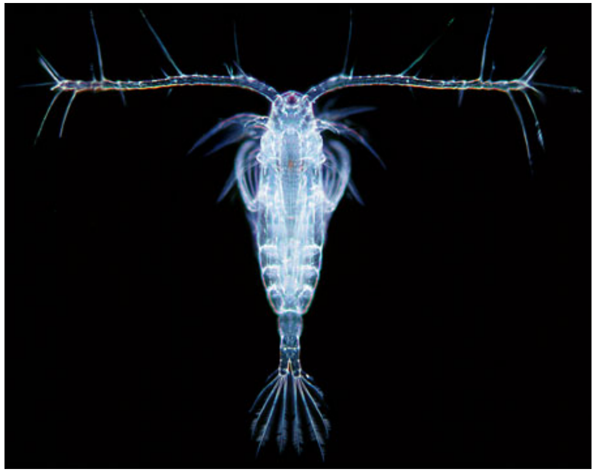
The Abdus Salam
International Centre for Theoretical Physics

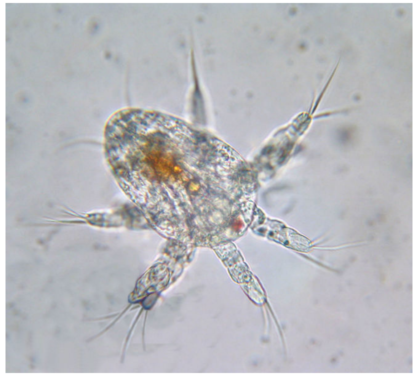
United Nations
Educational, Scientific and
Cultural Organization

Advanced School on Complexity, Adaptation and Emergence in Marine Ecosystems

IAEA
International Atomic Energy Agency

Mechanistic interactions in plankton, fitness and behaviour

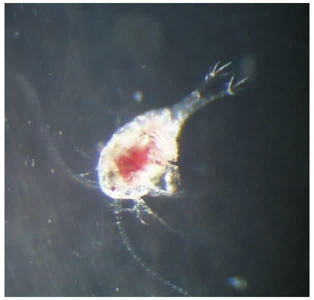


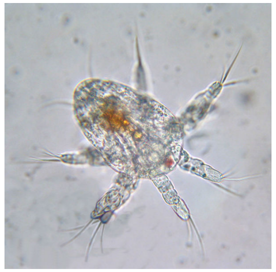



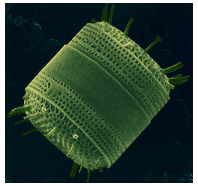
André W. Visser

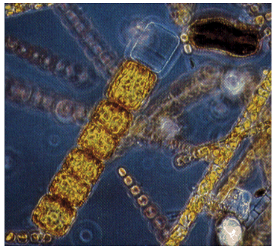
DTU Aqua
National Institute of Aquatic Resources

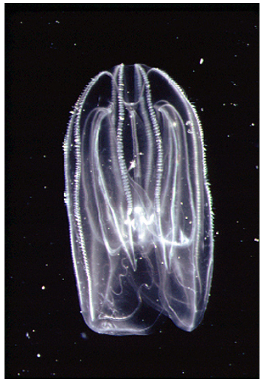
Marine organisms have a wide range of abilities, behaviours, and life strategies.


copepod


nauplius


diatom


diatom


ctenophore


ciliate


copepod


dinoflagellate

Energy source:
- light (autotrophy, photosynthesis),
- chemicals (autotrophy, chemotrophy) ,
- other organisms (heterotrophy),
- dead particles (detritivore),
- dissolved organic material (osmotrophy)

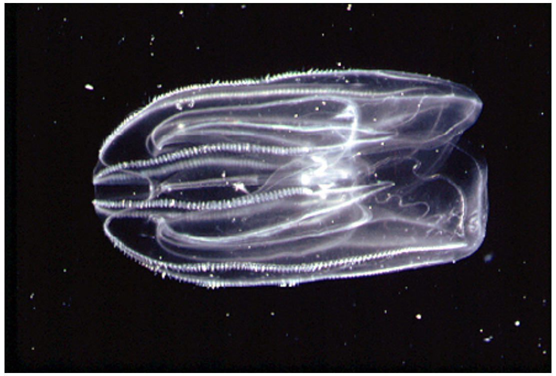
How they forage

Feeding mode:
- ambush, feeding current, cruise, suspension, filter

Sensing mode:
- visual, hydromechanical, chemical, tactile

Migration:
- daily, orthogenic, seasonal

Maternal care:
- broadcast spawner, egg-carrier



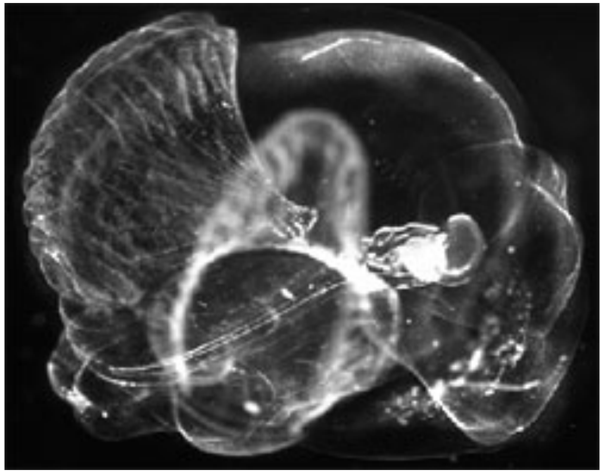
mnemiopsis

ctenophore

comb jellies

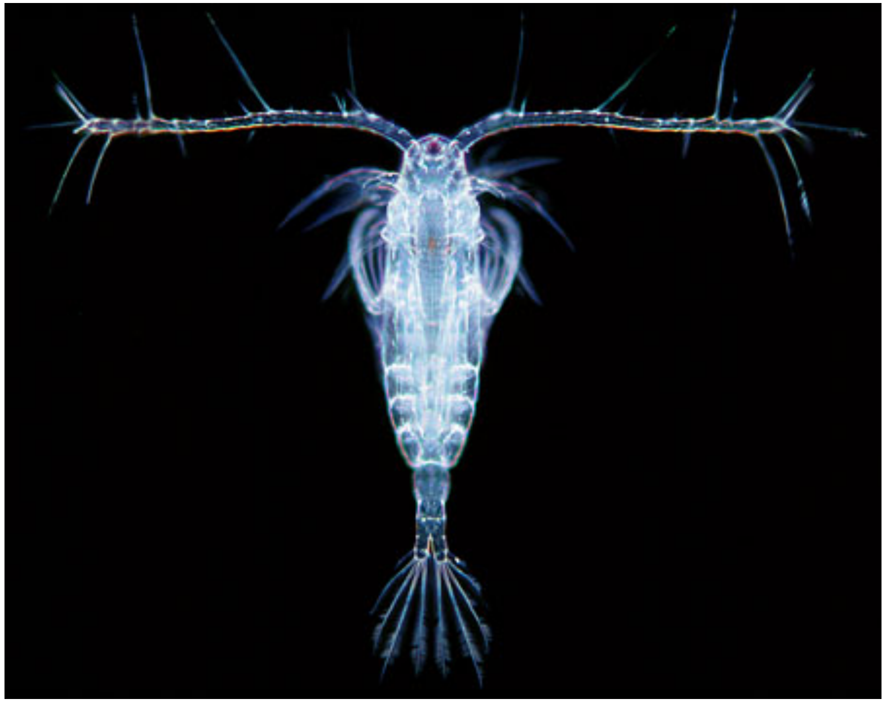
Larvaceans

Filter feeders:
mucus housing
through which
water is
pumped and
prey extracted



appendicularium

Copepod feeding modes



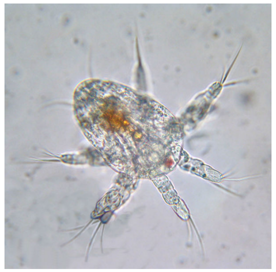
Suspension feeding: generate a feeding current and “pick out” prey items that approach.

Filter feeding: generate a current and filter out all prey items that can be sieved out.

Cruise feeding: swim to find a prey item.

