



A Tale of Two Copepods

by

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Comparative ecology of the copepods *Calanoides carinatus* & *Calanus agulhensis* in the southern Benguela and Agulhas Bank ecosystems

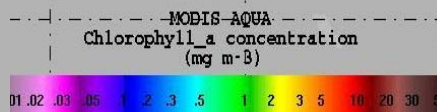


Southern Benguela

Jet current

Agulhas Bank

AGULHAS CURRENT

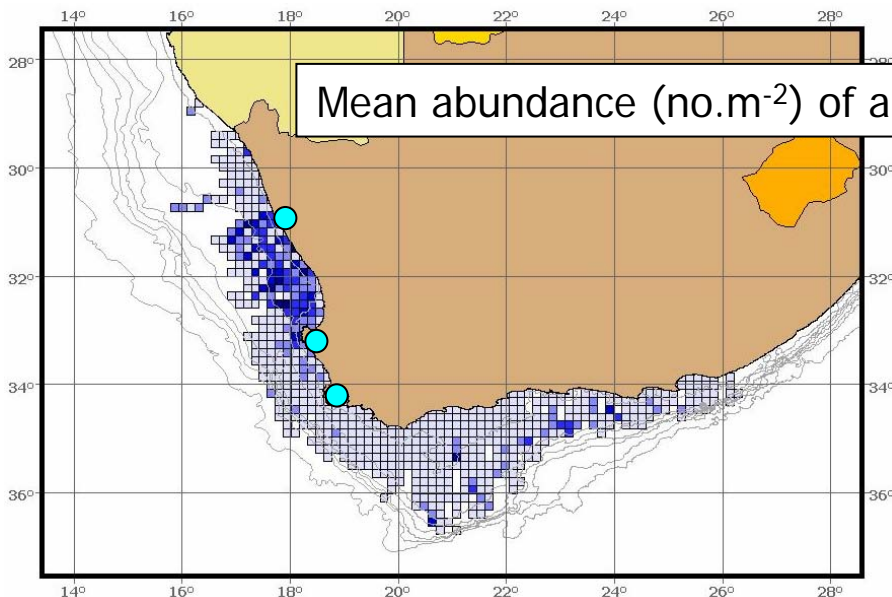


- Cool, variable, upwelling-dominated system
- High food abundance (2xAB) but variable (3xAB) due to pulsed upwelling
- More large cells than AB

- Warm and stable, typical of temperate shelf systems like Georges Bank
- Low food abundance but more consistent
- More small cells compared to West Coast

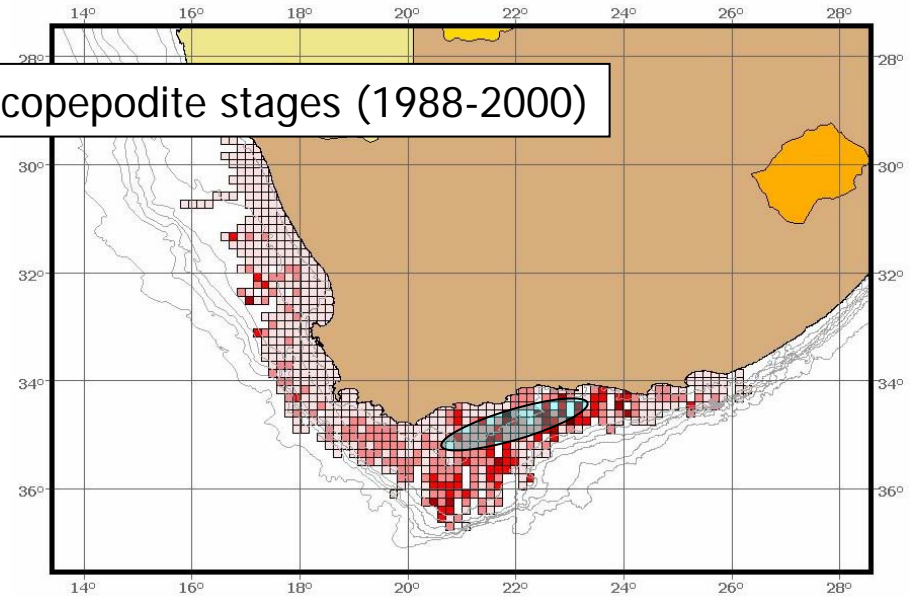
Calanoides carinatus

- Most abundant on central **West Coast**, downstream from **upwelling centres** ●
- May comprise up to **67%** of copepod biomass in **S. Benguela**
- Also found on outer Agulhas Bank, prob. transported from upwelling centres on East Coast, inshore of core Agulhas Current



Calanus agulhensis

- Centre of distribution on the central **Agulhas Bank (AB)**
- **~50-80%** copepod biomass
- Associated with quasi-permanent **cool ridge of upwelled water**: enhanced 1° production & retention
- Also occurs on West Coast, advected by jet current





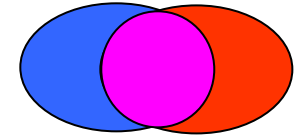
More on *Calanoides carinatus*

- **Opportunistic** species, characteristic of many **upwelling** systems
- Able to accumulate large **lipid stores**
- These enable it to undergo **diapause** - to overwinter at depth (>500 m) between upwelling seasons (e.g. NW Africa, Somalia)

Studies in the S. Benguela*:

