The evolutionary ecology of defence mechanisms in the pelagic zone

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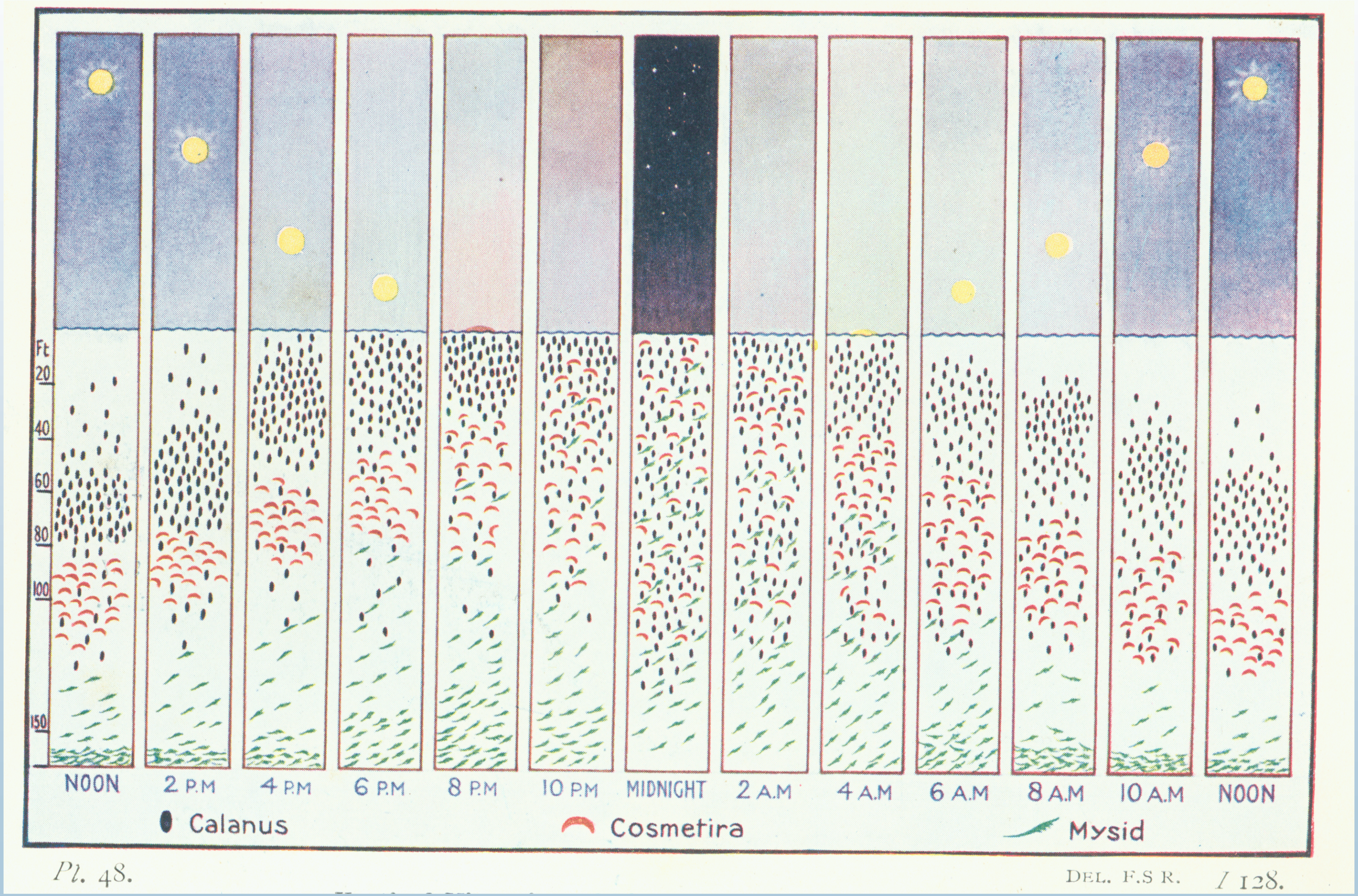
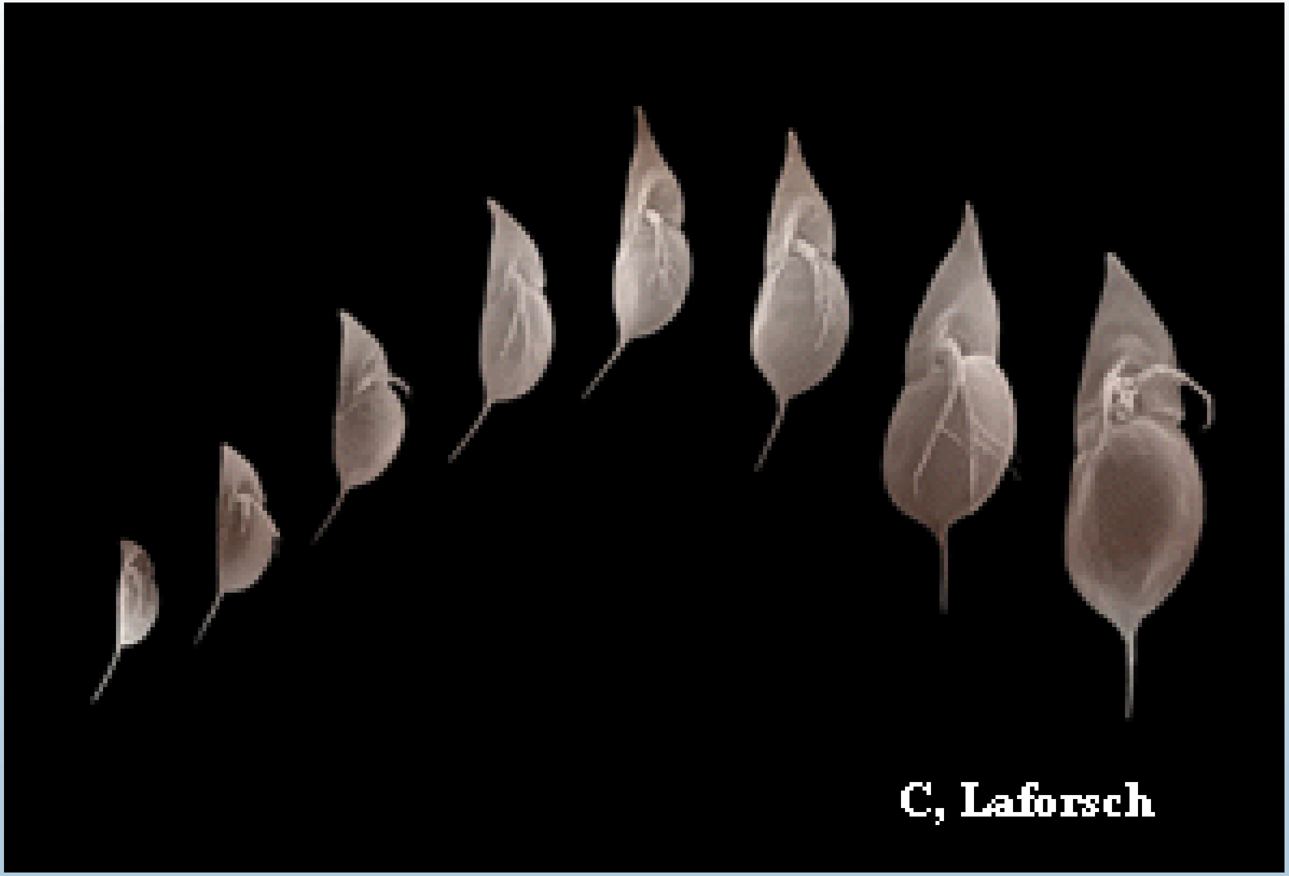
Two main topics

- Chemical communication
- Explanatory models of defence mechanisms


Vertical migration



Cyclomorphosis



Mechanisms

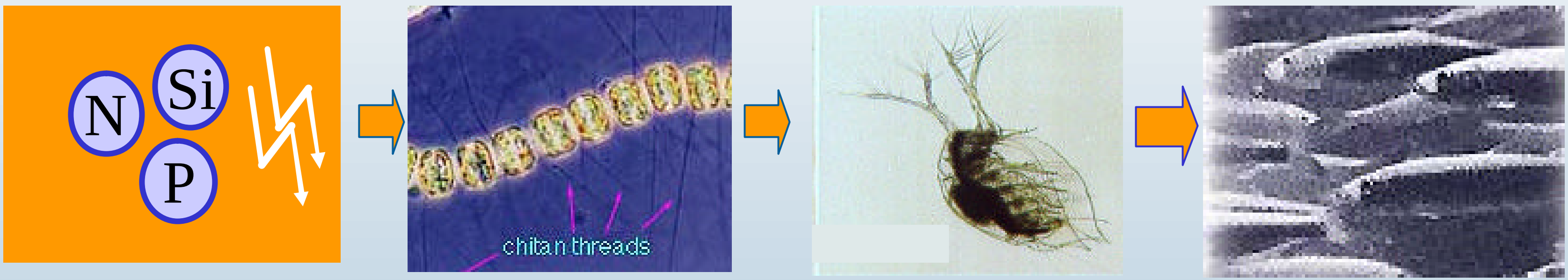
- How does this happen?
- Why does it happen?