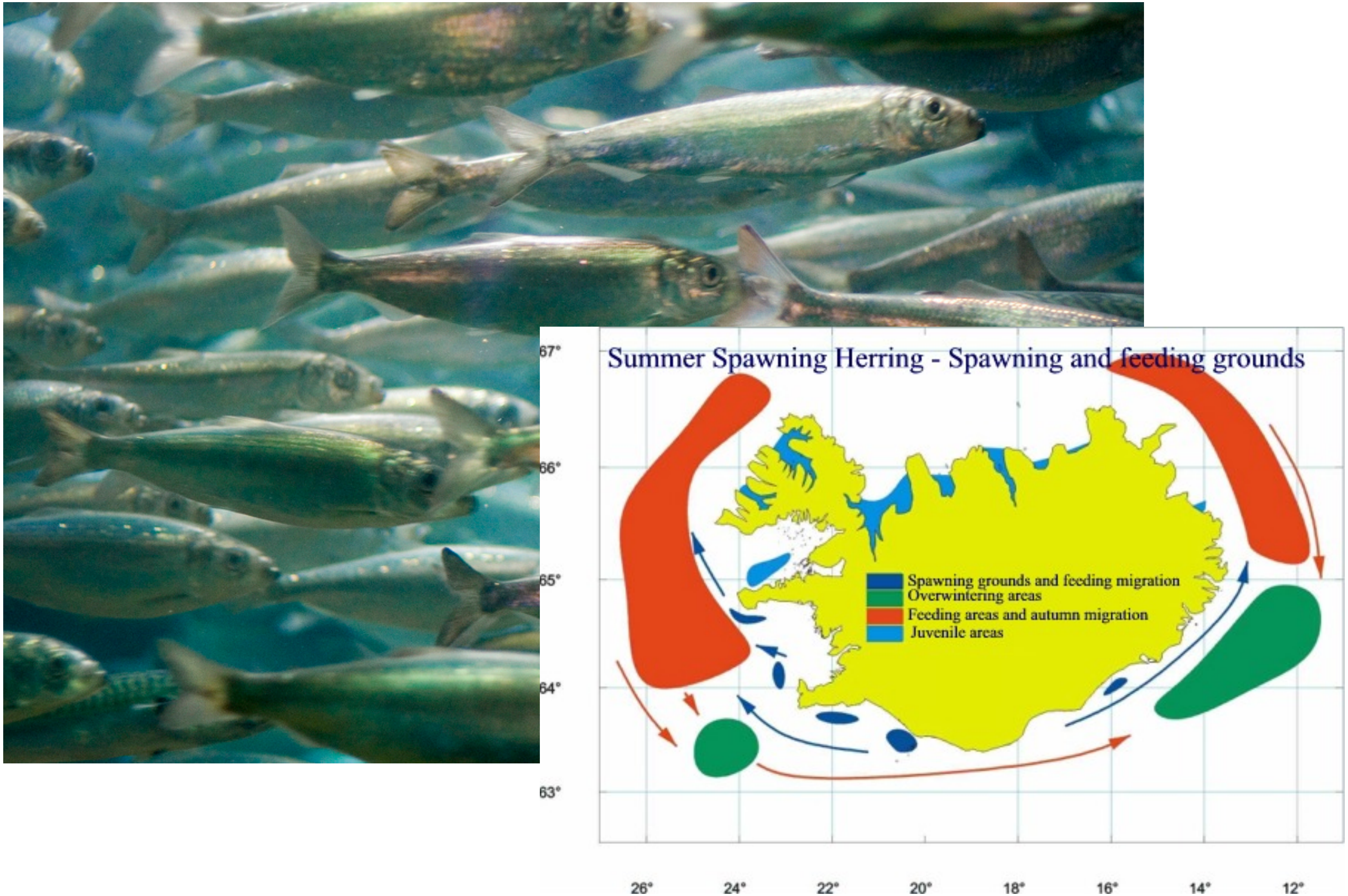
Ambush feeding: remain motionless and wait for prey to approach.

Success depends on the type of prey available

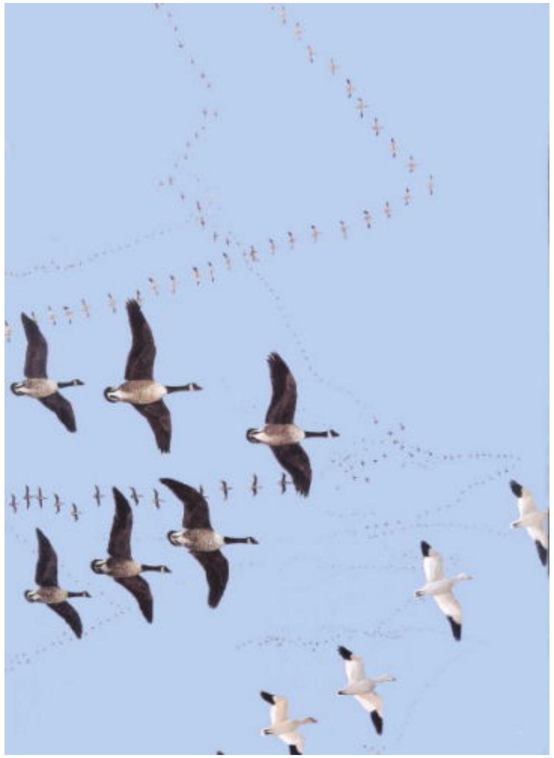


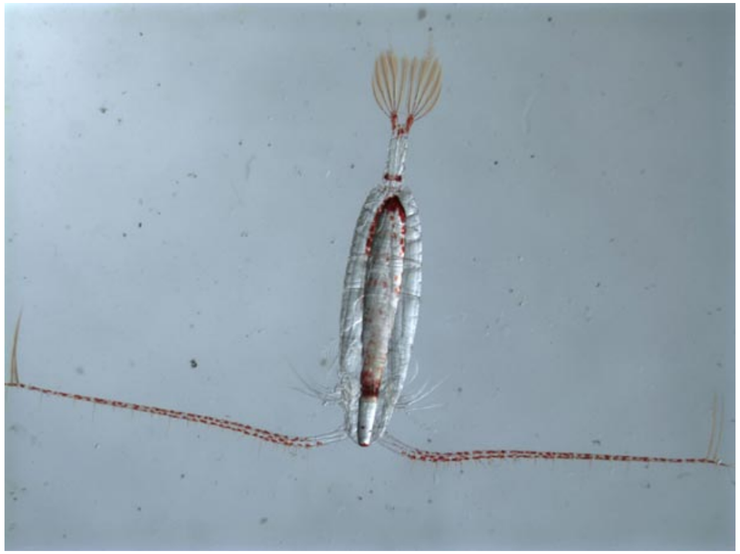
..and will be different for different life stages

Migration

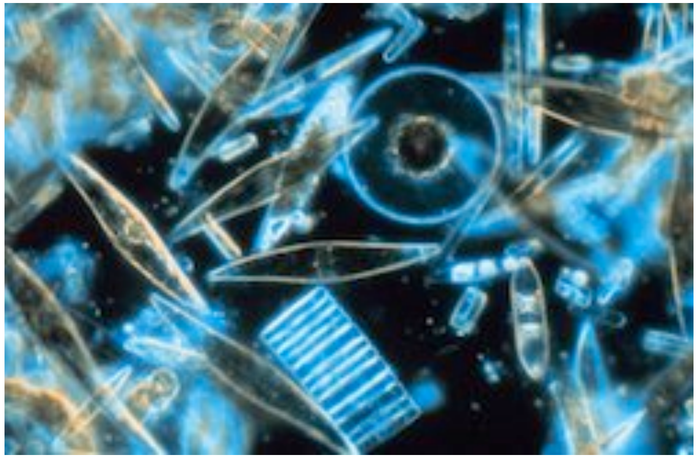

Summer Spawning Herring - Spawning and feeding grounds
Spawning grounds and feeding migration
Overwintering areas
Feeding areas and autumn migration
Juvenile areas
67°
66°
65°
64°
63°
26°
24°
22°
20°
18°
16°
14°
12°

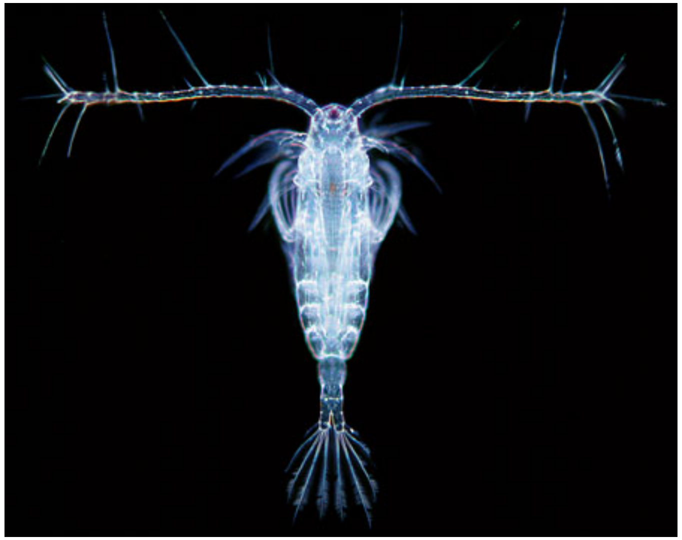
Migration





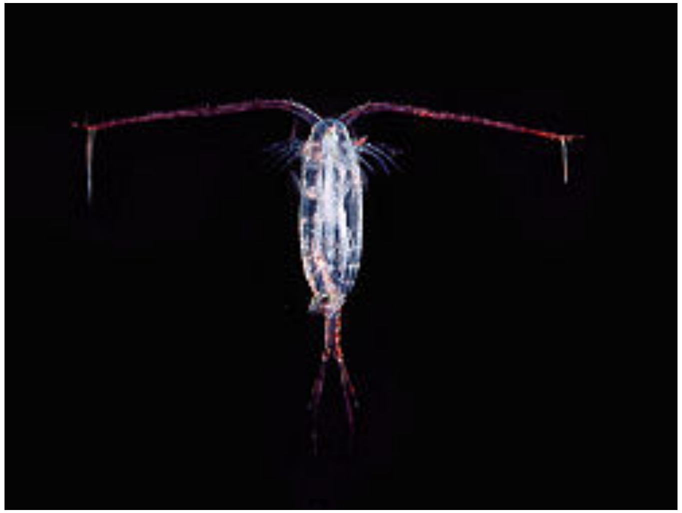
All of these behaviours and adaptations are plastic to a greater or lesser degree