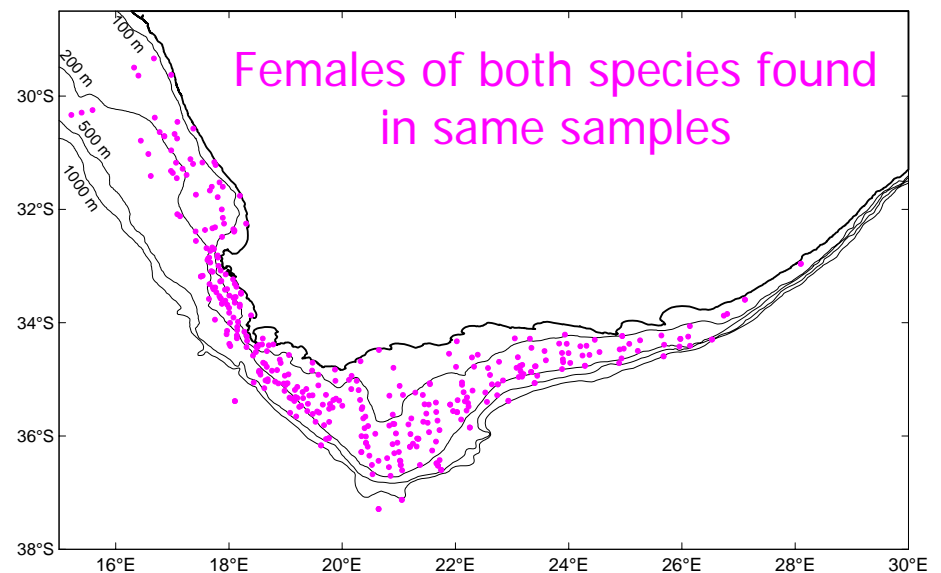
- **Rapid development** rate – **faster** than *Calanus* (2d@15°C; 4d@19°C)
- **Starts feeding** at an **earlier** stage than *Calanus* (N1 vs N3)
- It uses **diel vertical migration** (DVM) to **maintain population** close to shore in highly advective upwelling environment, using subsurface onshore return flow

* Armstrong *et al.* 1991; Borchers & Hutchings 1986; Peterson *et al.* 1990a&b; Peterson & Painting 1990; Richardson & Verheye 1998; Verheye 1989; Verheye *et al.* 1991; Verheye & Field 1992; Walker & Peterson 1991.



Overlap in distribution

- Both species found throughout the year in South African shelf waters, and their distribution ranges often **overlap**, however:
- On the **Agulhas Bank** *Calanus* always >> *Calanoides*
- On the **West Coast** shelf *Calanoides* always >> *Calanus*
- Suggests that each species is **better adapted** to its "home range" or **niche** in one or more ways, allowing it to out-compete the other on a long-term basis
- Several **hypotheses** as to why this may be the case



Hypotheses:



Environment/Habitat:

(Southern Benguela vs. Agulhas Bank)

1. Temperature (Cool vs. Warm)
2. Food abundance (High vs. Low)
3. Food size/type (Large vs. Small)
4. Food variability (Variable vs. Consistent)

Behaviour:

5. Vertical migration* (*Calanoides* Yes vs. *Calanus* No)

* DVM by *Calanus agulhensis* not previously studied



Hypothesis 1 - Temperature

Calanoides egg production (EP) is **inhibited** by **warm** temperatures typical of the **Agulhas Bank**; conversely, *Calanus* egg production is reduced at **cooler** temperatures characteristic of the **Benguela upwelling region**.

Effect:

Cool temperatures: *Calanoides* EP > *Calanus* EP

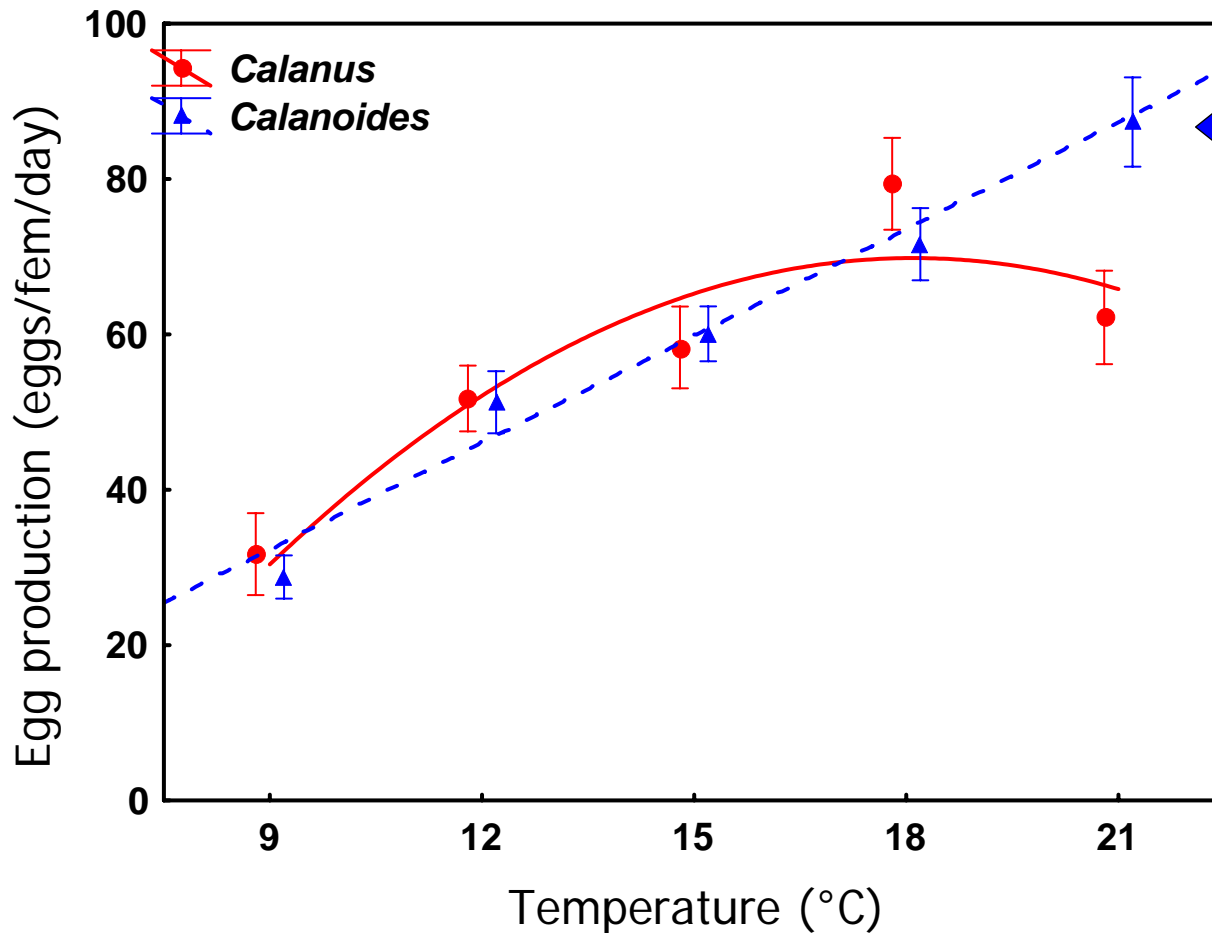
Warm temperatures: *Calanus* EP > *Calanoides* EP

Test:

Measure **EP at different temperatures** (9-21°C) in the laboratory under **non-limiting food** conditions.