Mechanisms

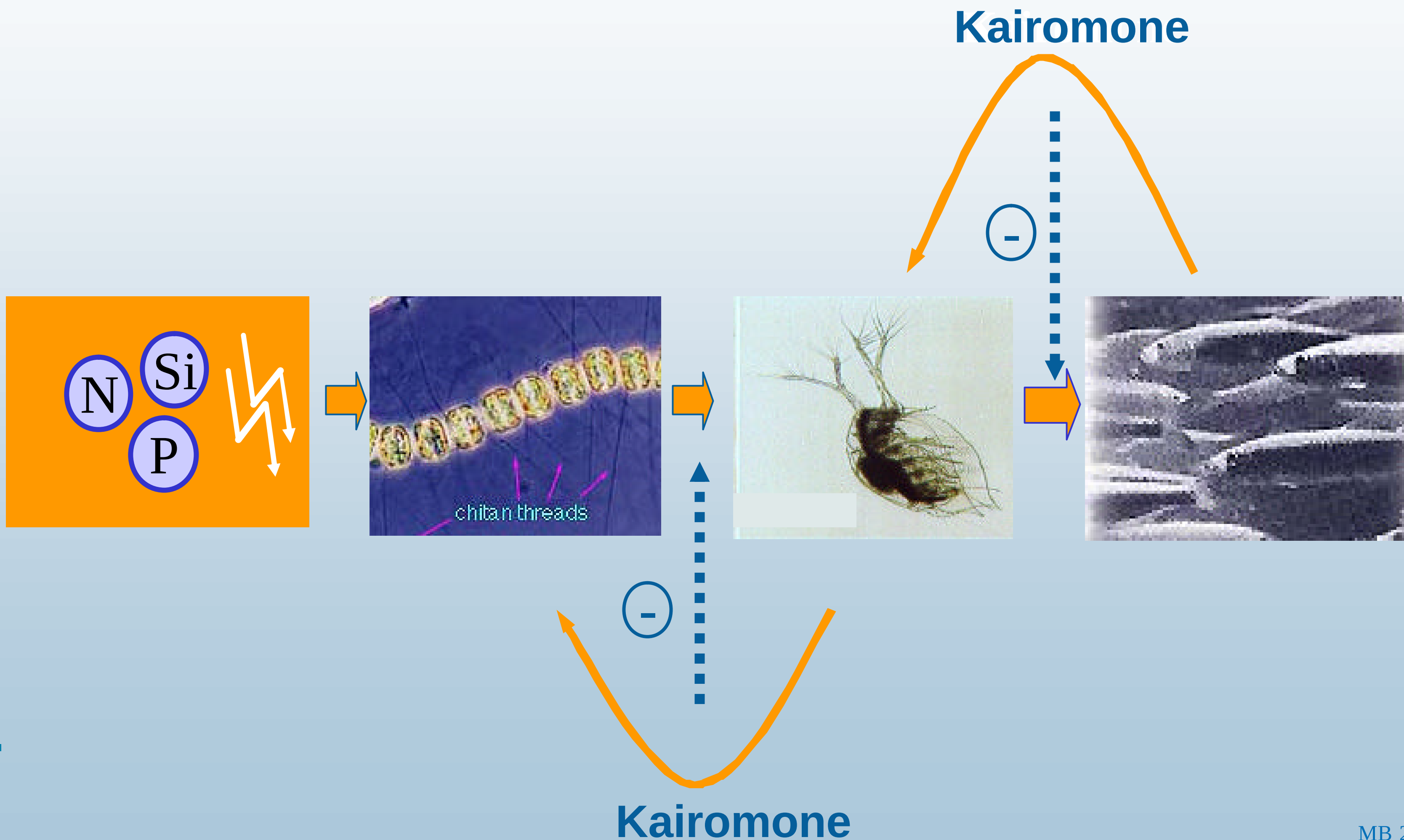
- Vertical migration
  - Why?
    - Food, Predator avoidance, UV-avoidance, temperature tolerance, metabolic efficiency
  - How?
    - Light, gravity

- Cyclomorphosis
  - Why?
    - Buoyancy, Predator avoidance, Swimming
  - How?
    - Temperature

A simplified marine foodweb



A more complicated simple marine food web



Infochemicals

- Intraspecific: pheromones are chemicals produced by one individual of a species, received by another individual of that species and eliciting a behavioral and/or physiological response in the receiver (sex, aggregation, alarm)

- Interspecific

Interspecific messengers

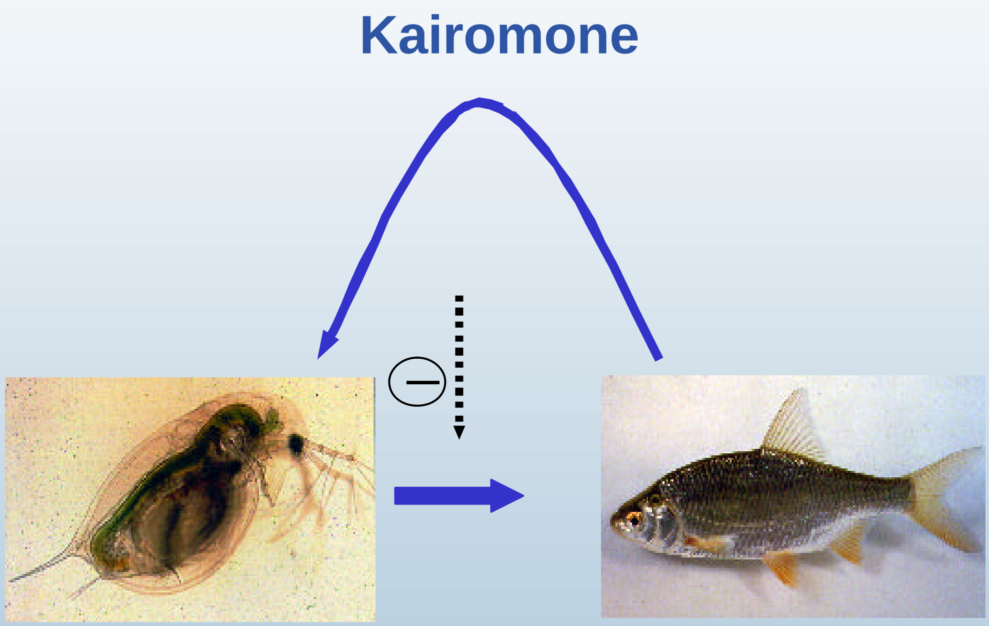
- Allomones are interspecific chemical messengers that benefit the emitter (feeding deterrents, chemical mimicry)
- Synomones operate between species and benefit both the emitter and the receiver (floral odours, alarm substances)
- Kairomones are interspecific chemical messengers that benefit the receiver (to follow)

Kairomones

- Which role do these infochemicals play in aquatic foodwebs?

- What is the nature of these substances?

The interaction fish-zooplankton



Potential adaptations to predation

- Life-history
  - size and age at maturity
  - size and number of offspring
  - mode of reproduction
- Morphology
  - morphological defences such as spines and helmets
- Behaviour
  - increased alertness
  - diel vertical migration

The waterflea (*Daphnia*)

Johann Swammerdamm,
der Arzneykunst Doctor von Amsterdam,
Bibel der Natur,
worinnen
die Insekten in gewisse Classen vertheilt,
sorgfältig beschrieben, zergliedert, in saubern Kupferstichen vorgestellt,
mit vielen Anmerkungen über die Seltenheiten der Natur erleutert,
und
zum Beweis der Allmacht und Weisheit des Schöpfers
angewendet werden.
Nebst
Hermann Boerhave
Vorrede von dem Leben des Verfassers.
Aus dem Holländischen übersetzt.

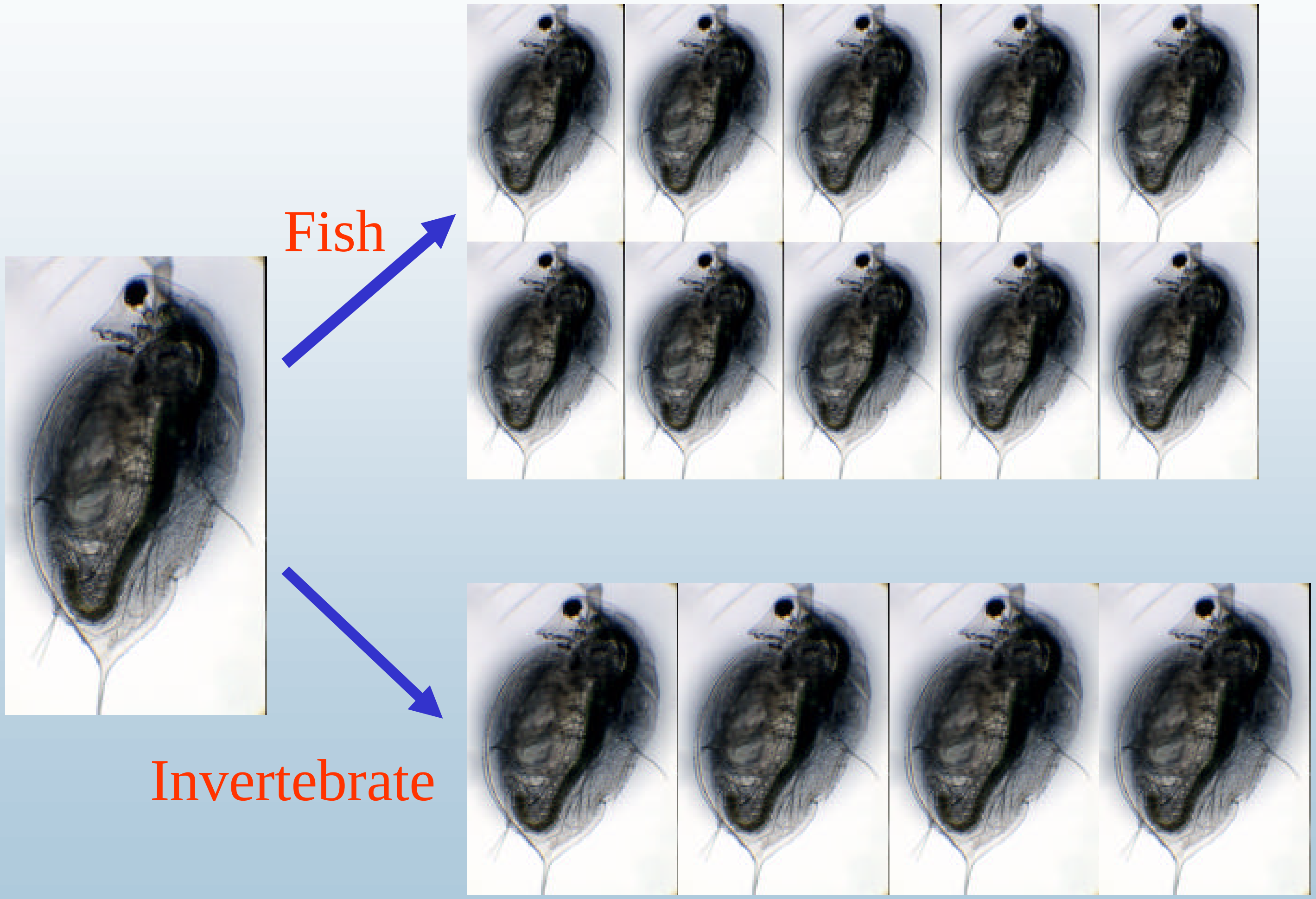
(Swammerdamm 1752)