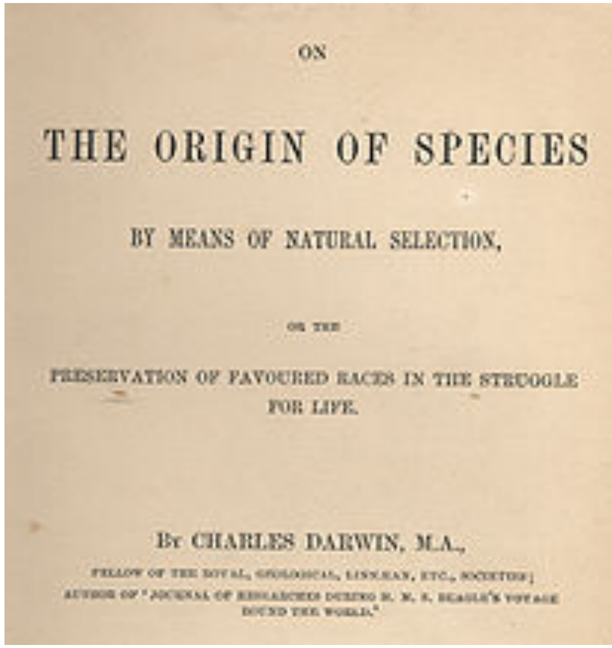


Phenotypic plasticity is the ability of an organism to change its phenotype in response to changes in the environment, either its biotic or abiotic components. Expressed in changes of either morphology or behaviour (reaction norms).

Why do organisms do what they do ?



copepod



ON

THE ORIGIN OF SPECIES

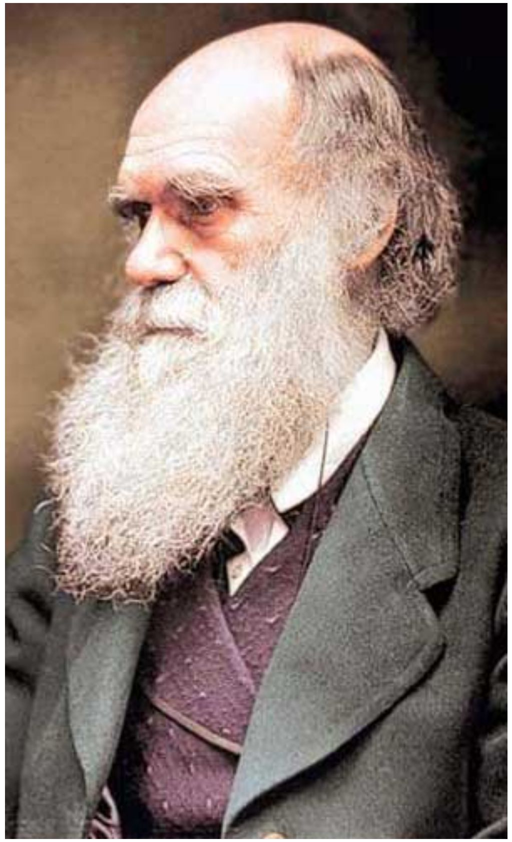
BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'



They do what they do in order to best promote their fitness.

Rationalization of behaviour !!

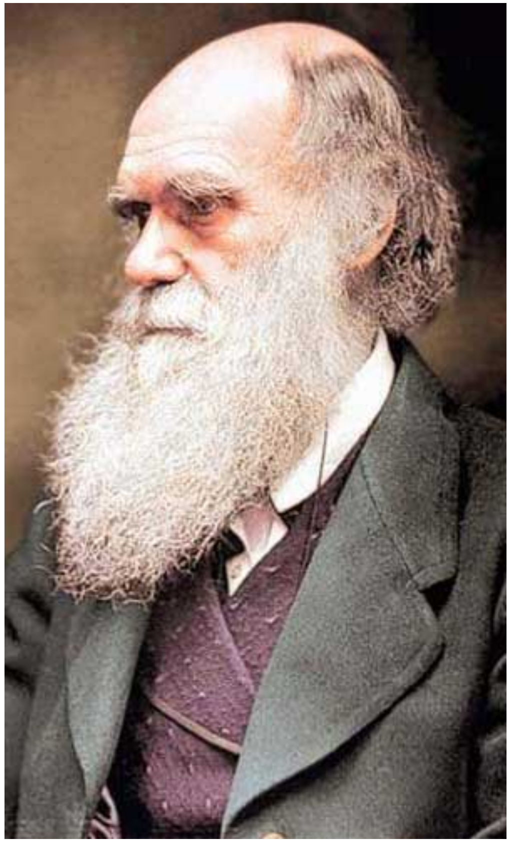
Darwin's central concept

Fitness: **a measure of how well an individual organism can survive and reproduce**

The driving force of evolution and the origin of species

.. not just the geologic past

The echoes of evolution can be seen in how animals behave today



Estimating fitness

Mathematically, fitness is not easy to define

Fisher's Reproductive value

Having survived up to "now", what is the probable number of offspring an organism will have over its expected future lifetime?

Probability of surviving

$$r_0 = \int_{t_0}^{\infty} a(t) f(t) dt$$

Reproduction rate: number of offspring/time

Maximizing r_0 at all times is *probably* the best strategy

Sir Ronald Aylmer Fisher

Statistician
Evolutionary biologist
Geneticist
Eugenics promoter

If an organism has no expectations of improving either its survival potential or reproductive rate over what it has "now", then

Expected reproductive value

$$r_0' = \int_{t_0}^{\infty} a e^{-m(t-t_0)} dt$$

$$= \left[-\frac{a}{m} e^{-m(t-t_0)} \right]_{t_0}^{\infty}$$

$$= \frac{a}{m}$$

Note: $\frac{1}{m}$ is the expected future lifespan of the organism

Total number of expected offspring over its expected future life span

Ratio of instantaneous reproductive rate to mortality rate

Estimating fitness

Expected fitness $$r_0\text{¢} = \frac{a}{m}$$

Factors effecting expected fitness:

The **environment**:

- **physical**: temperature, light, turbulence,
- **biotic**: how much food, type of food, how many predators, type of predators, competitors, parasites….

The **state** of the organism itself:

- maturity, gut fullness

The **behavioural** options it chooses:

- foraging strategy, feeding mode, migration, mating strategy

Estimating fitness

The net rate of energy income = gross income - energetic cost

Expected fitness $r_0' = \frac{a}{m} = g\frac{\dot{E}}{m} = g\frac{\dot{E}_{in} - \dot{E}_{cost}}{m}$

The energetic cost of producing a single surviving offspring

$$\text{Fitness} \approx \frac{\text{Benefit} - \text{Cost}}{\text{Risk}}$$

Fitness reflects a trade-off between the benefits, costs and risks of an individual's choice of behaviour played out in a specific environmental setting

An organism should choose its behaviour so as to maximize its fitness

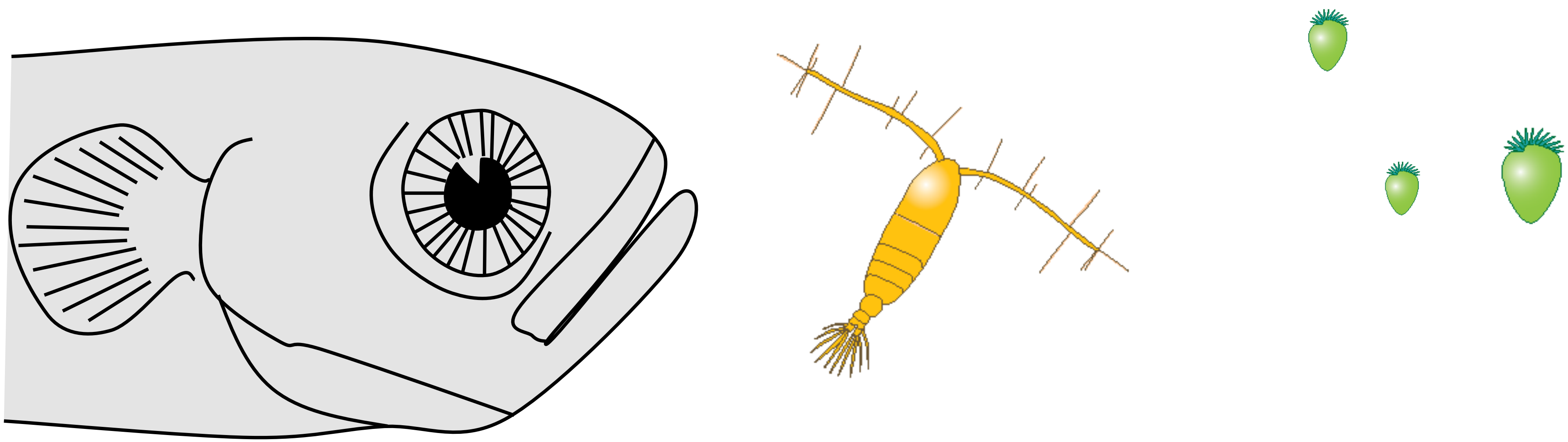
Natural selection has provided organisms with behavioural algorithms that do just that