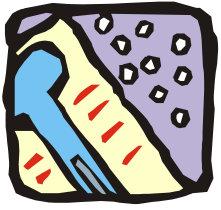


Hypothesis 1 - Temperature



2. *Calanoides* experienced **greater mortality** than *Calanus* at this temp.

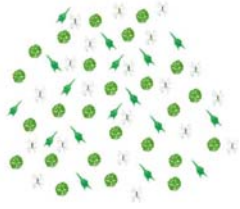
1. Food-satiated rates of EP were similar for both species across a broad temperature range (9-18°C), but at 21°C *Calanoides* had significantly faster rates of EP than *Calanus*.



Hypothesis 1 - Temperature



- Hypothesis **rejected**.



Hypothesis 2 – Food abundance

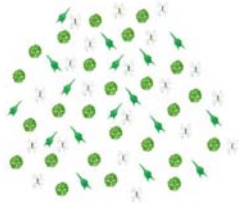
Calanus can attain **satiation** at a lower food concentration than *Calanoides*.

Effect:

Calanus requires **less food** than *Calanoides* to achieve **maximum rates of EP**, thus *Calanoides* will be at a **competitive disadvantage** on the **Agulhas Bank** (low food) compared to the **southern Benguela** (high food).

Test:

Compare **food concentrations** in the ocean required for both species to achieve **satiation** (and **max.** rates of **EP**).

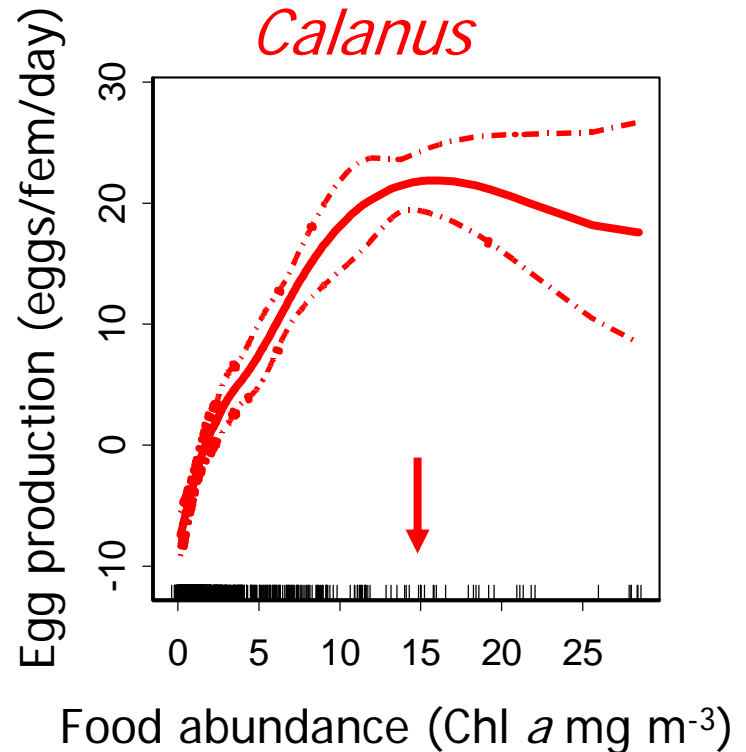
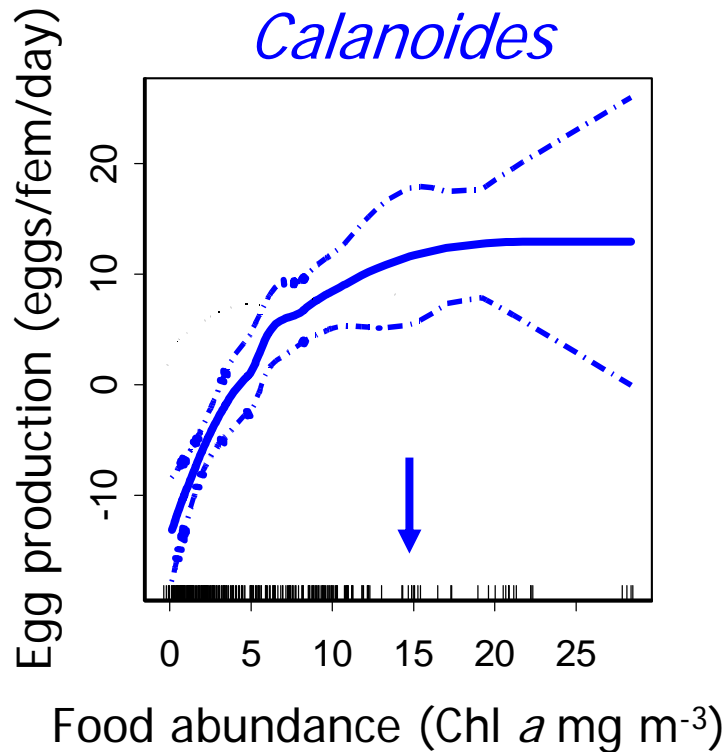


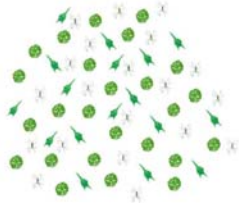
Hypothesis 2 – Food abundance



(a) Rates of Egg Production (EP) in the ocean (ambient food conc.)