Life-histories

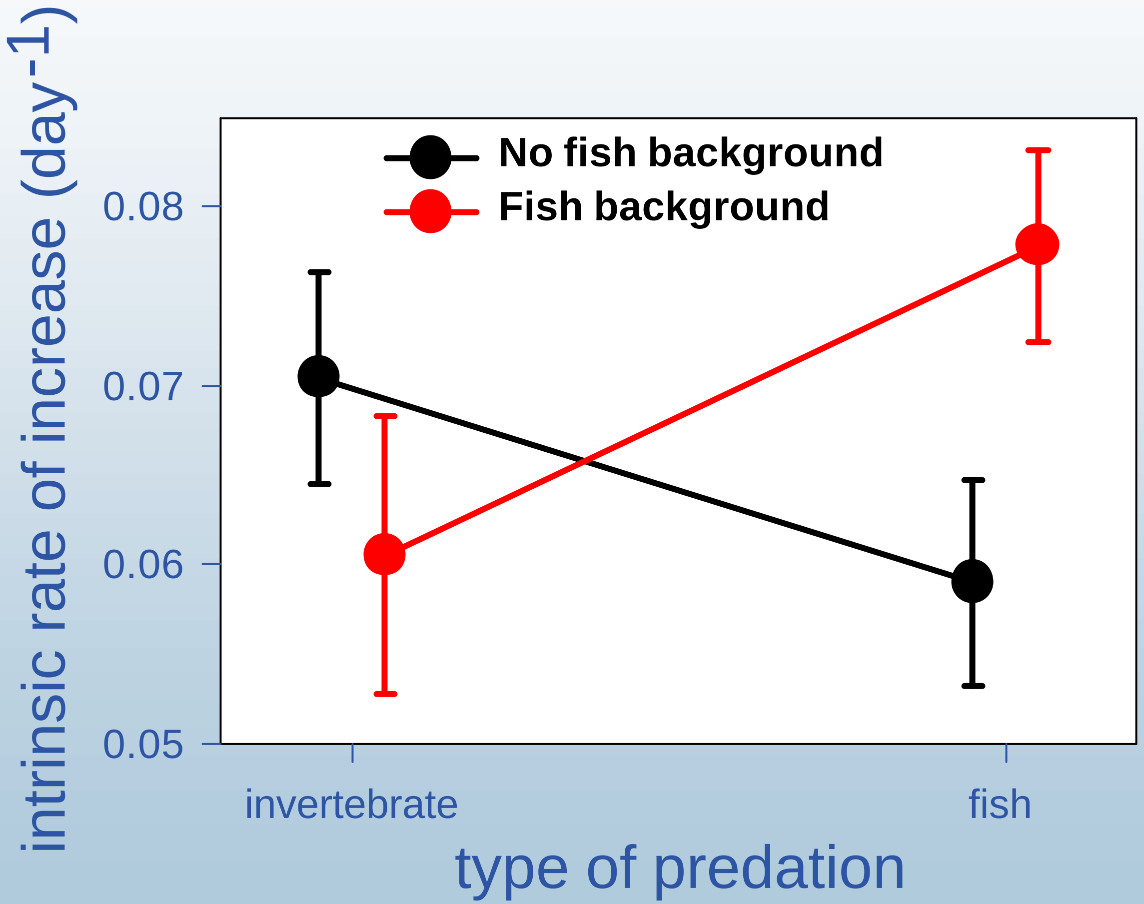
- Most fish feed positively size-selective
  - Stay smaller
  - Produce smaller offspring, earlier

- Many invertebrate predators feed negatively size-selective
  - Attain larger size
  - Produce larger offspring , later

Life-histories



Consequences

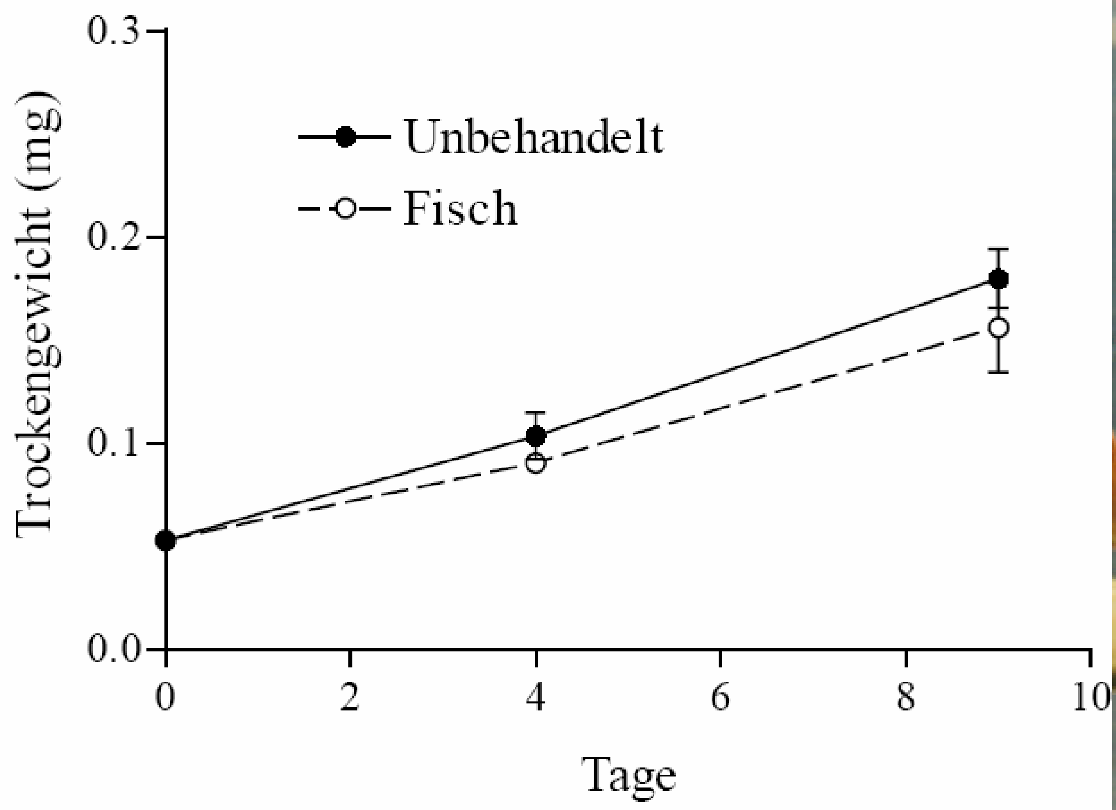


MB 2006

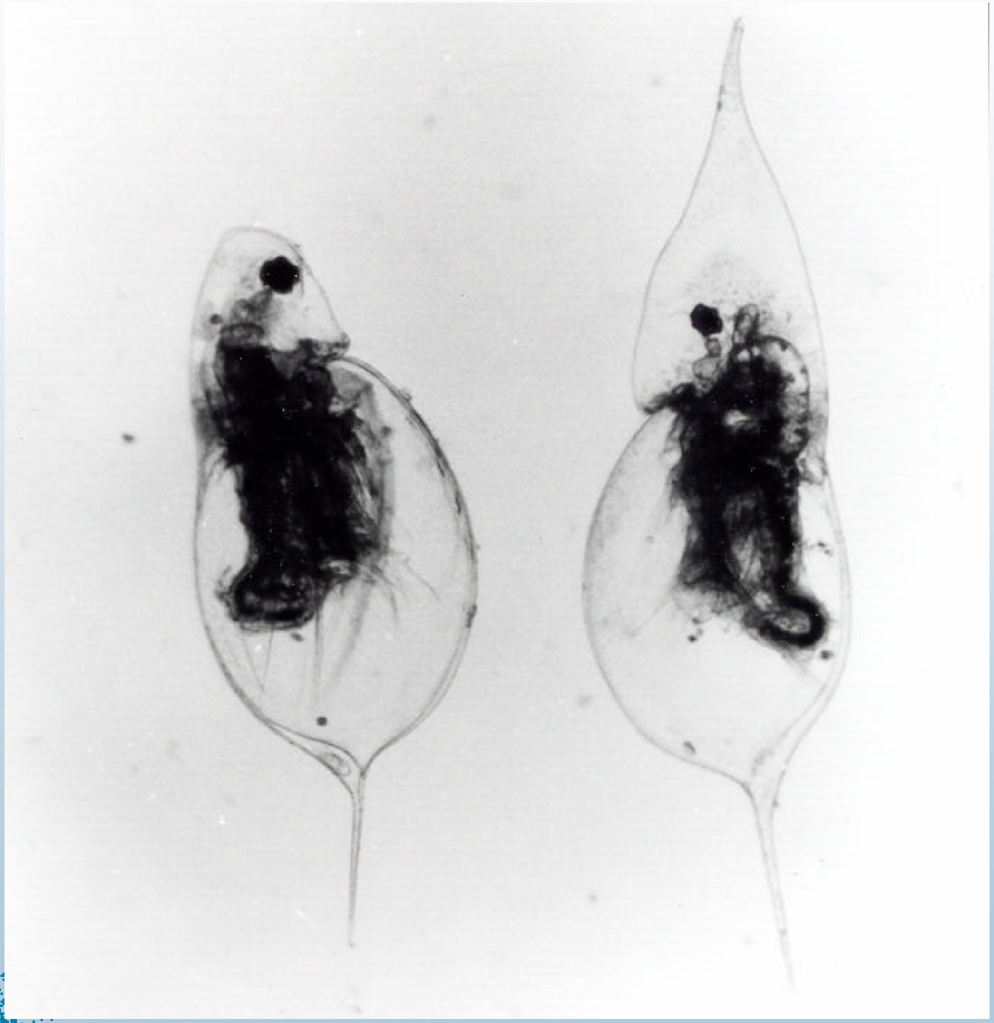
And in the sea?