Trade-offs in foraging behaviour

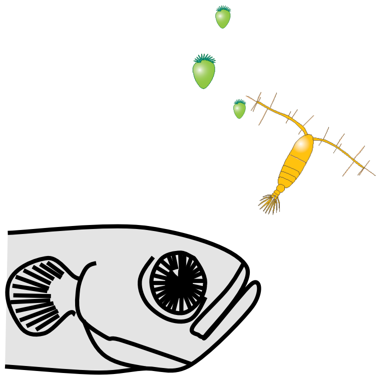
$$\textbf{Fitness} \approx \frac{\textbf{Benefit} - \textbf{Cost}}{\textbf{Risk}}$$

Encounters with prey

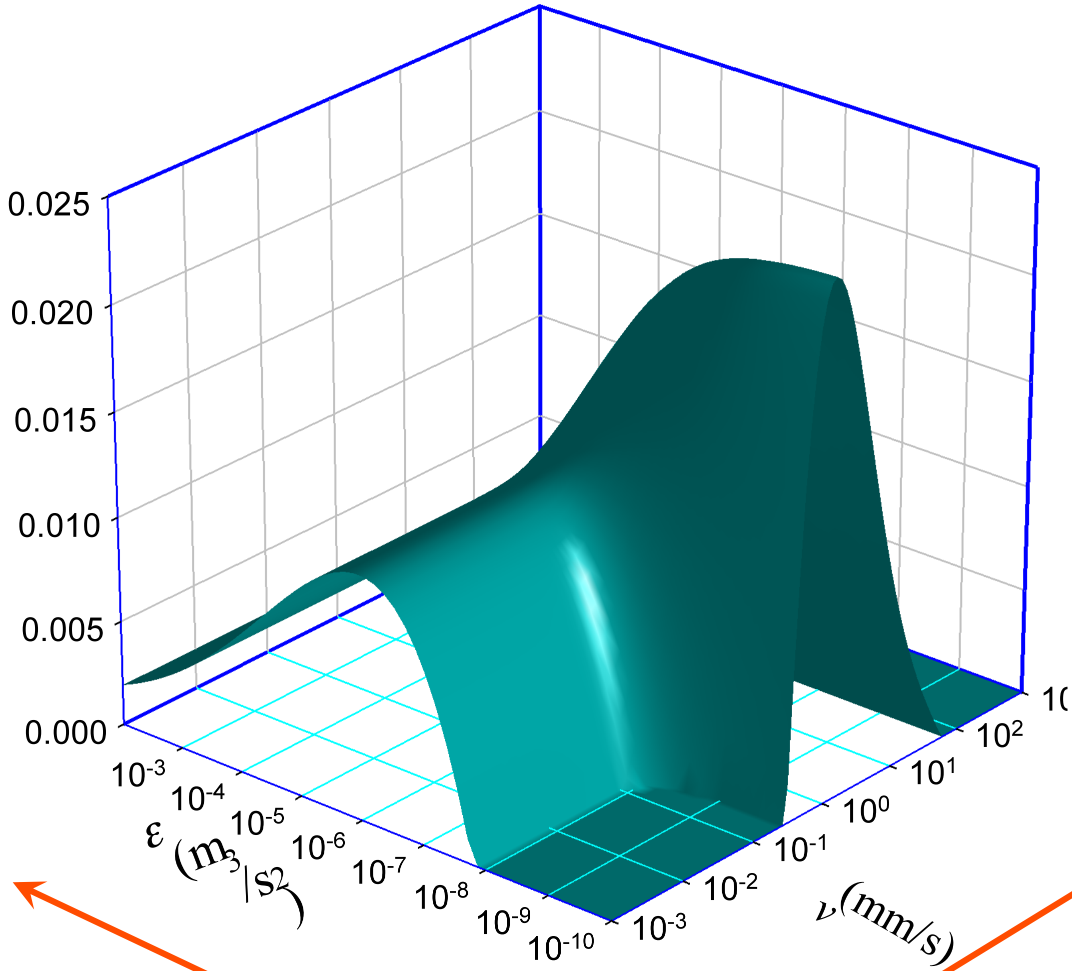
Encounters with predators



Trade-offs in foraging behaviour



Fitness landscape for an adult copepod

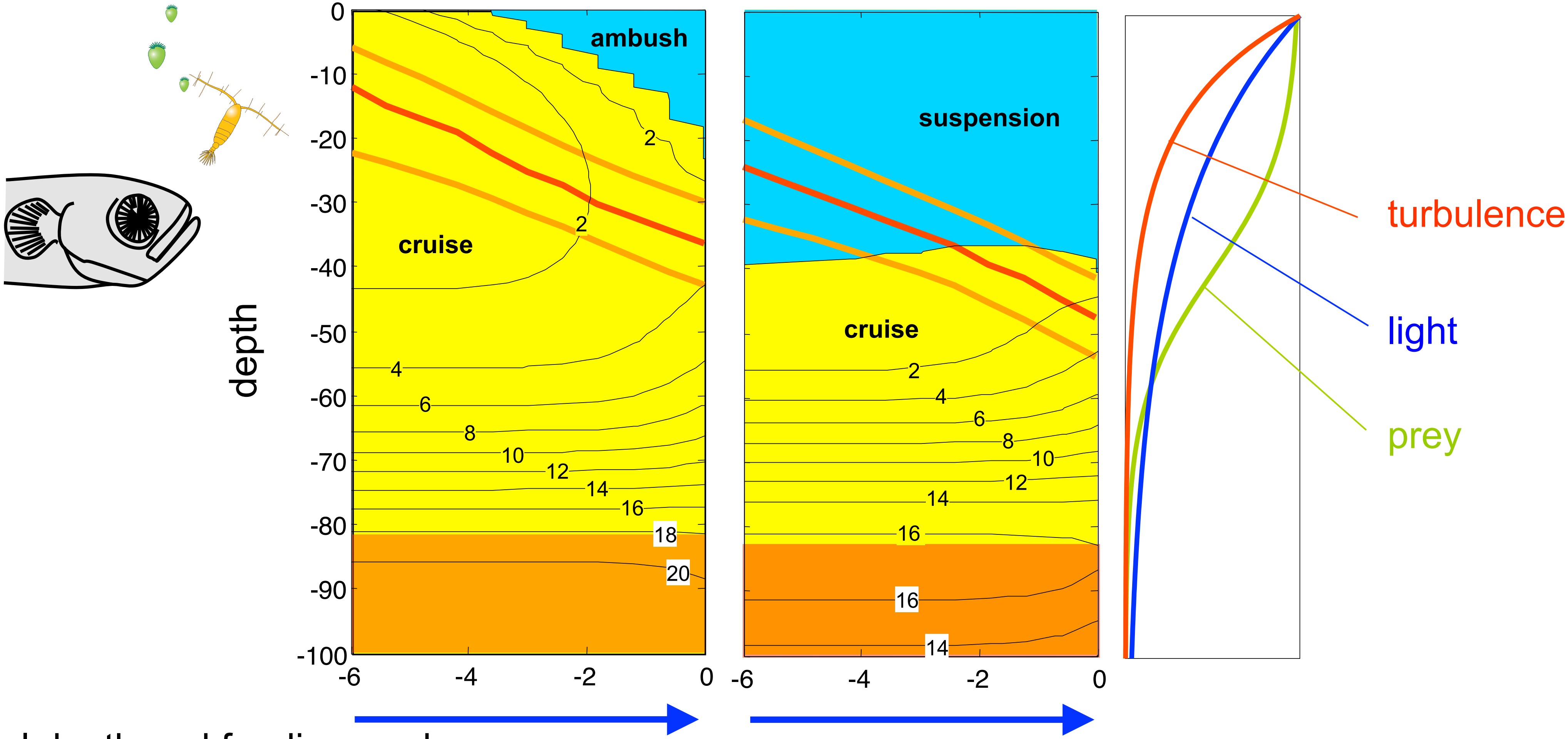


turbulent dissipation rate

swimming speed (foraging effort)