GAMs: Similar response – max EP at same food concentration





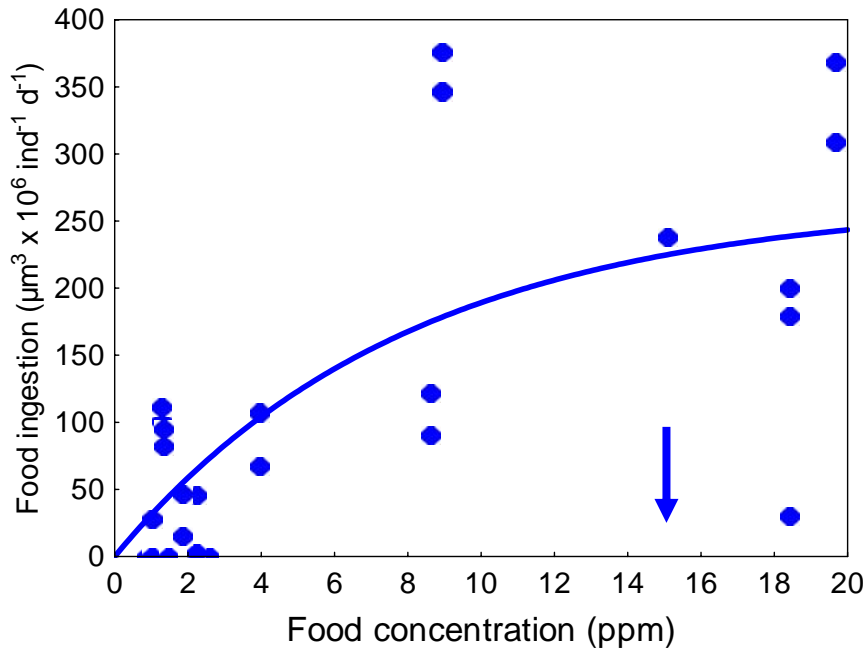
Hypothesis 2 – Food abundance



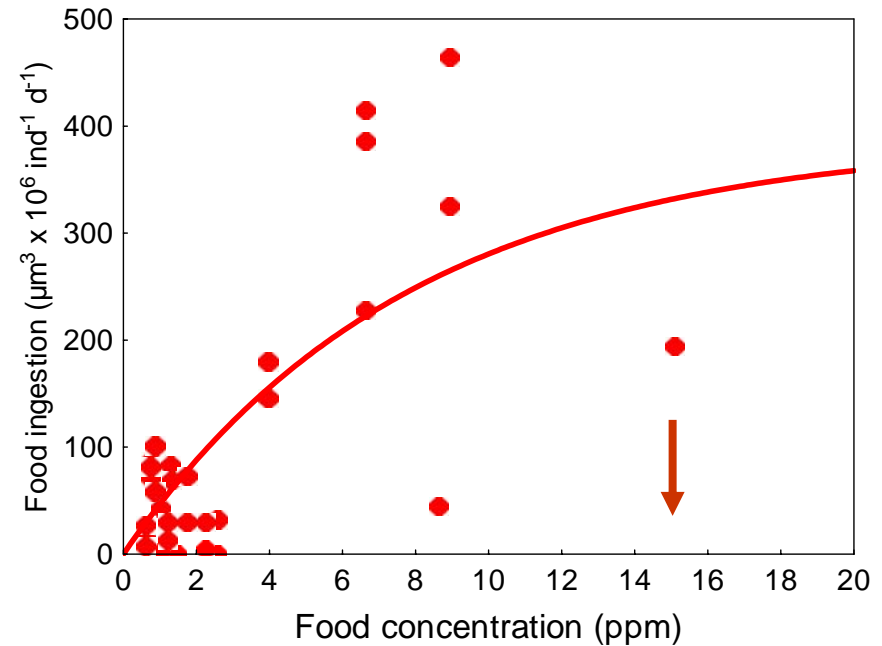
(b) Ingestion Rates in the ocean (ambient food concn)

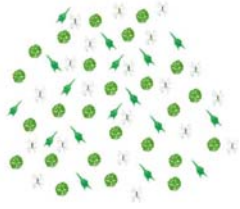
Similar response – max ingestion rate at same food concentration

Calanoides



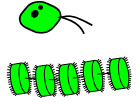
Calanus





Hypothesis 2 – Food abundance

- Both species displayed a **similar functional response** to food concentration in terms of **egg production** and **ingestion rates**
- Hypothesis **rejected**

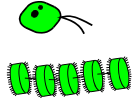


Hypothesis 3a – Food size

Calanoides feeds **less efficiently** than *Calanus* on **small cells** typical of **low food** concentrations associated with the **Agulhas Bank**

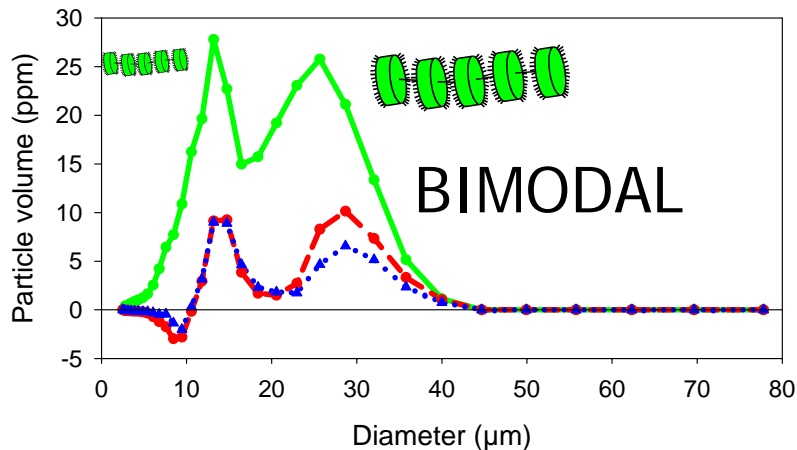
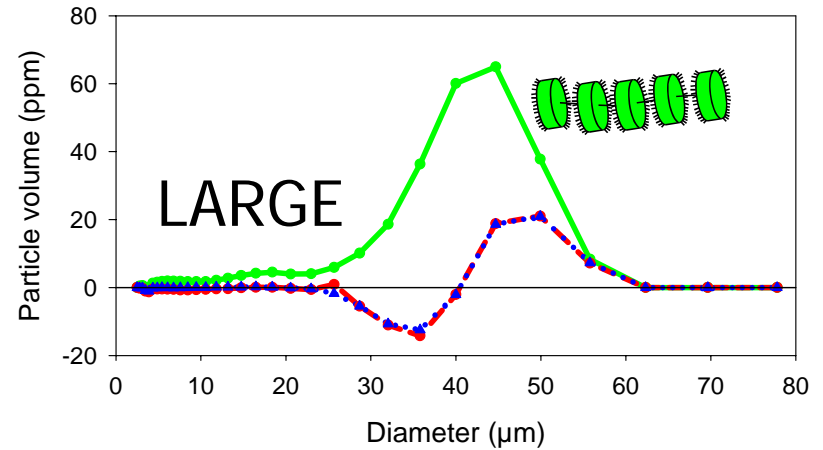
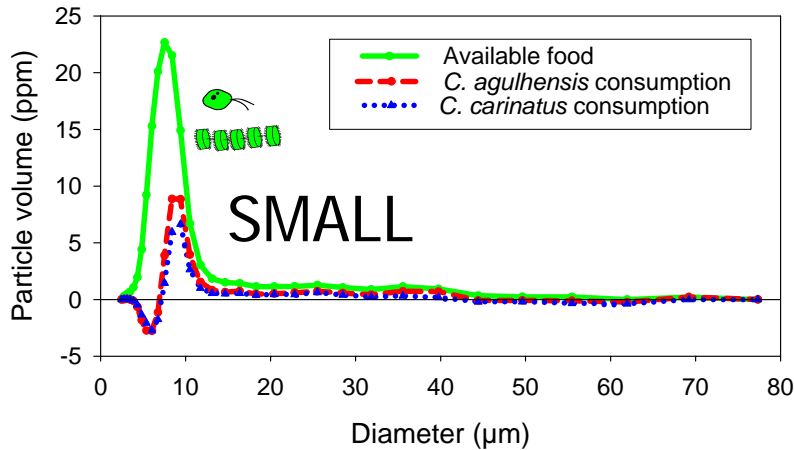
Effect: *Calanoides* ingestion and EP rates are **low** compared to *Calanus* when the phytoplankton food is dominated by **small cells**, thus *Calanoides* is energetically disadvantaged on the **Agulhas Bank**.