- Megalopa of the blue crab (*Callinectes sapidus*) shorten or lengthen the time to metamorphosis depending on external cues

More Sea examples



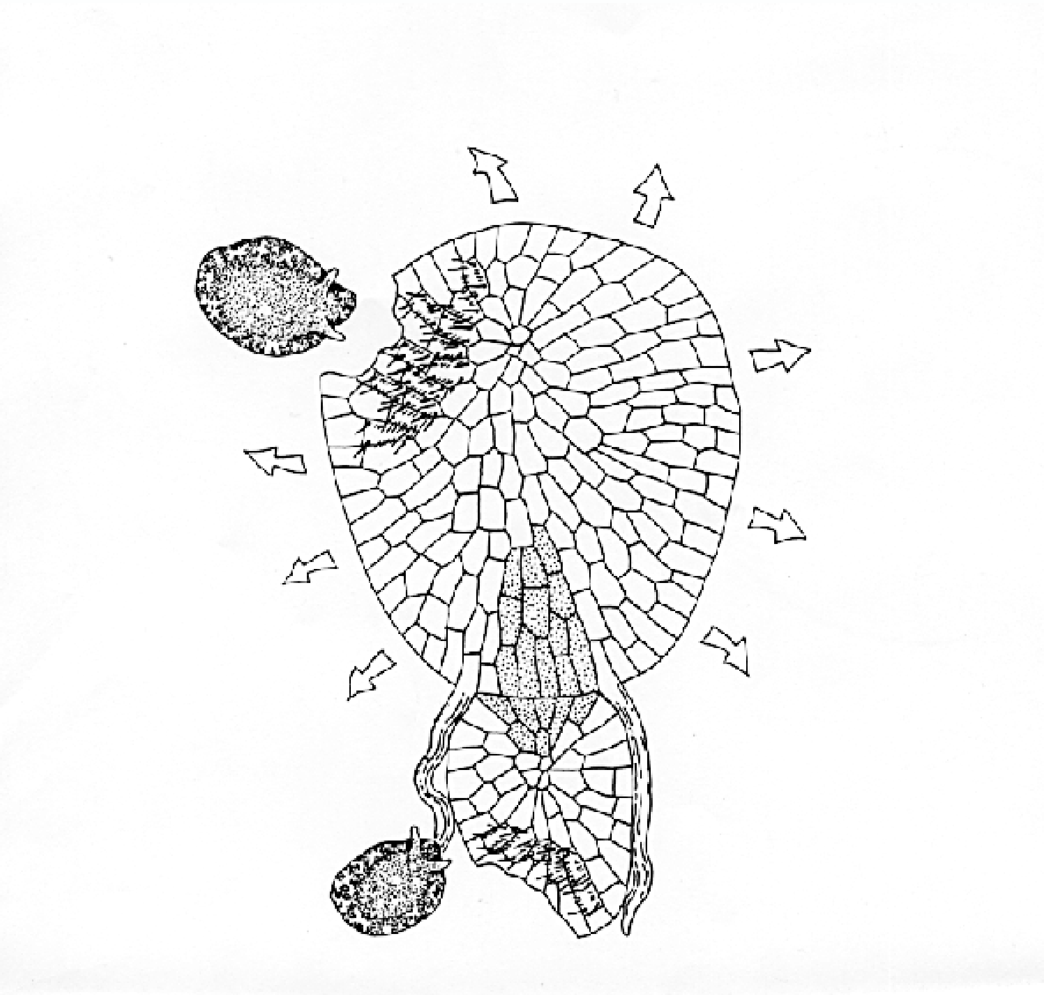
Morphology

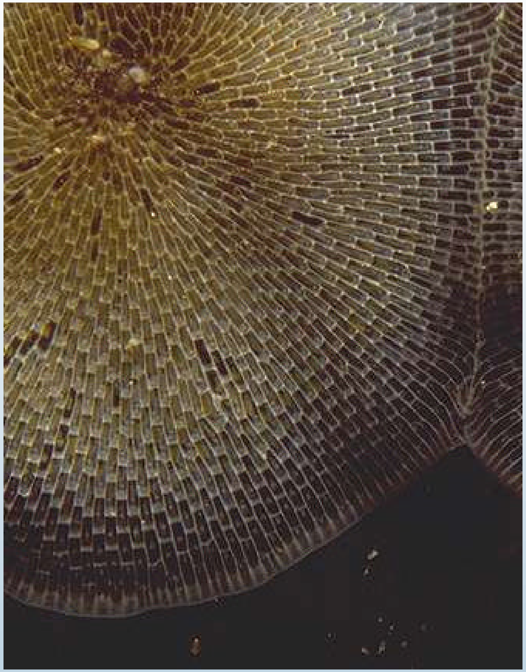


And in the sea?

- I know of no examples of morphological changes as a result of predator kairomones in the pelagic zone in marine systems

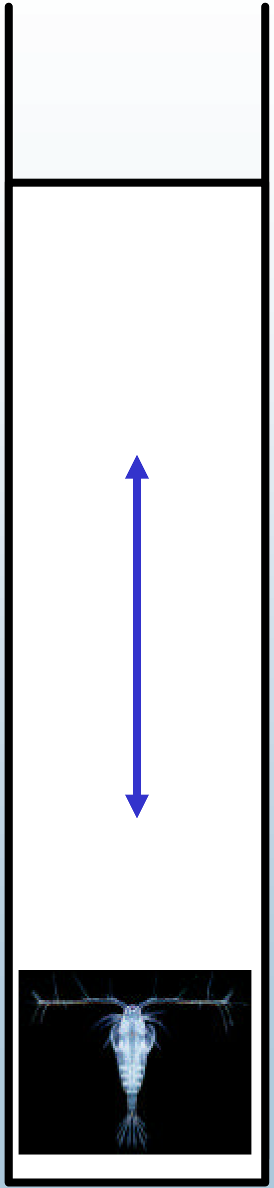
And in the sea?



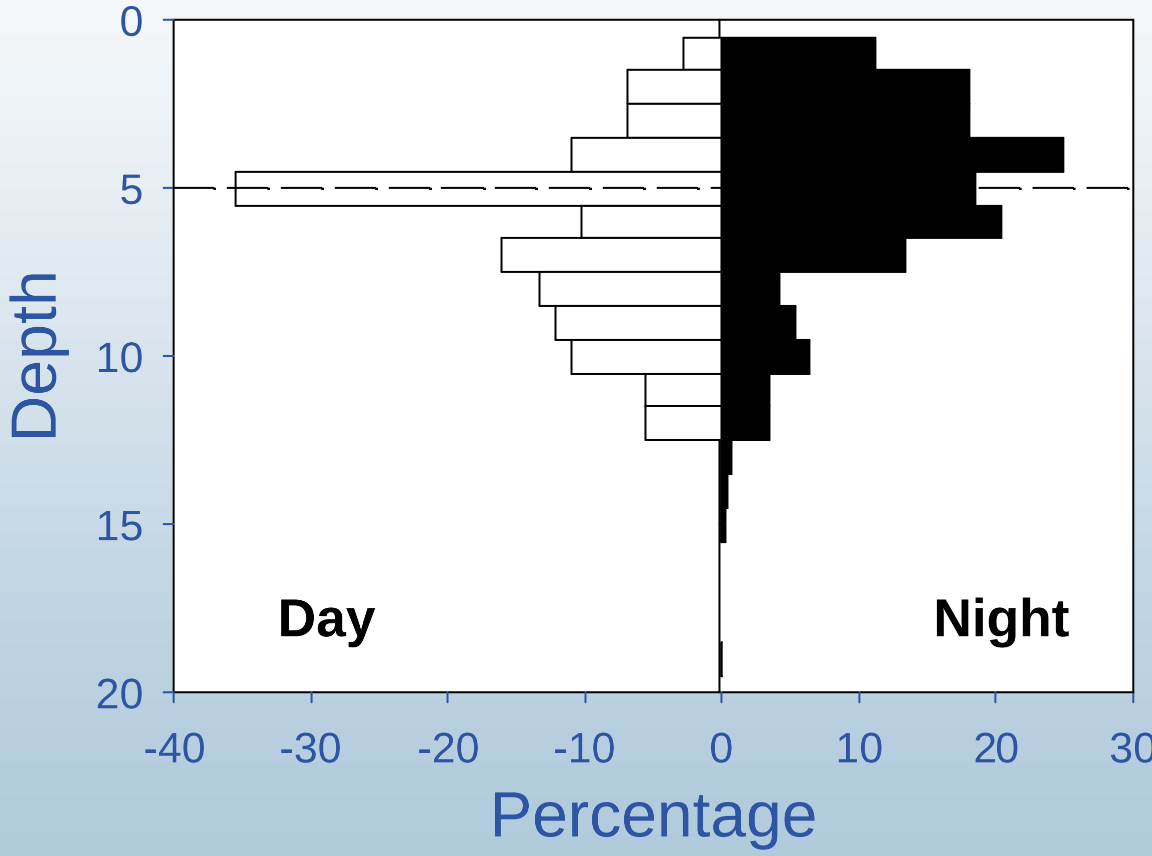


- Marine bryozoan (*Membranipora membranacea*) forms spines ans stolons to avoid predation by snails (Photos C.D. Harvell)