Visser, Mariani, Pigolotti, JPR 2009

Trade-offs in foraging behaviour



timal depth and feeding mode

Surface turbulent dissipation rate

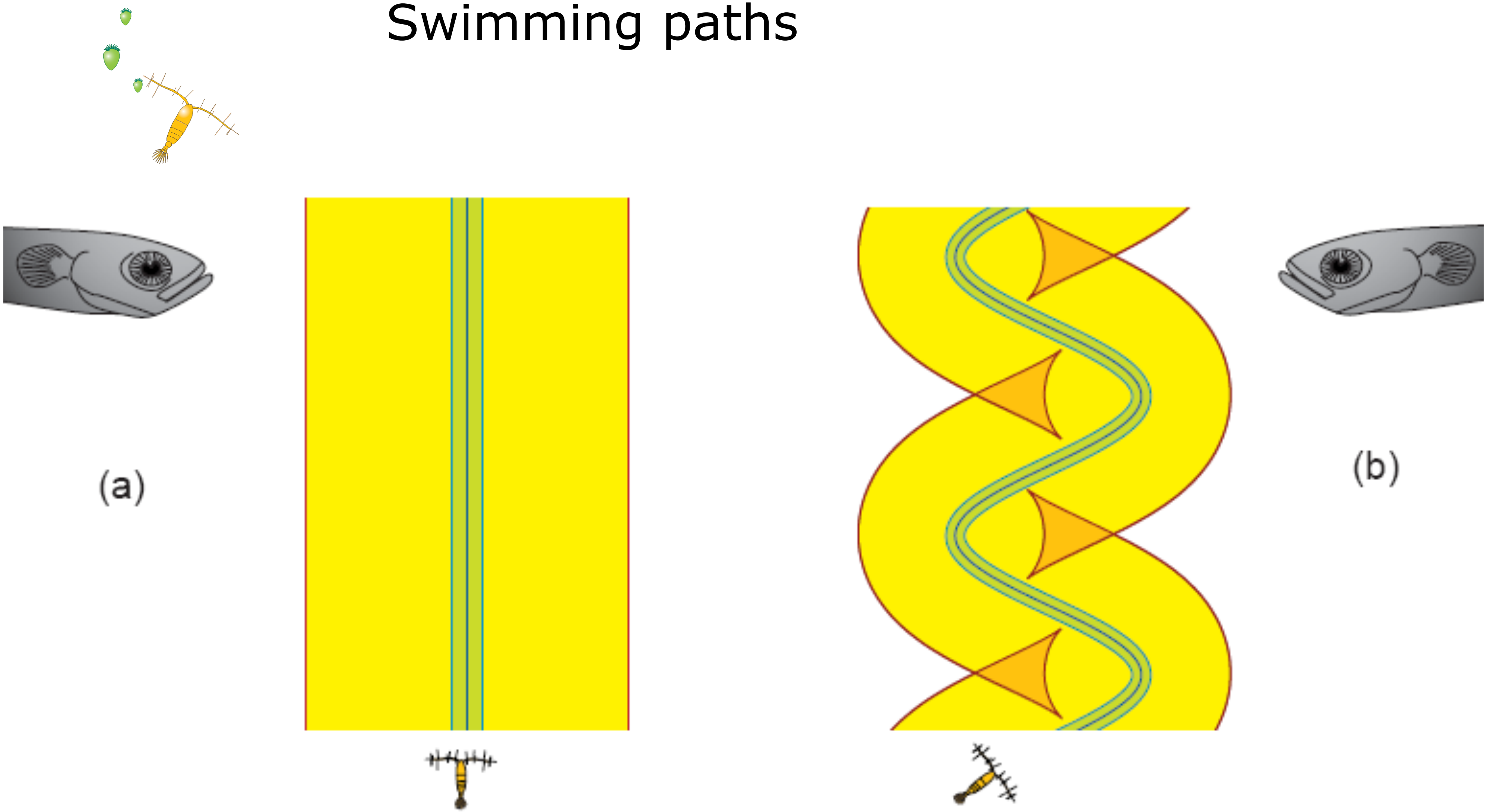
Neutrally buoyant copepod in the presence of a rheotactic predator