Test: Measure ingestion and EP rates over a **range of food sizes** in the ocean, including small- (<10 μm) cell-dominated food types

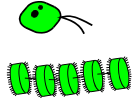


Hypothesis 3a – Food size

Particle removal in the ocean (ambient food concentrations)



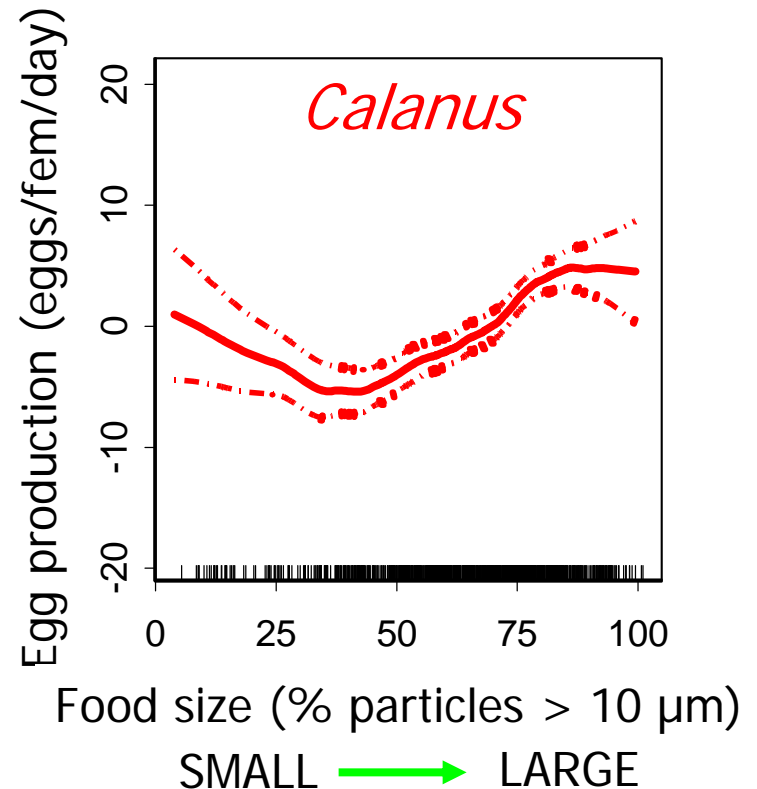
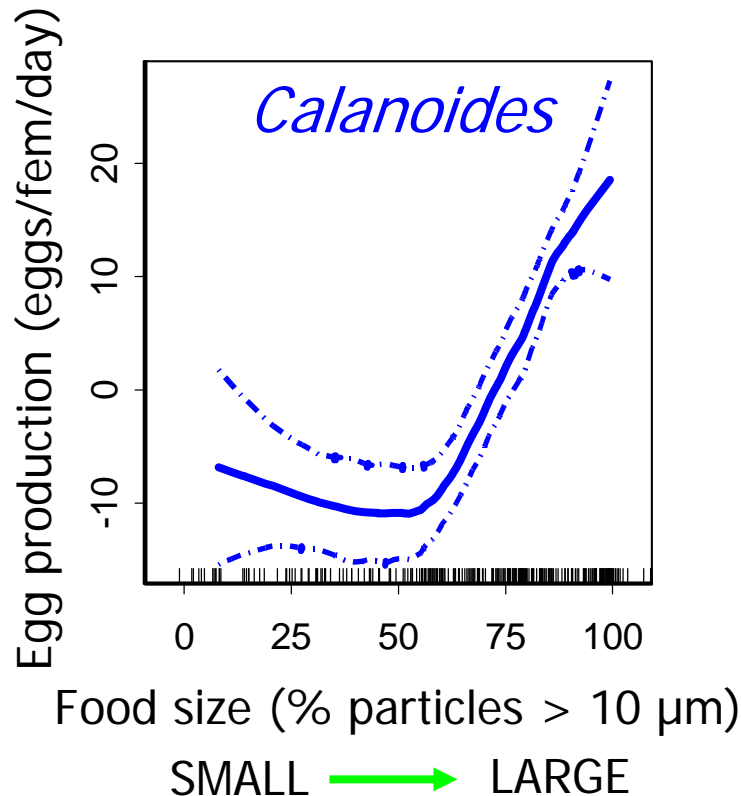
Both species displayed similar feeding behaviour in terms of particle size selection, and generally appeared to prefer the larger particles that dominated the food biomass



Hypothesis 3a – Food size

GAMs:

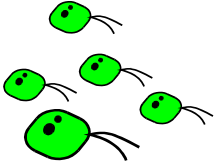
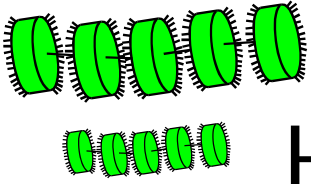
Particle size **very important** for egg production by *Calanoides*
Particle size **not very important** for egg production by *Calanus*





Hypothesis 3a – Food size

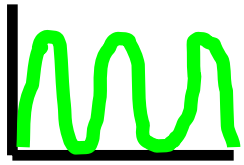
- Ingestion rate by *Calanoides* was ~ half that of *Calanus* during the small particle experiment, suggesting that *Calanoides* may feed less efficiently than *Calanus* on **small cells**
- Hypothesis **not rejected**.