Behaviour



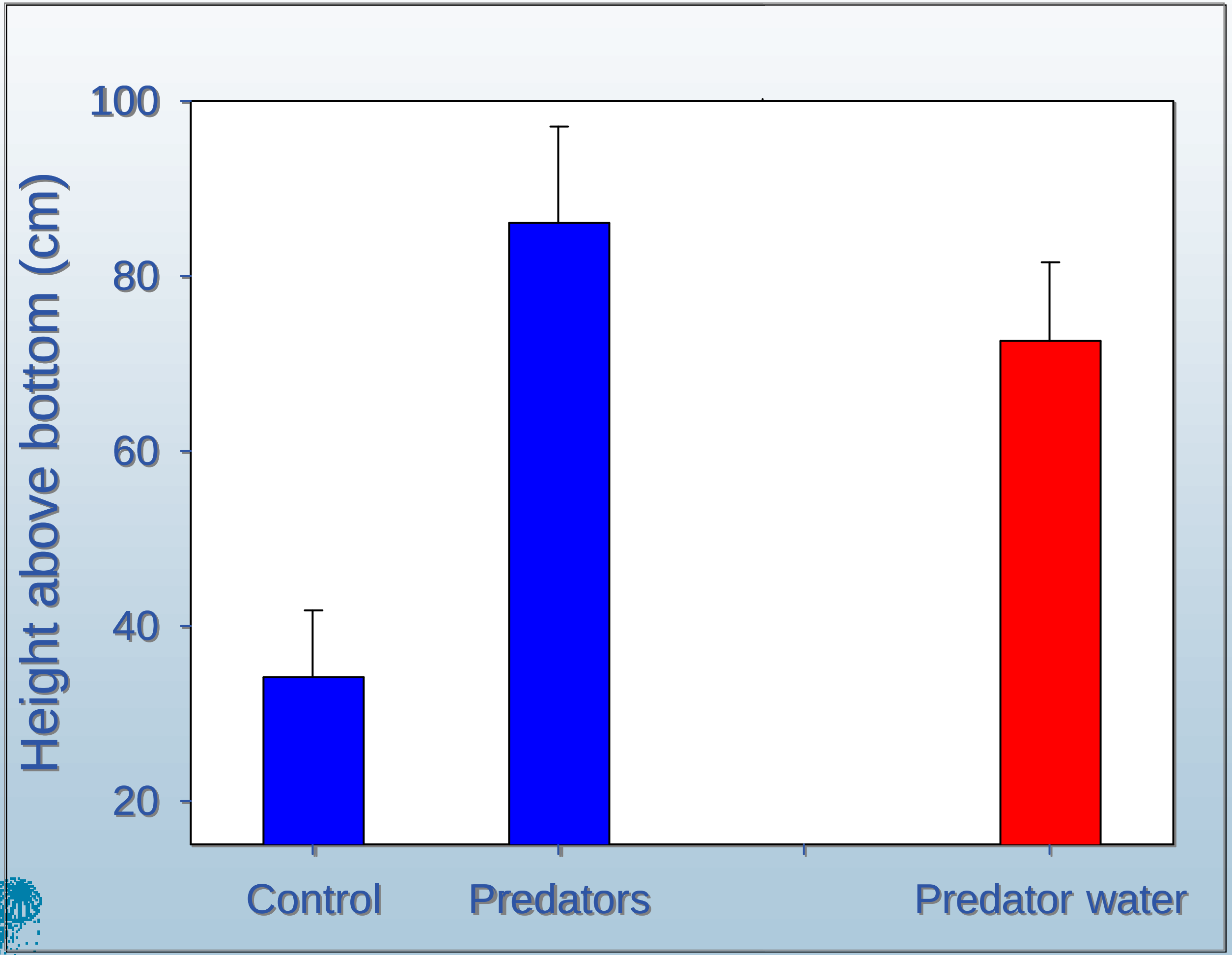
Vertical migration



And in the sea?

Marine crab (*Rhithropanopeus harrisii*) migrates up and down, depending on the tide

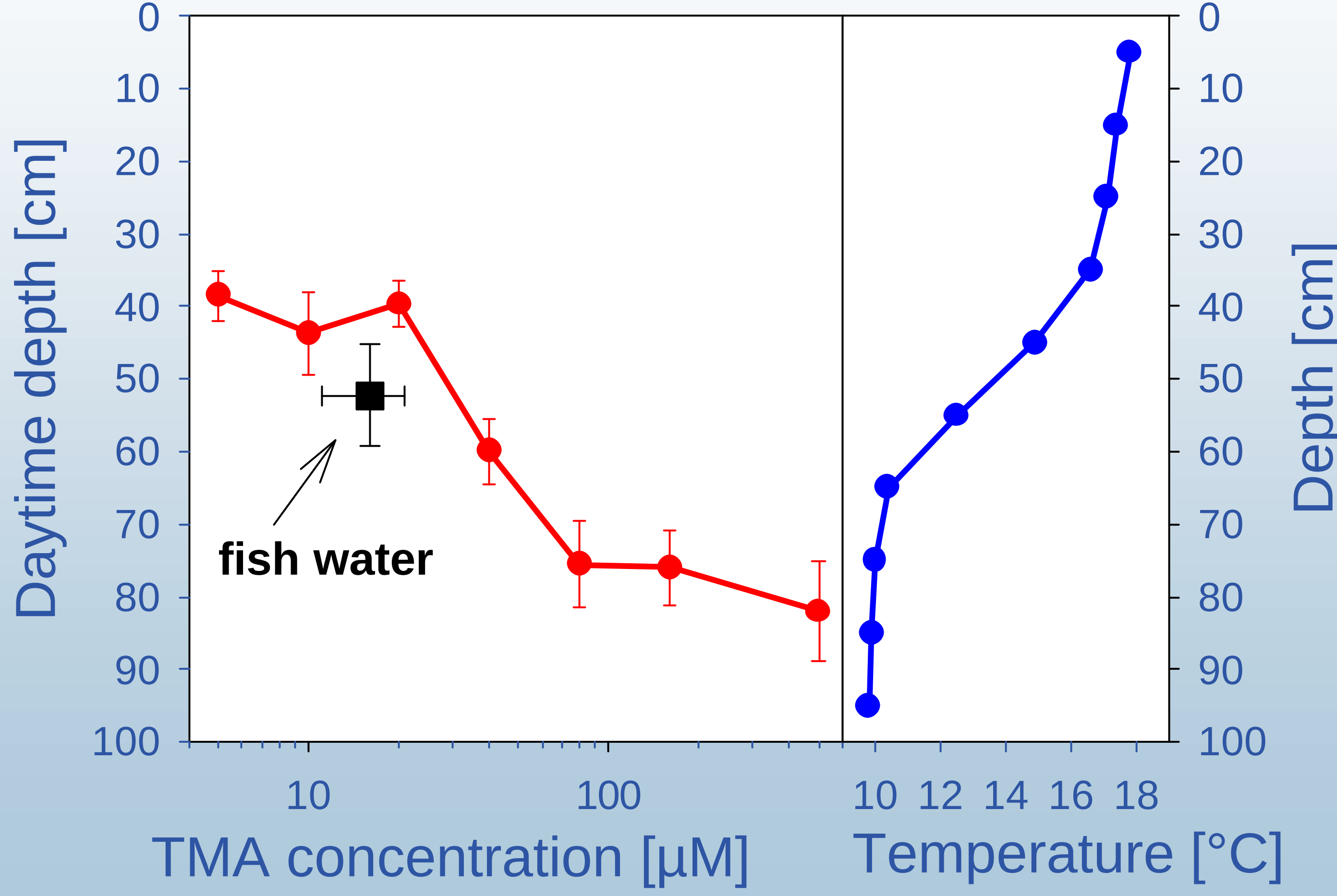
More examples in the sea



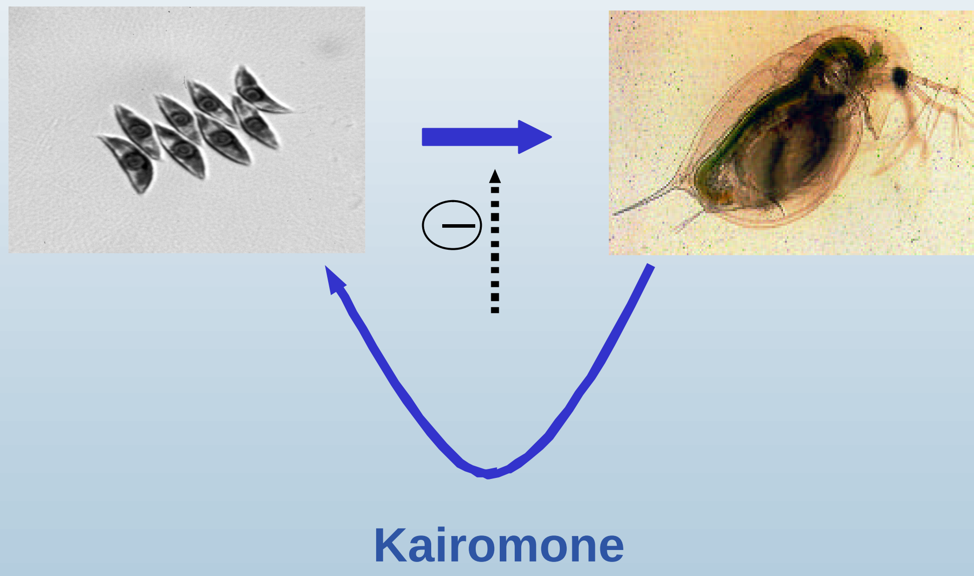
The nature of the kairomones

- We have very little idea
  - disaccharide degradation products of predator mucus containing sulfated and acetylated amines (Forward & Rittschof)
  - TMA (Boriss)
  - Not TMA, but something else (von Elert)

What is the nature of these kairomones



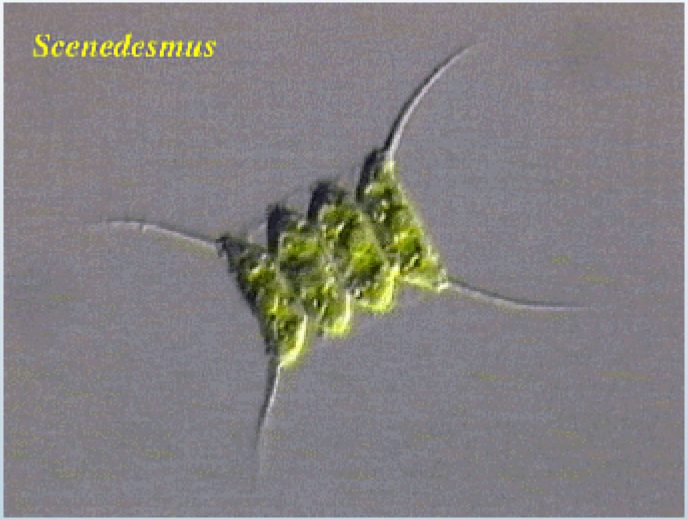
The interaction zooplankton-algae



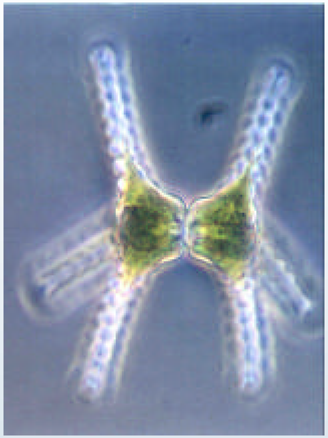
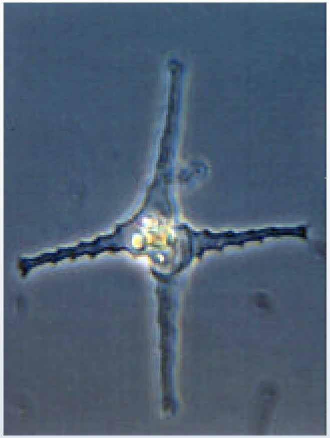
Potential adaptations to predation

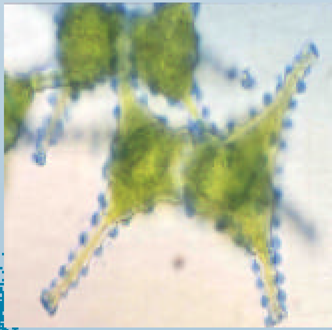
- Morphology
  - morphological defences such as spines
- Behaviour
  - vertical migration
- Life-history
  - Colony size
  - mode of reproduction