Negatively buoyant copepod in the presence of a visual predator

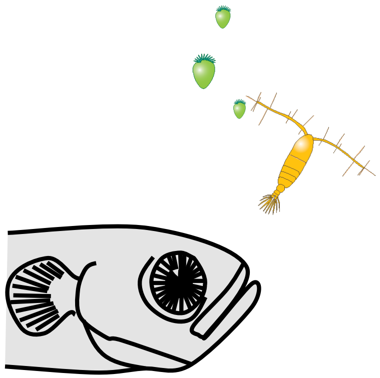
Visser, Mariani, Pigolotti, JPR 2009

Trade-offs in foraging behaviour

Swimming paths

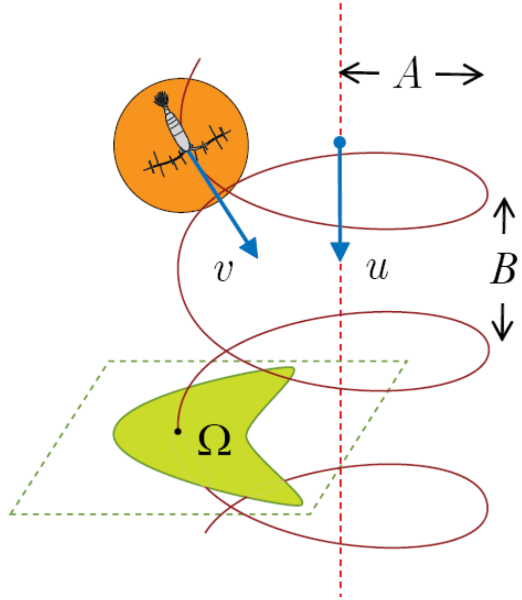


Trade-offs in foraging behaviour

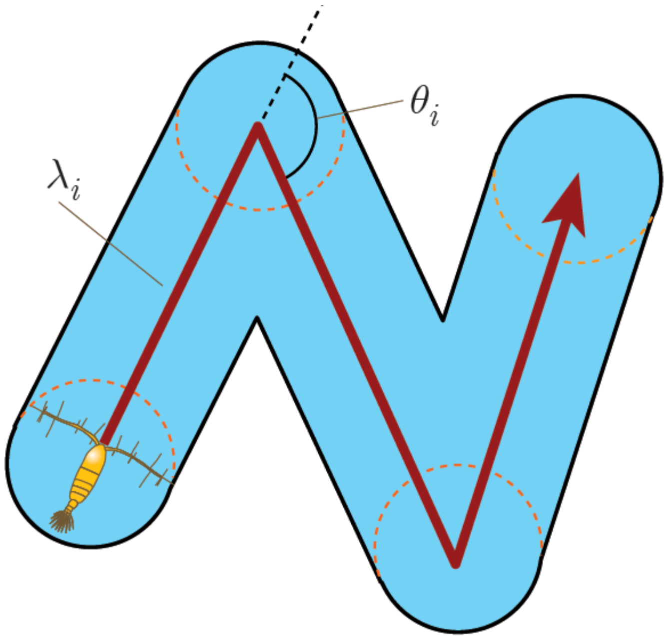


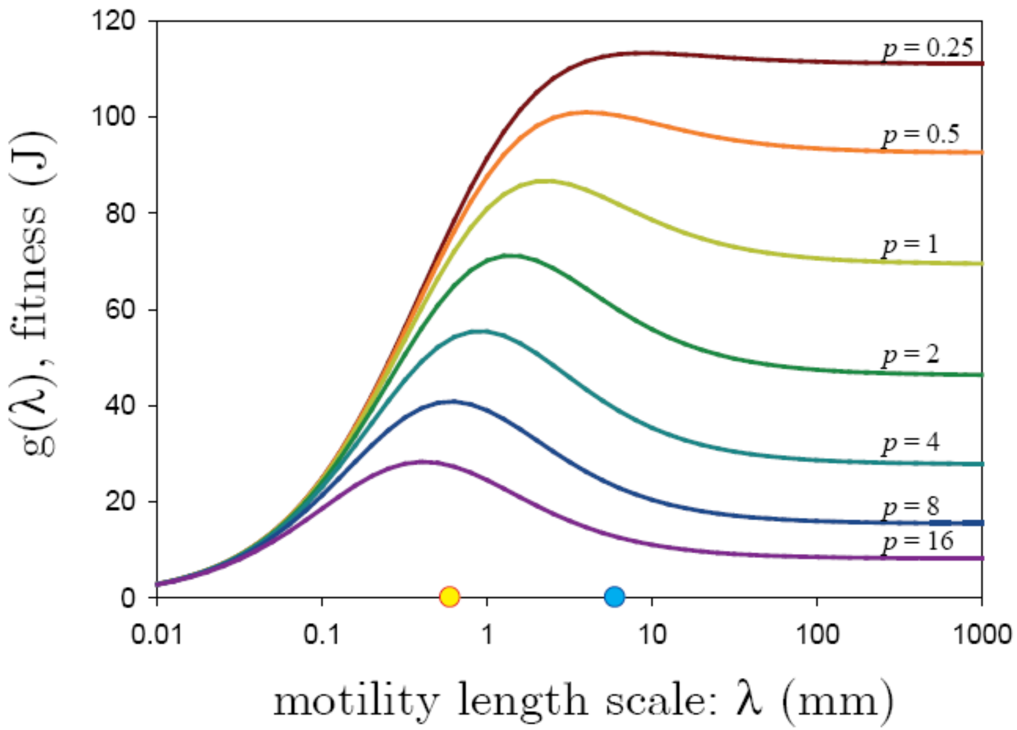
Swimming paths

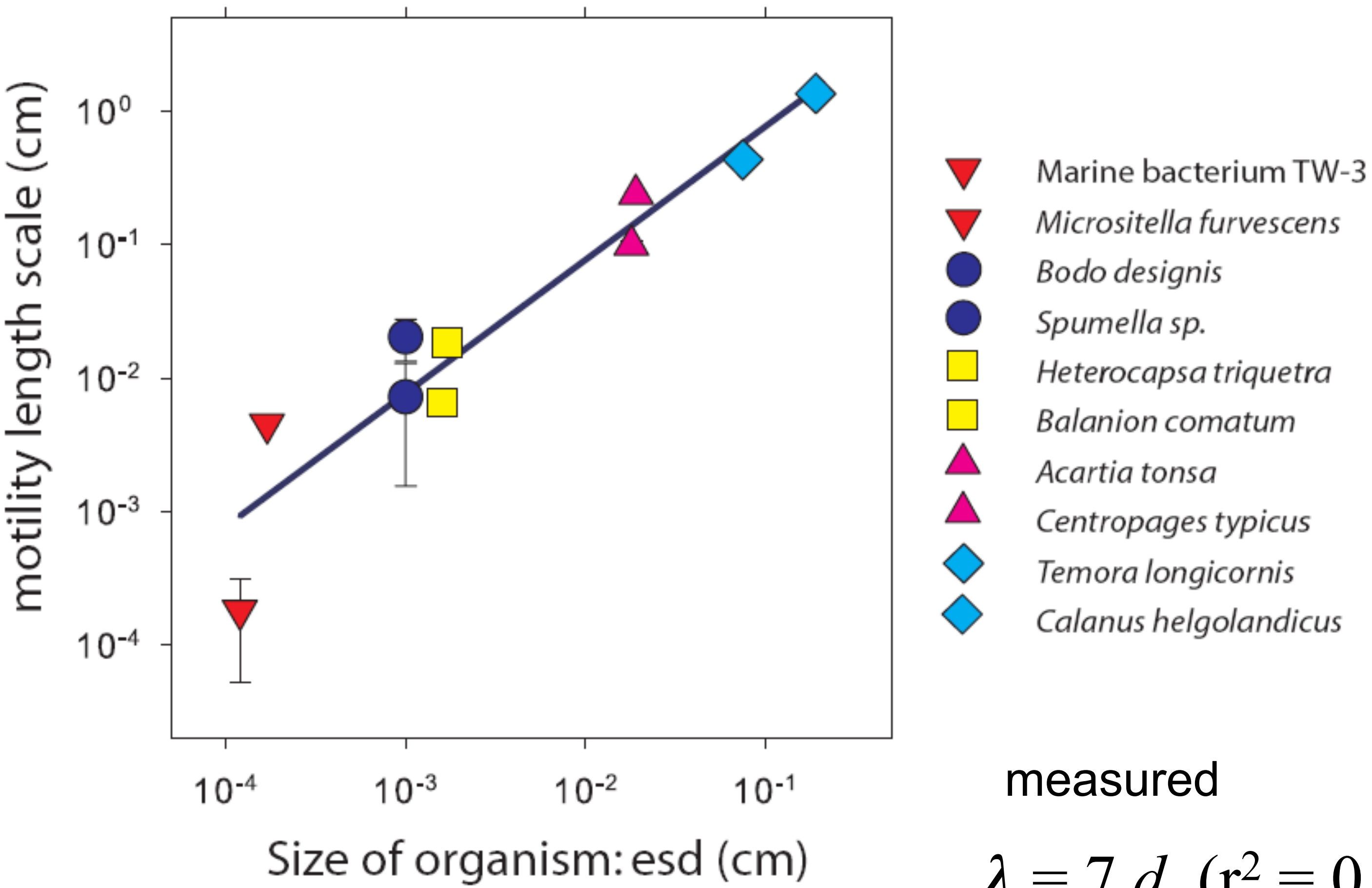
helical



random walk







measured

$$\lambda = 7\,d \quad (r^2 = 0.90)$$

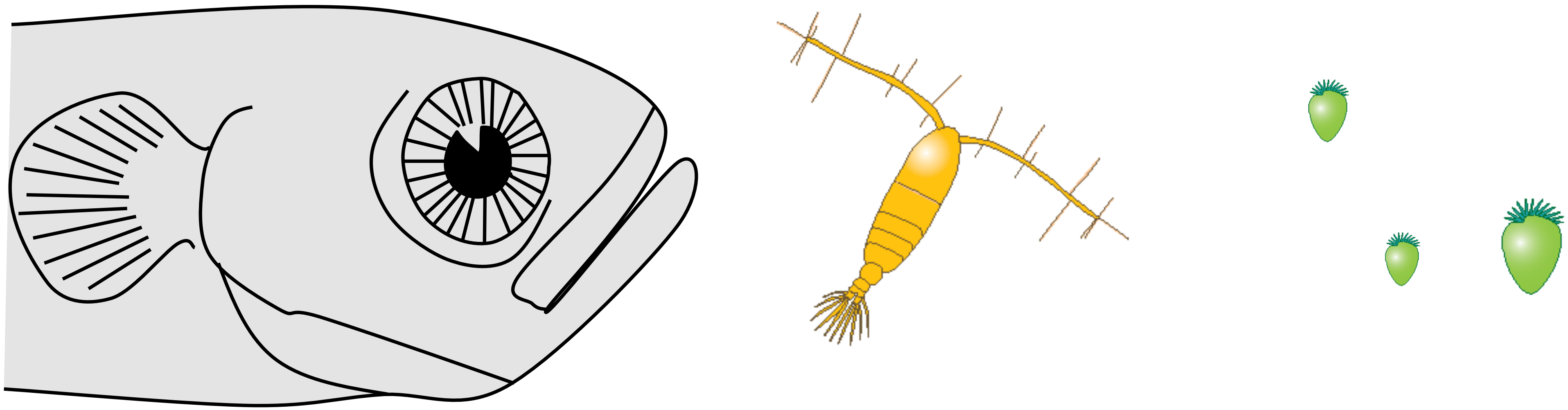
predicted

$$\lambda^* \approx 6 \times \text{size of organism}$$

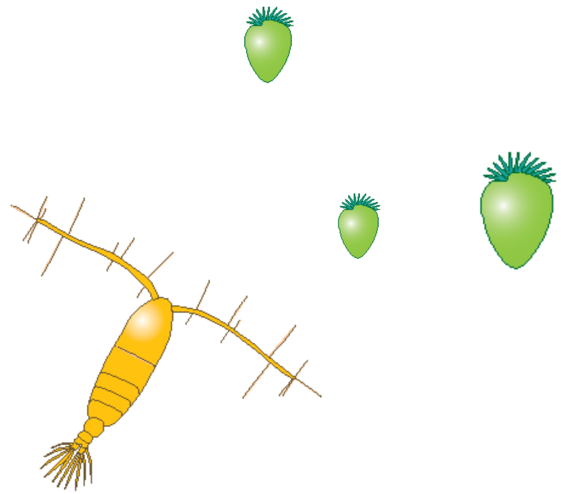
A concrete example

How fast should a planktonic organism swim given that

(1) Swimming allows an organism to search its environment for food: the faster it swims, the more volume it searches, and the more food it gets, the **benefit**
(2) It **costs** energy to swim.
(3) Swimming also increases the organism's predation **risk** as it makes it more conspicuous, and increases the probability of it blundering into a predator.



The benefit swimming



Energy derived from ingested food

Encountered prey $$Z = pR^2Cv$$

But this is not the same as ingestion rate

Hollings II functional response $$I = \frac{Z}{1 + t\,Z}$$

Handling time (→ t)

Energy income $$E = eI = e\frac{pR^2Cv}{1 + t\,pR^2Cv}$$

Cost of swimming

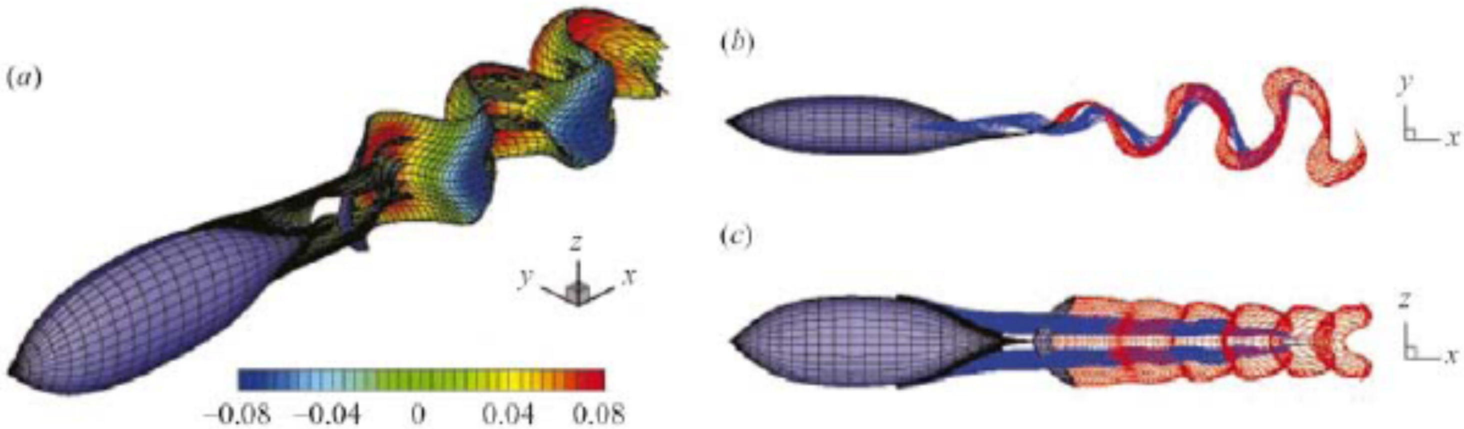


Figure 7: Formation of the wake sheets of a simulated straight-swimming tuna – *(a)* the wake sheets contoured by the distribution of dipole strength, *(b)* the top and *(c)* side views of the position of the wake sheets shed from the tail (red) and the dorsal/ventral median fins (blue) [8].