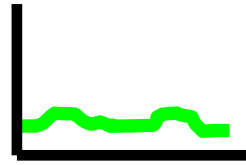
Hypothesis 3b – Food species

- Microscope analyses of some grazing experiments using natural food assemblages suggests that the two copepods **prefer different food species**, presenting the possibility of **resource partitioning** under diverse food conditions
- Results suggest that *Calanus* may have a greater tendency towards **omnivory** than *Calanoides*, and that **microzooplankton** (e.g. ciliates) may have an important role in supplementing nutritional requirements of *Calanus* when **phytoplankton abundance is low**
- Hypothesis **not rejected**





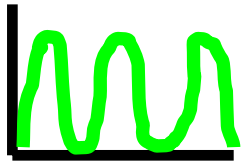
Hypothesis 4 – Food variability



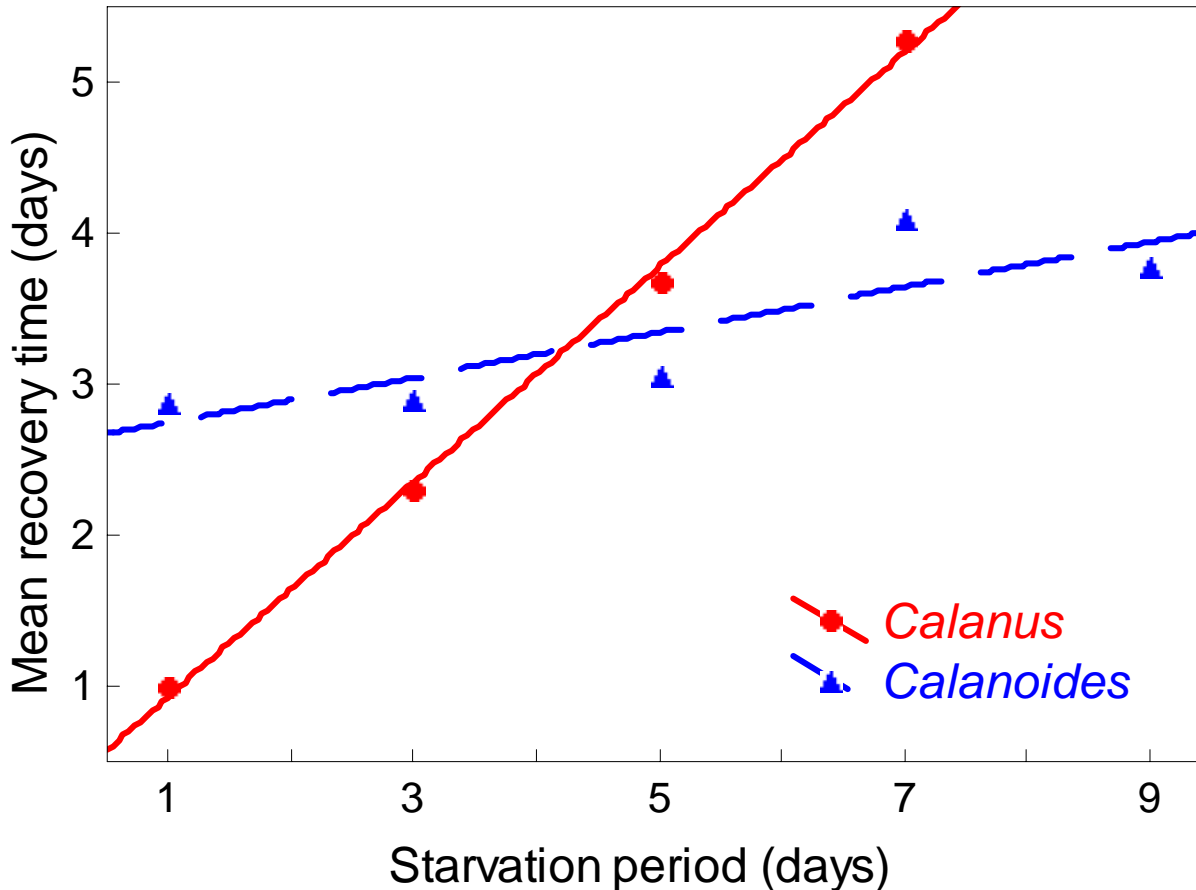
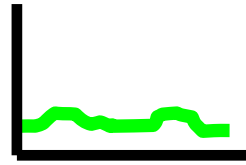
Calanoides is better adapted to the **pulsed food** environment characteristic of the **southern Benguela** upwelling region; conversely, *Calanus* is better adapted to more **consistent food** availability typical of the **Agulhas Bank**

Effect: EP by *Calanus* recovers more slowly, or does not recover, from **intermittent food** availability characteristic of a pulsed upwelling system, thus *Calanus* is energetically disadvantaged on the **West Coast**

Test: Measure recovery of EP in the laboratory following different periods of **starvation** (1-9 days)

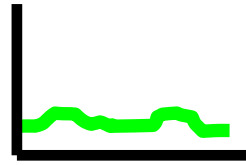
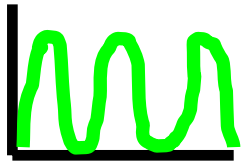


Hypothesis 4 – Food variability



Short (1-3 day) periods of starvation: *Calanus* regained normal EP faster than *Calanoides*.