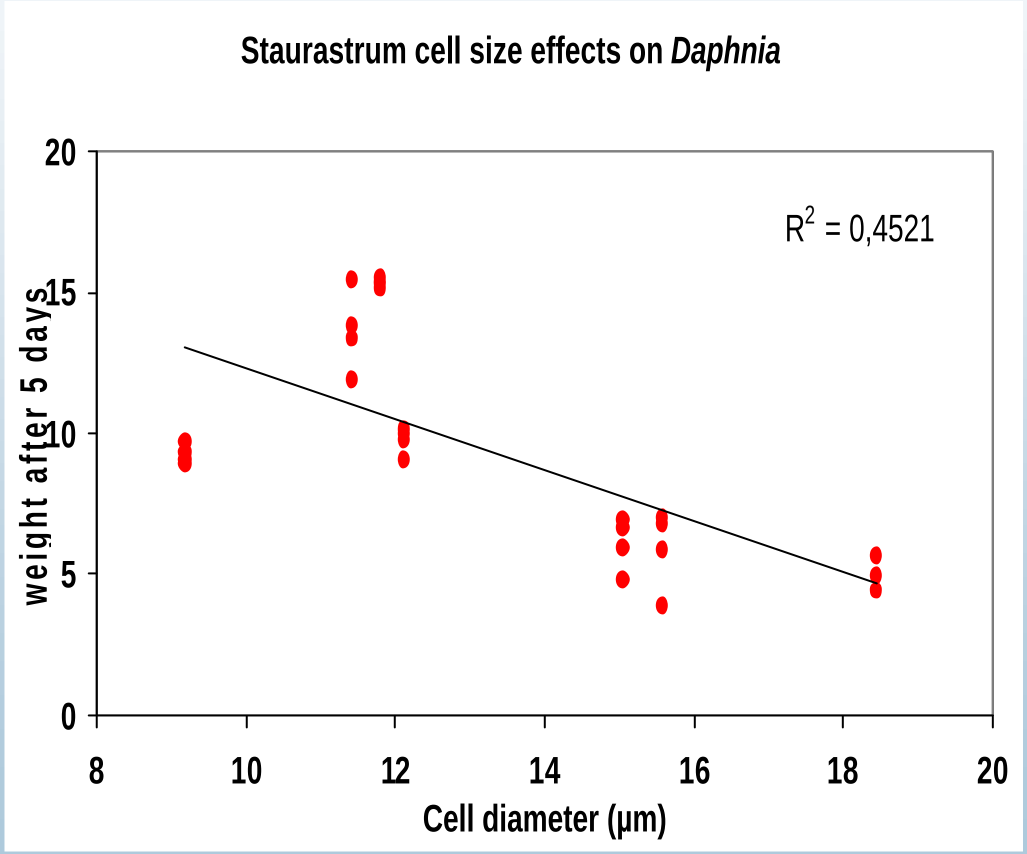
Morphology



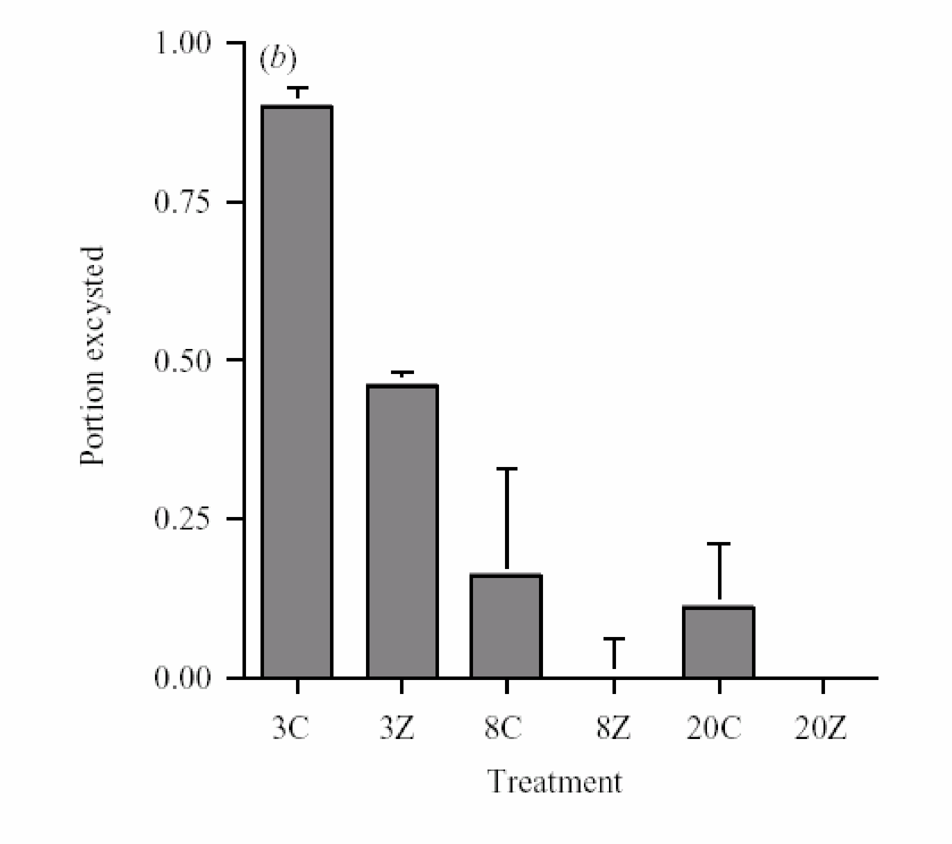
Morphology



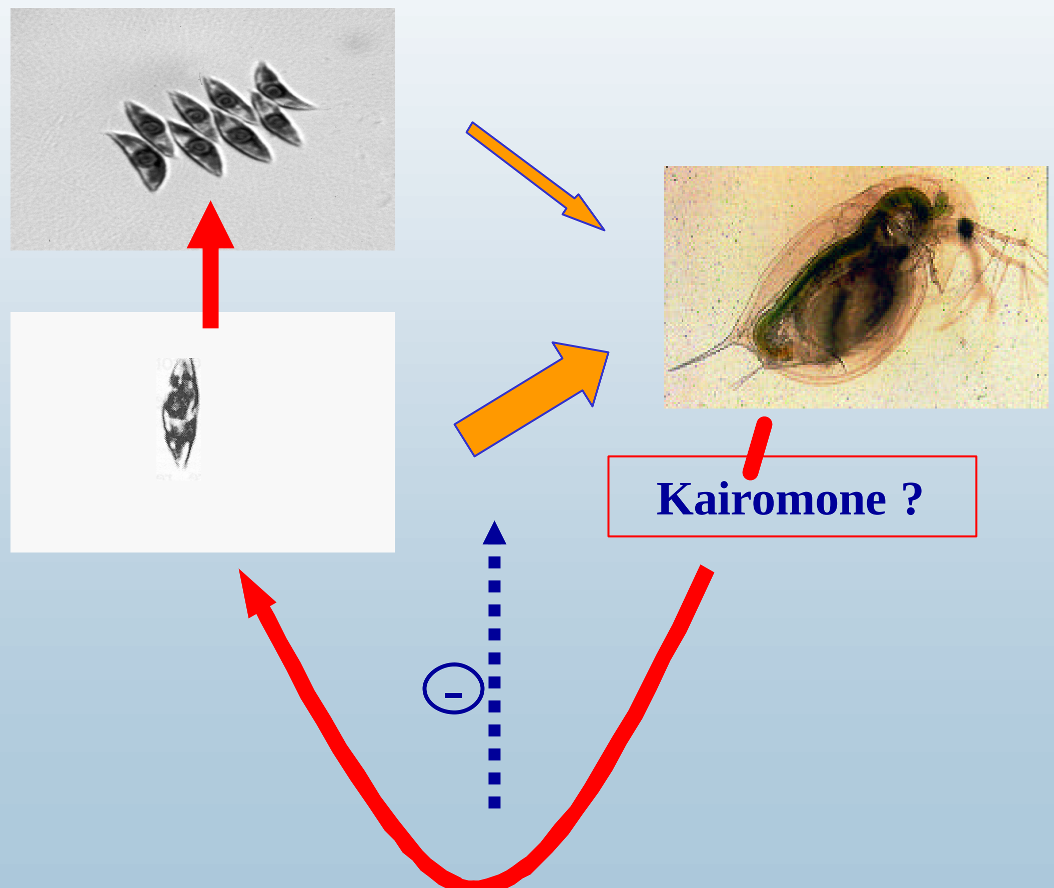


Staurastrum cell size effects on *Daphnia*
$R^2 = 0,4521$
weight after 5 days
20
15
10
5
0
8
10
12
14
16
18
20
Cell diameter (µm)