In order to move though a fluid, an organism has to do **work** against resistance of the fluid

work has units of energy (Joules) = force x distance

The rate of doing work is power, and has units Joules/second = Watts

Cost of swimming

The resistance experienced by a moving organism depends on

(1) The nature of the fluid
(2) The size of the organism
(3) How fast it moves

For small organisms like plankton, water seems like syrup – it is sticky

viscosity

Dynamic viscosity m $kg\ m^{-1}\ s^{-1}$

Kinematic viscosity $h = \frac{m}{r}$ $m^{2}\ s^{-1}$

Reynolds number $Re = \frac{rUL}{m} = \frac{\text{fluid density x speed x size}}{\text{dynamic viscosity}}$

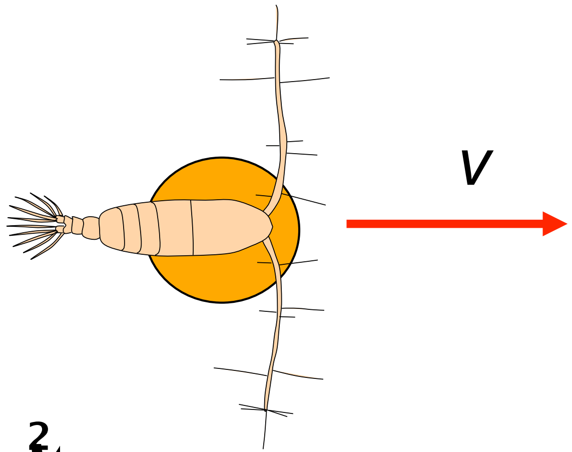
Cost of swimming

At low Reynolds numbers $$Re = \frac{av}{\eta} < 1$$

kinematic viscosity of water

$$drag = 6\pi a \eta v$$

Equivalent spherical radius



$$power = 6\pi a \eta v^2$$

But converting internal energy to forward motion is very inefficient

Efficiency ε is typically only 1%

$$cost = m + \frac{6\pi a \eta v^2}{\varepsilon}$$

where m is the base metabolic cost

Risk of swimming

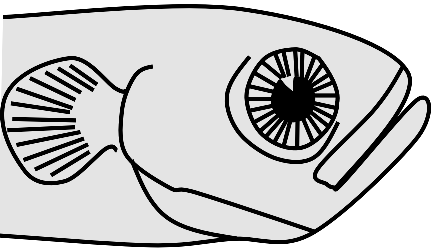
By swimming, the organism not only increases its encounter with prey, but also with its predators

If the predator itself swims with speed u, and has a detection distance to the organism X, then the organism's encounter rate with predators is

$$Z_{pred} = pX^2P\sqrt{u^2 + v^2}$$

..where P is the concentration of predators

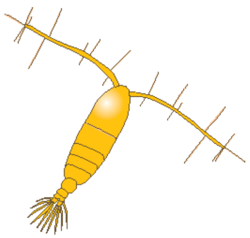
The overall mortality rate of the organism can thus be written as



$$m = m_0 + j\,pX^2P\sqrt{u^2 + v^2}$$

Background mortality rate in the absence of predators

Proportion of encounters that lead to capture



Fitness

Is the life time number of off spring an individual produces

= the probability of surviving * the rate of production integrated over a life span

An instantaneous parameter that reflects this in principal is

reproduction rate

energy per offspring

energy acquisition rate

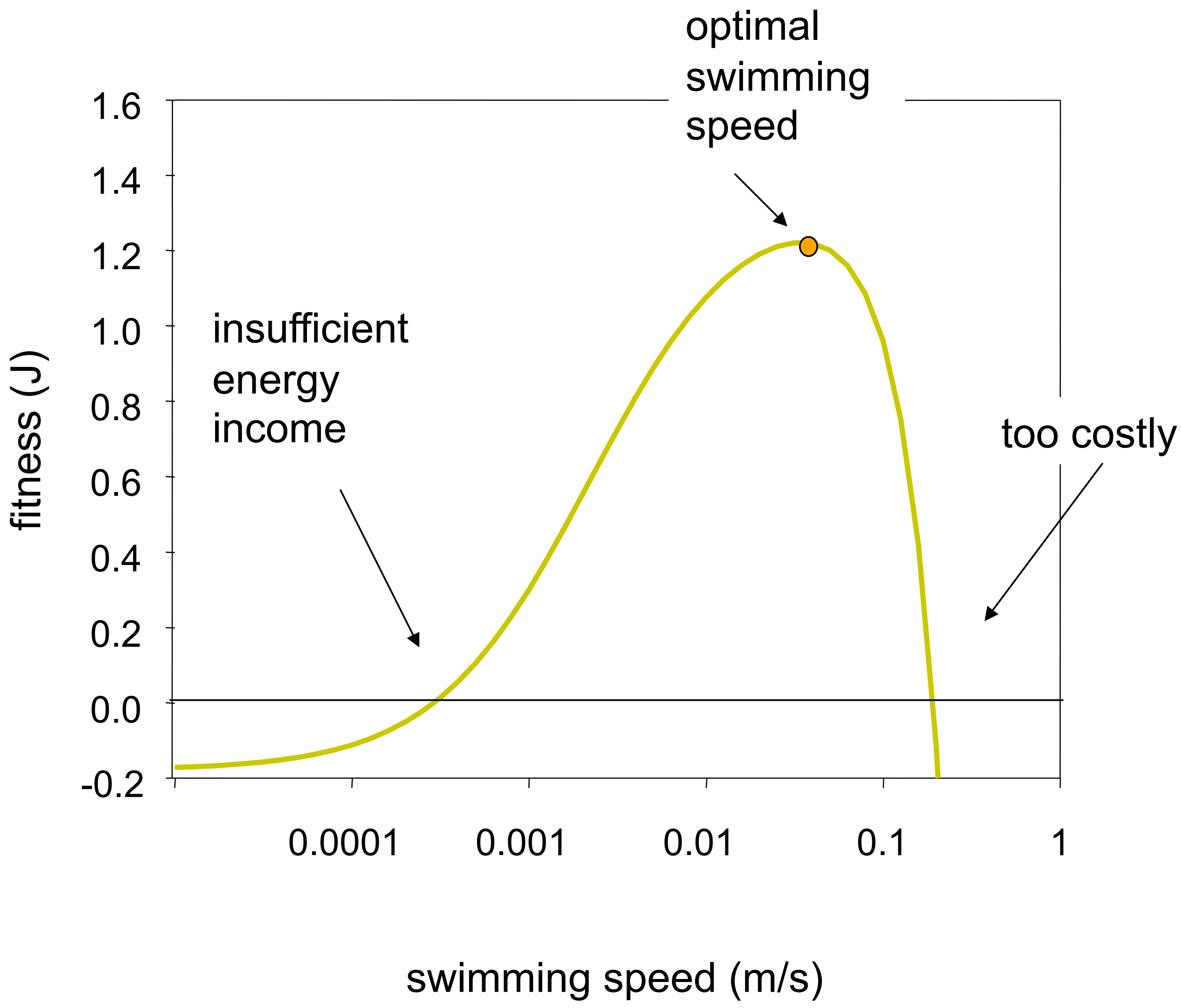
$$g = \frac{a}{m} = g\frac{\dot{E}}{m}$$

mortality rate

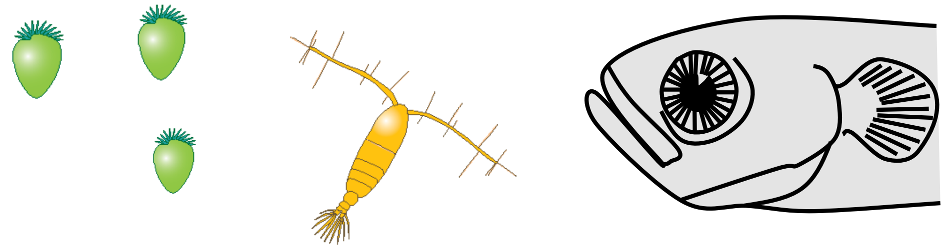
$$g = g\frac{e\frac{s_c C v}{1 + t s_c C v} - m - q v^2}{m_0 + j s_p P \sqrt{u^2 + v^2}}$$