Long (7-9 day) periods of starvation *Calanoides* regained normal EP faster than *Calanus*. Some *Calanus* did not recover at all from 9 days without food.



Hypothesis 4 – Food variability

- *Calanoides* terminated egg production much sooner than *Calanus* when food was removed, whereas *Calanus* continued to lay eggs for several days in FSW
- *Calanoides* was probably able to regain max. EP faster than *Calanus* following longer periods without food due to greater lipid reserves
- Hypothesis not rejected



Hypothesis 5 – Vertical migration

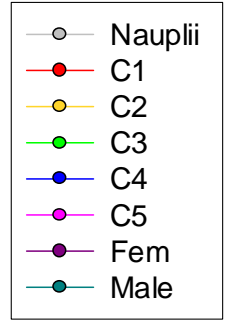
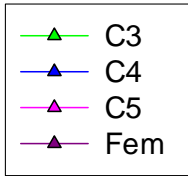
Calanus does not display ontogenetically-based (stage-based) diel vertical migratory (**DVM**) behaviour on the **Agulhas Bank**.

Effect: *Calanus* may be unable to use **DVM** as a **retention mechanism** on the West Coast, as has been demonstrated for *Calanoides*, and thus would be prone to substantial **advective loss** from the **Benguela upwelling system**

Test: Explore **DVM** of *Calanus* on the **Agulhas Bank**, and explore DVM of both species under the **same conditions**.

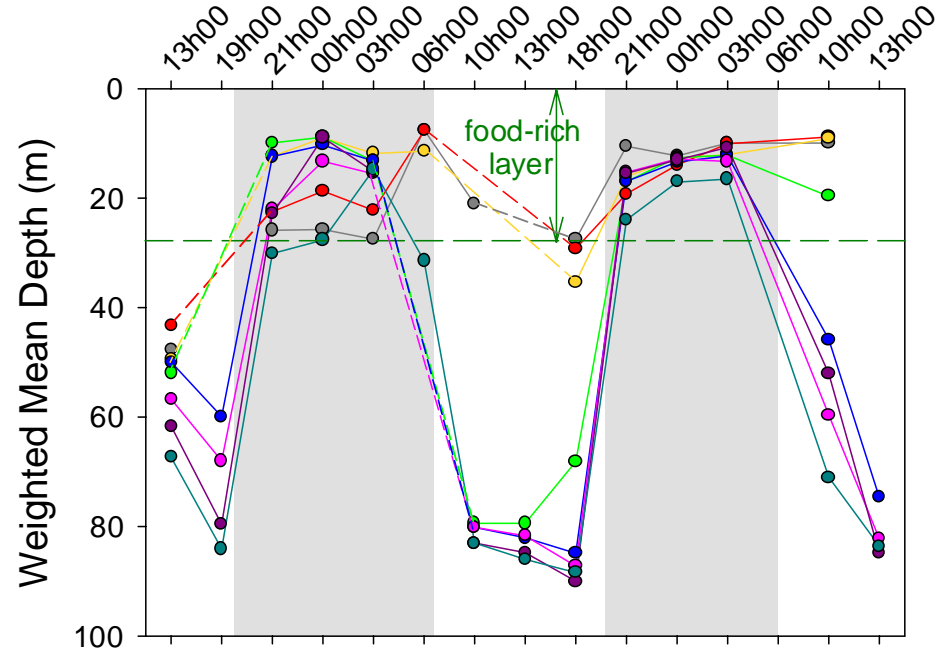
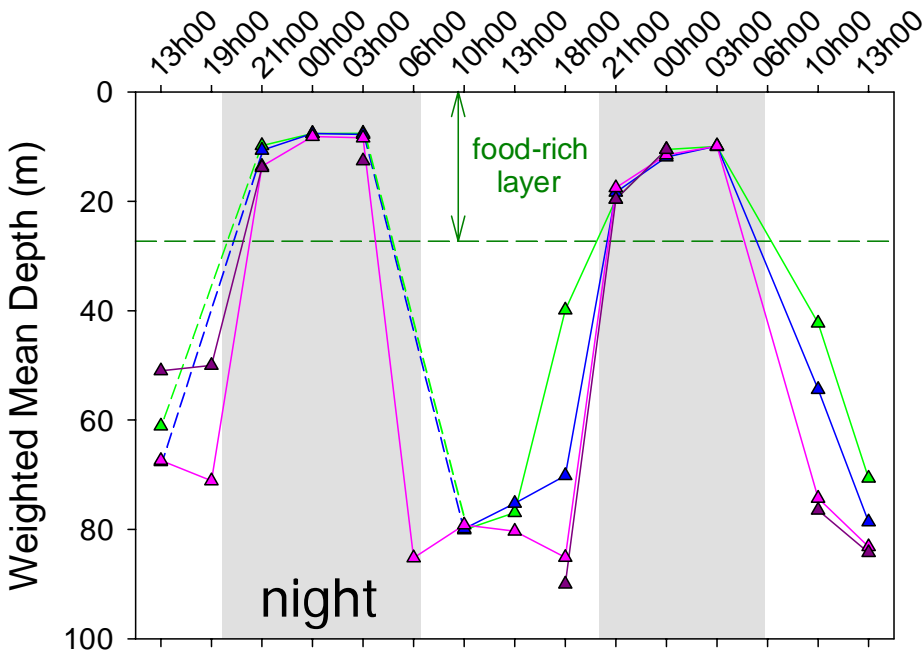
Hypothesis 5 – Vertical migration

Similar patterns of DVM. Ascend at sunset to feed at night in the upper food-rich layer. Descend at sunrise to avoid detection by visual predators (fish).