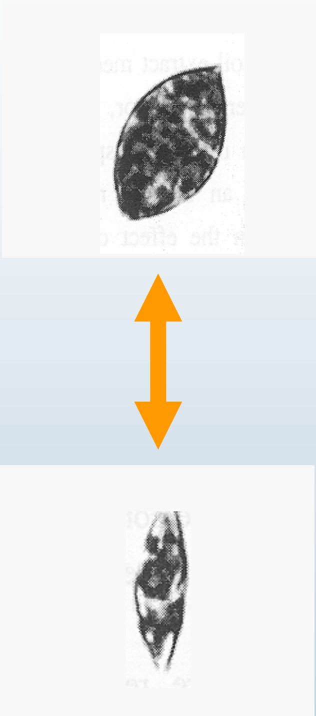
Life-history

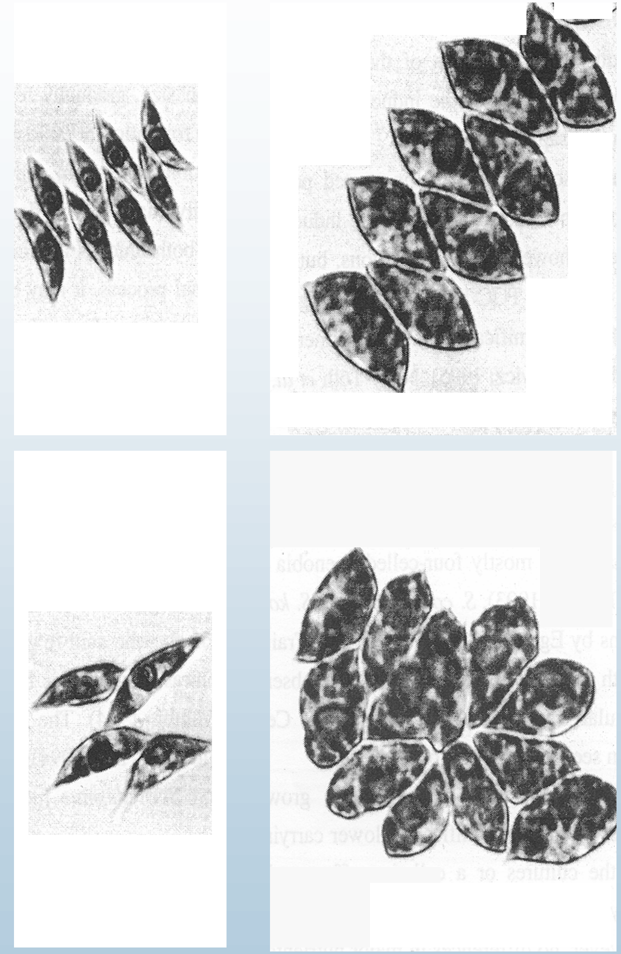


Hatching in *Peridinium* *(Rengefors)*

Colony size



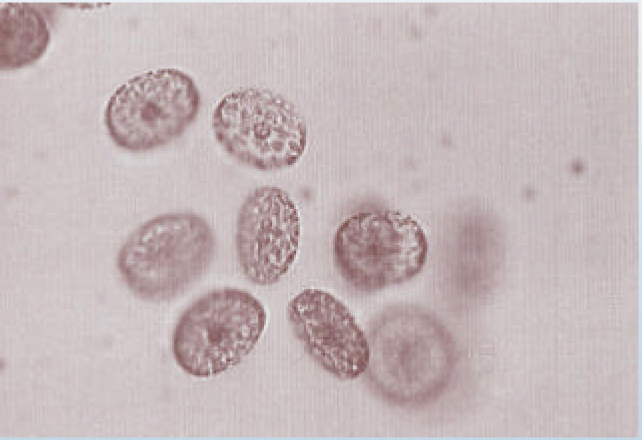




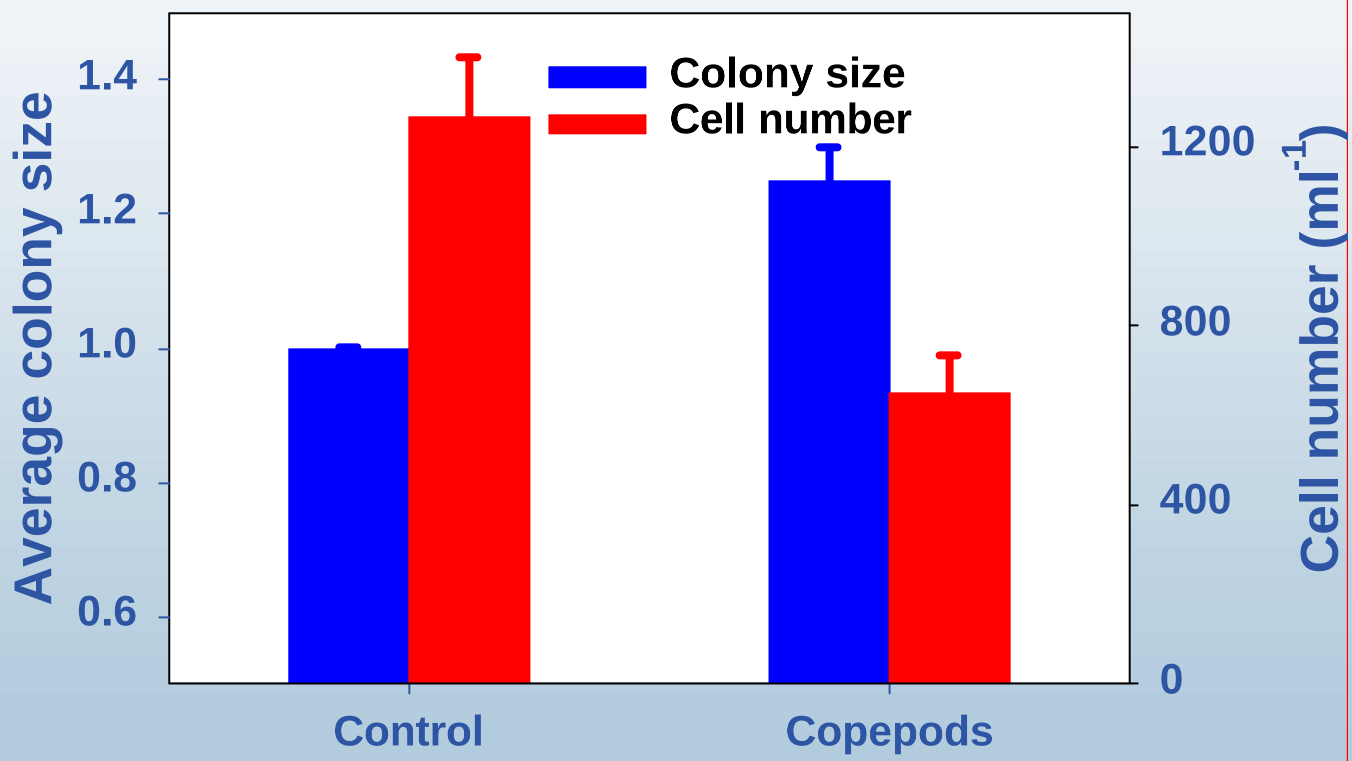
Single cells

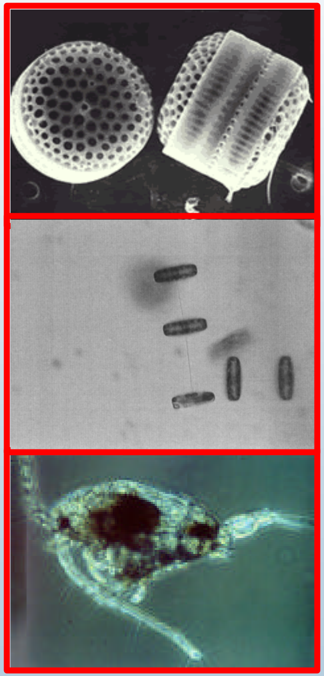
coenobia

And in the sea?