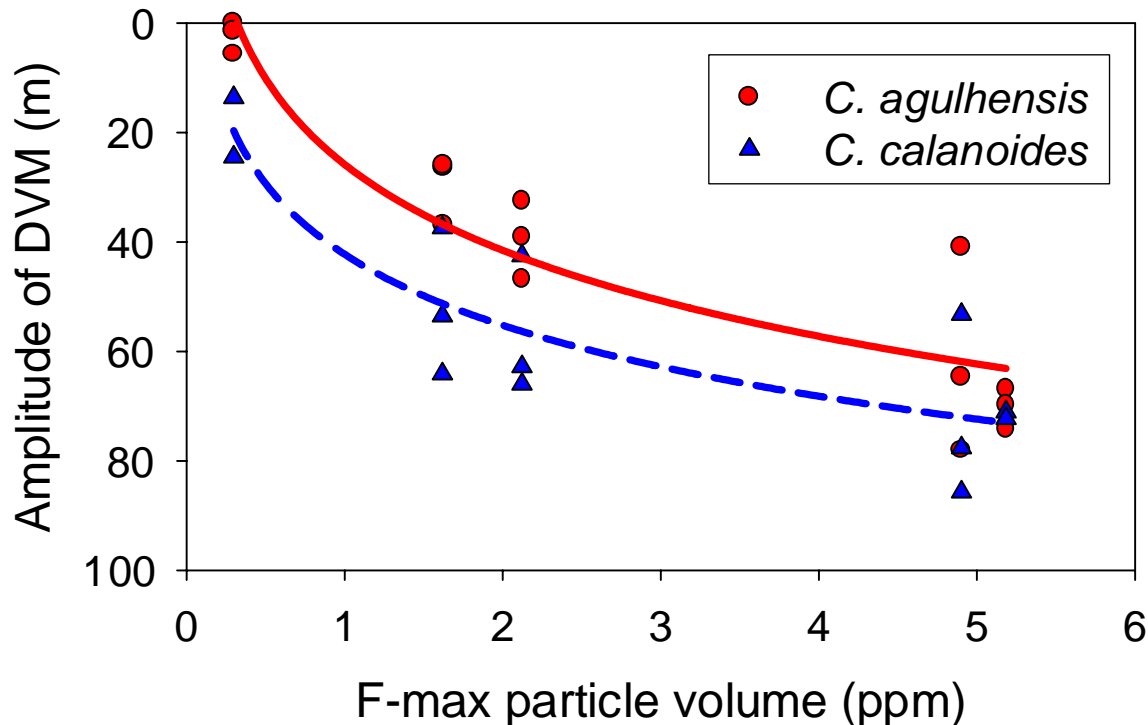
Calanoides

Calanus



Hypothesis 5 – Vertical migration

Amplitude of DVM = Difference in depth of copepods between midnight and midday (10h00).



Amplitude of **DVM** was significantly related to **food concentration**.

Both species delayed their daytime descent when food abundance was relatively poor.

Calanoides had a significantly **greater** amplitude of **DVM** compared to *Calanus*.



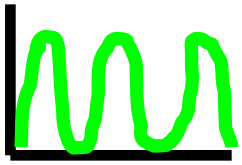
Hypothesis 5 – Vertical migration

- Both species displayed **similar patterns** of stage-based **DVM** under the same environmental conditions
- Hypothesis **rejected**



Results:

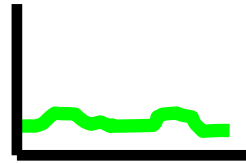
1. Temperature: **NO** (similar functional response)
2. Food abundance: **NO** (similar functional response)
3. Food size/type: **YES** – both seem to prefer larger cells, but *Calanoides* may feed less efficiently on small cells, and cell size is more NB to *Calanoides* EP. *Calanus* may be more omnivorous
4. Food variability: **YES** (*Calanus* recovered faster from short periods without food; *Calanoides* recovered faster from long periods → lipids)
5. Vertical migration: **NO** (although greater DVM by *Calanoides* = faster swimmer)



Conclusions: *Calanoides*

- *Calanoides carinatus* is able to **opportunistically** exploit localized upwelling events and the associated rapid food growth, because of its **rapid development** and **early feeding by its nauplii**.
- Its **preference for large cells** (and possible inefficiency wrt small cells) makes it well-matched to the greater prevalence of large-cells in the **southern Benguela**
- However, because of its ability to accumulate **large lipid reserves**, it is also able to **withstand long periods without food**, or with poor food abundance, and can **recover rapidly** when conditions improve.
- These characteristics enable it to **thrive** in an **unpredictable and variable food environment** such as that in the southern Benguela upwelling region.

Conclusions: *Calanus*



- *Calanus agulhensis* appears to be **less opportunistic**, and is limited by **slower development** rates and **delayed first-feeding**.
- Since food size appears to be less important, it may **feed more efficiently on small cells**, as has been shown for other *Calanus* congeners, and may depend more on **omnivory**.
- When food abundance declines it does not completely halt reproduction, but **continues to produce eggs at slow rates**, and is able to resume moderate rates of egg production fairly quickly when food again becomes abundant.
- It is thus **well suited** to an environment where **food abundance is generally low but relatively consistent**. However, it **does not accumulate large energy reserves**, and thus females **cannot withstand long periods without food**, which are more likely on the variable West Coast.



The Big Picture

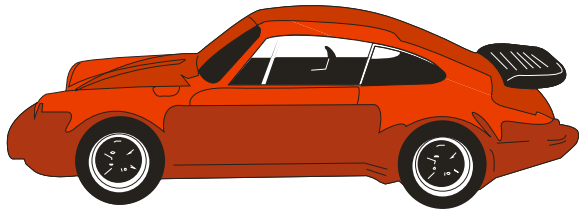
The abundance of *Calanoides* in the West coast upwelling region is enhanced by seeding from resting stages, local retention through ontogenetically-based vertical migratory behaviour, and adaptation to the variable food environment, including rapid development and the accumulation of lipid reserves.

The abundance of *Calanus* on the Agulhas Bank is favoured by enhanced growth rates, production and retention associated with the Agulhas Ridge, and adaptation to low but consistent food availability.

These characteristics result in the two copepods being less suited to their non-core areas, and at a competitive disadvantage if they are transported to these regions. They are at an additional disadvantage in their non-core areas because they tend to occur at the **margins** of these regions, where the risks of **starvation, advection and/or predation** are greater.

If copepods were cars...

Calanoides carinatus



- **Porsche**
- Fast acceleration
- Expensive to run

Calanus agulhensis



- **Beetle**
- Slow but reliable
- Fuel efficient

A stage curtain with a sunset background. The curtain is dark red with a gold fringe at the top and a gold tassel on the left side. The background is a gradient of orange and yellow, suggesting a sunset. The text "The End" is written in a gold, serif font in the center of the curtain.

The End