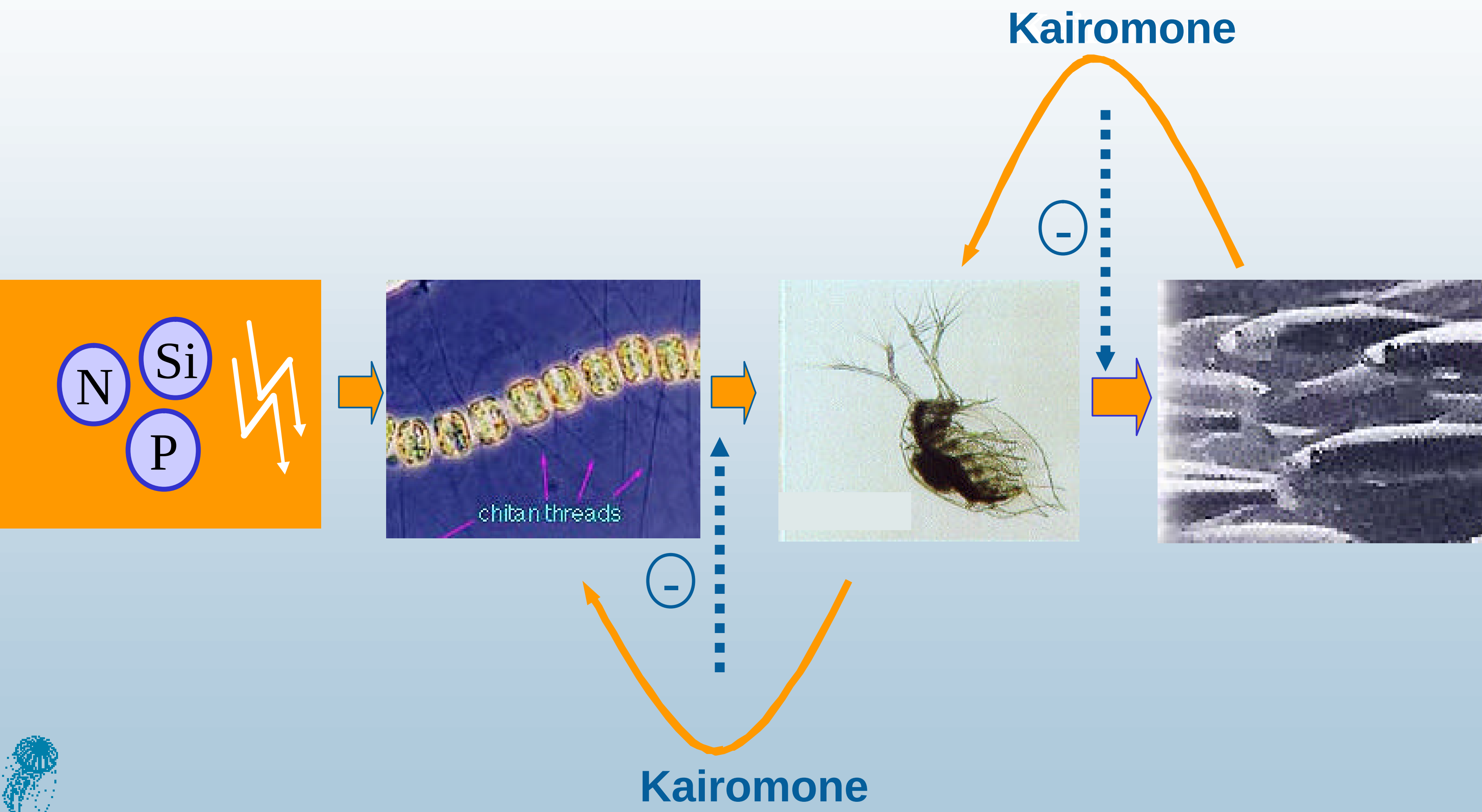


Reaction of *Thalassiosira* to Copepods



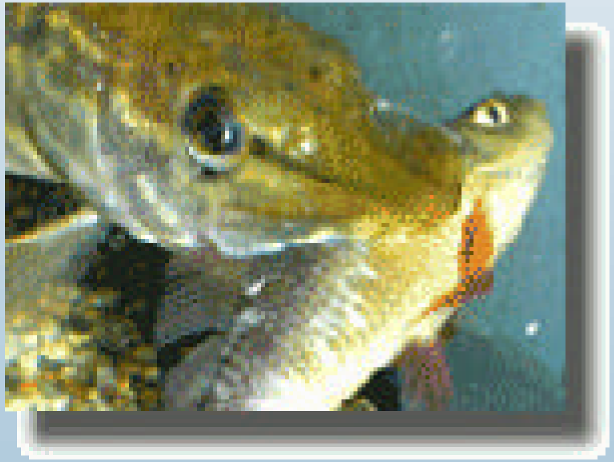


A very complicated simplified food web

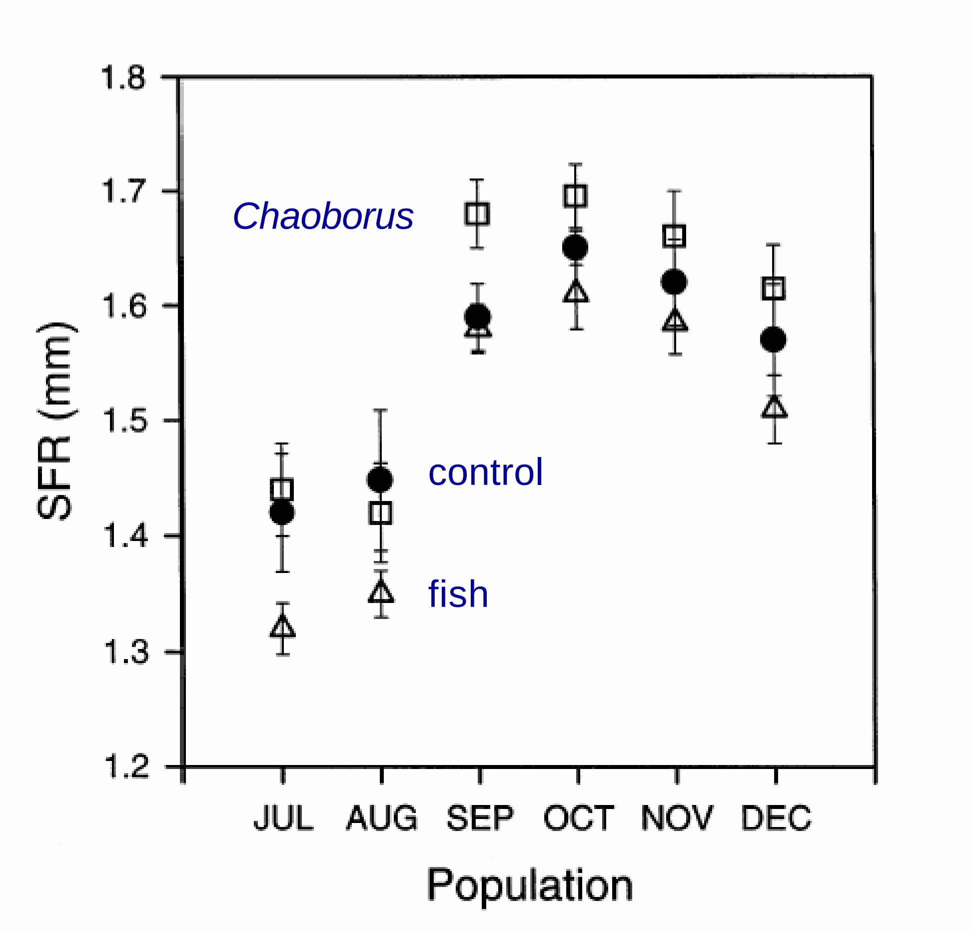


Why induced responses?

- Change!
- Physiological costs
- Ecological costs



Change



Stibor & Lampert 2000

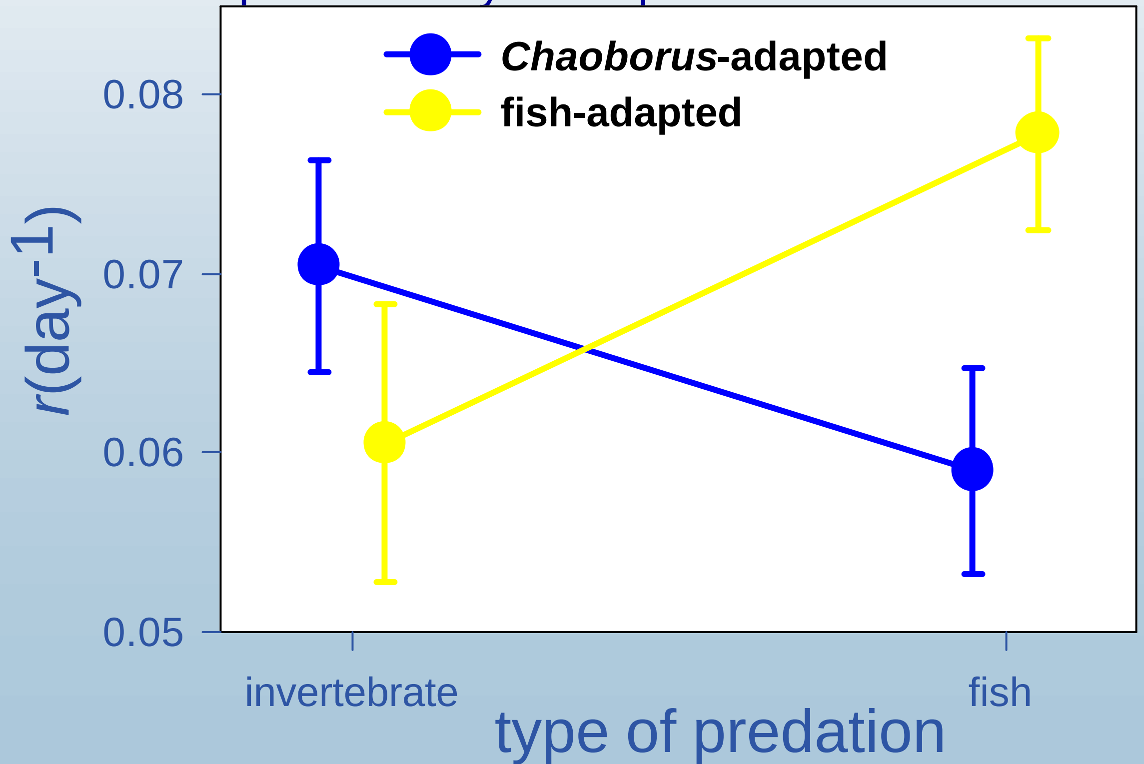
Physiological costs

- Costs attached to the response (increased energy consumption)
- Costs attached to the production of substances (trade-offs: other substances cannot be produced)
- Auto-toxicity
- Genetic costs (pleiotropy)

- These are very difficult to measure as a decreased growth rate might be part of the response
- Currency?

Ecological costs

- What are the ecological costs of being wrongly defended?
  - Increased predation by other predators?



MB 2006

Explanatory models

- If a trait is to be selected for the benefits of this trait in terms of fitness gain should be more than the costs incurred to display the trait
- Early theories: secondary metabolites are waste overflow products
- Modern: production comes with costs, hence there need to be benefits, but costs are difficult to measure

Explanatory models of defence mechanisms

When to invest in defence?

- Plant Apparency Model (PAM)
- Resource Availability Model (RAM)
- Carbon Nutrient Balance Hypothesis (CNBH)
- Environmental Stress Theory (EST)
- Growth Differentiation Balance Hypothesis (GDBH)
- Optimal Defence Theory (ODT)

Plant Apparency Model (PAM)

- Feeney 1976; Rhoades 1979

- Large, common, or predictable plants cannot hide from predators
- As a result, they are very likely to come under attack
- Hence, apparent plants should invest more in defence than non-apparent ones

Resource Availability Model (RAM)

- Coley et al. 1985

- Those species that evolved in nutrient-rich environments are fast growers, that can replace lost tissue with ease, and should hence not invest in defence
- Low-nutrient species (slow growers) should invest more

Carbon Nutrient Balance Hypothesis (CNBH)

- Bryant et al. 1983; Tuomi et al. 1988
- Under light (carbon) limiting conditions plants should invest in growth and reproduction
- Under nutrient limitation (excess photosynthetic products) plants should invest in low-nutrient secondary metabolites

Environmental Stress Theory

- Rhoades 1979

- Stress causes a reduction in the availability to acquire resources
- As a result, stress should result in a decrease in the secondary metabolites

Growth Differentiation Balance Hypothesis (GDBH)

- Loomis 1953; Herms & Mattson 1992

- Trade-off between differentiation and growth
- Differentiation occurs after growth
- Young, actively growing tissues should contain low levels of secondary metabolites

Optimal Defence Theory (ODT)

- Feeny 1975; Rhoades 1979
- Organisms should defend themselves in such a way that they **maximize their fitness**
- Younger individuals and younger parts of a plant are generally more nutritious and should be defended more heavily

Difficult to apply to planktonic algae?

- What is an apparent uni-cellular organism?
  - Bloom-forming
- Do we know where species evolved?
  - Current distribution
- Mostly single-celled organisms: so no differentiation
  - Different phases of a bloom

Predictions: PAM

- Those species that form large predictable blooms should invest in defences, but single individuals are probably defended by numbers in a bloom, so?

- Evidence: those algal species that produce toxins are very often not the dominating species or produce large blooms
- Bloom-forming species often do not produce toxins

Predictions: RAM

- Species occurring in coastal (or other more productive) regions are faster growers and hence should produce less heavily in defence mechanisms
- Evidence: toxic algae occur close to the coast very often, even though the algae that produce them are often indeed not the fastest growers

Predictions

- ODT: fast growing populations (pre-bloom) should invest most heavily in defence, because they are more nutritious, but most likely the predation rates are higher later in the bloom, so?
- GDBH: algae in late bloom (‘mature’) should be more defended
- Evidence: virtually absent. Probably because much of the predictive capacity focuses on when the algae are found, not when they produce substances

Predictions

- CNBH: algae should produce most of their defence substances, which are often low in nitrogen (except PSP toxins; saxitoxin 33% N), under excess carbon and limiting nitrogen

- EST: nutrient limitation is stress, and hence will lead to a lower production of toxins

- Evidence: there are many examples that toxin production increases under nutrient stress

So?

- Carbon Nitrogen Balance Hypothesis explains the production patterns, but does it really?

- It does not explain why, it merely explains the timing of toxin production when it comes to resources, but not to timing of the need.
- ODT predicts: produce when needed, perhaps we should combine these two models

- Predator induced toxicity in microalgae?

Kunstformen der Natur (Haeckel 1899)

Behind the morphological diversity, already observed by Haeckel, there is a plethora of other diversity, which we are only starting to understand. Furthermore, this diversity is not constant, but can change as a result of environmental conditions