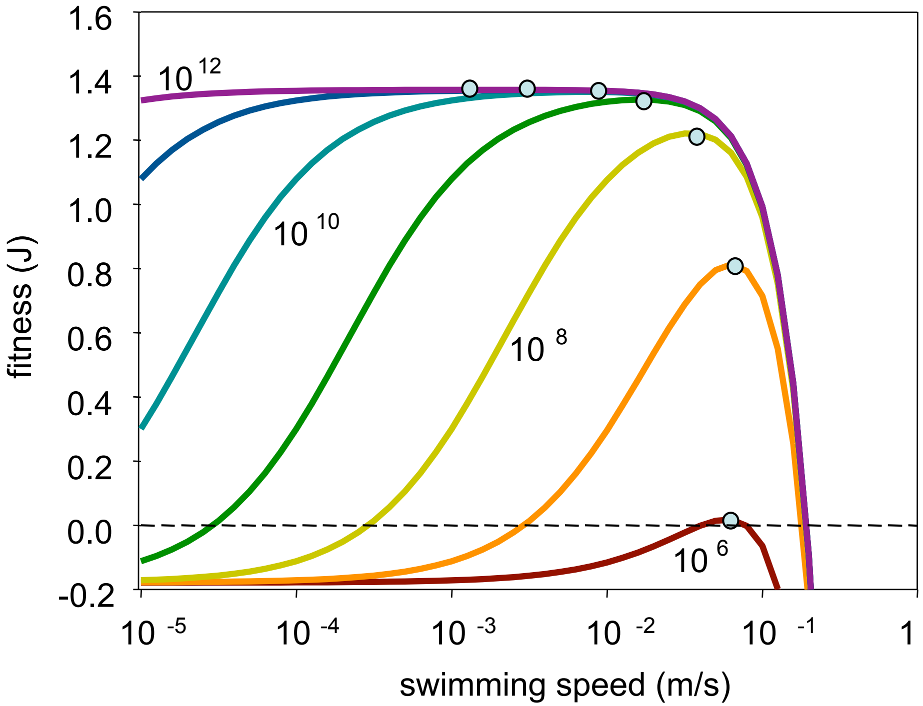
The value of *V* that maximizes this parameter is an estimate of the optimal swimming speed

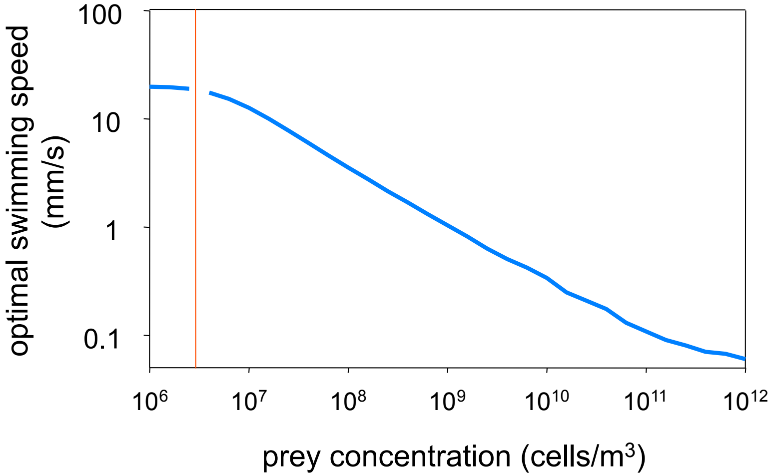
Optimal swimming speed

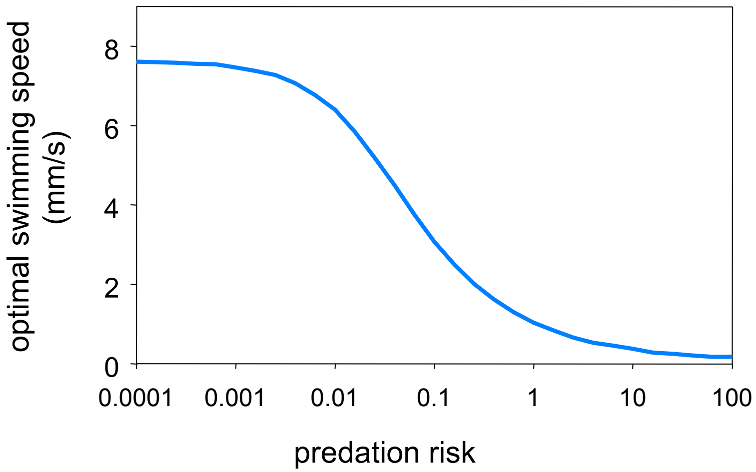


Optimal swimming speed









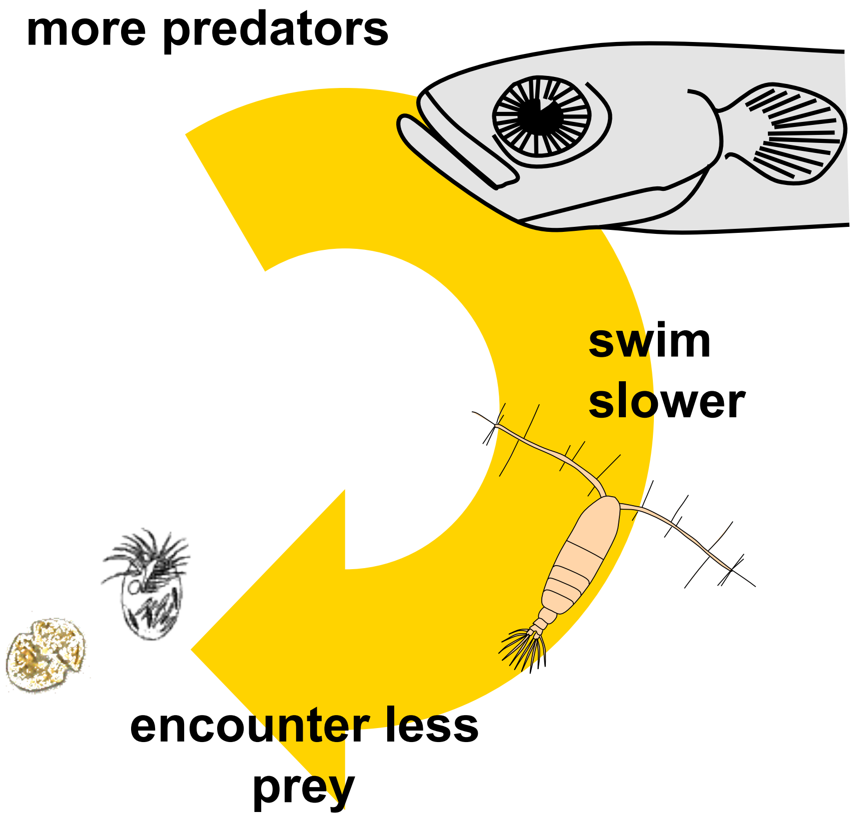
Swim slower as both predator and prey concentration increase

Visser JPlankonRes 2007

Optimal swimming speed

Optimization has cascading effects on trophic interaction through out the ecosystem

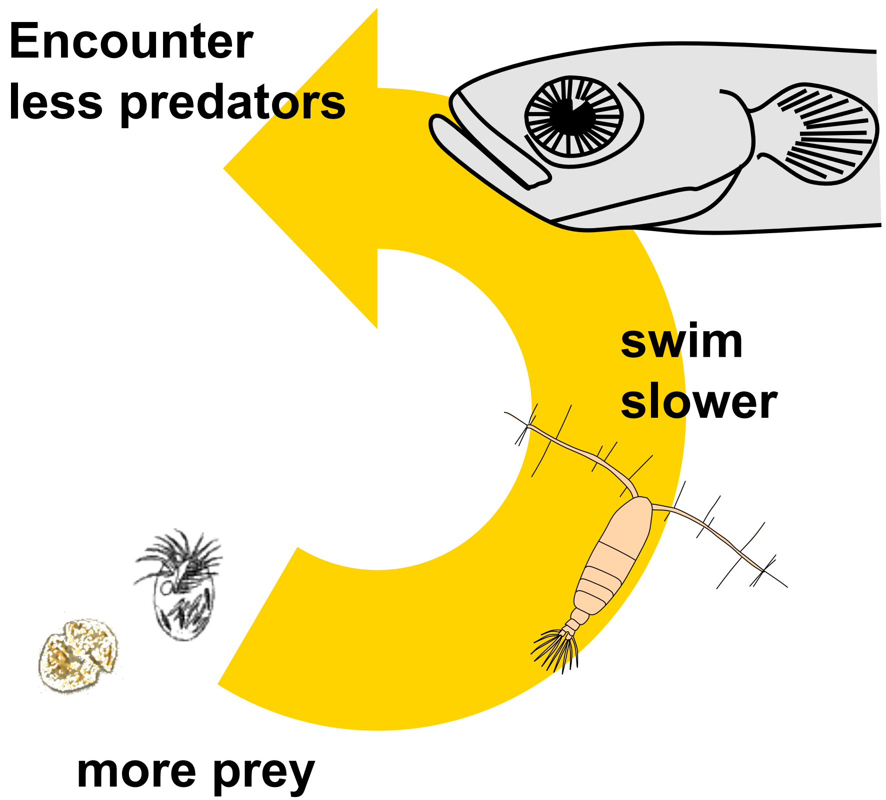
grazing pressure is influenced by number density of the grazer's predators



Optimal swimming speed

Optimization has cascading effects on trophic interaction through out the ecosystem

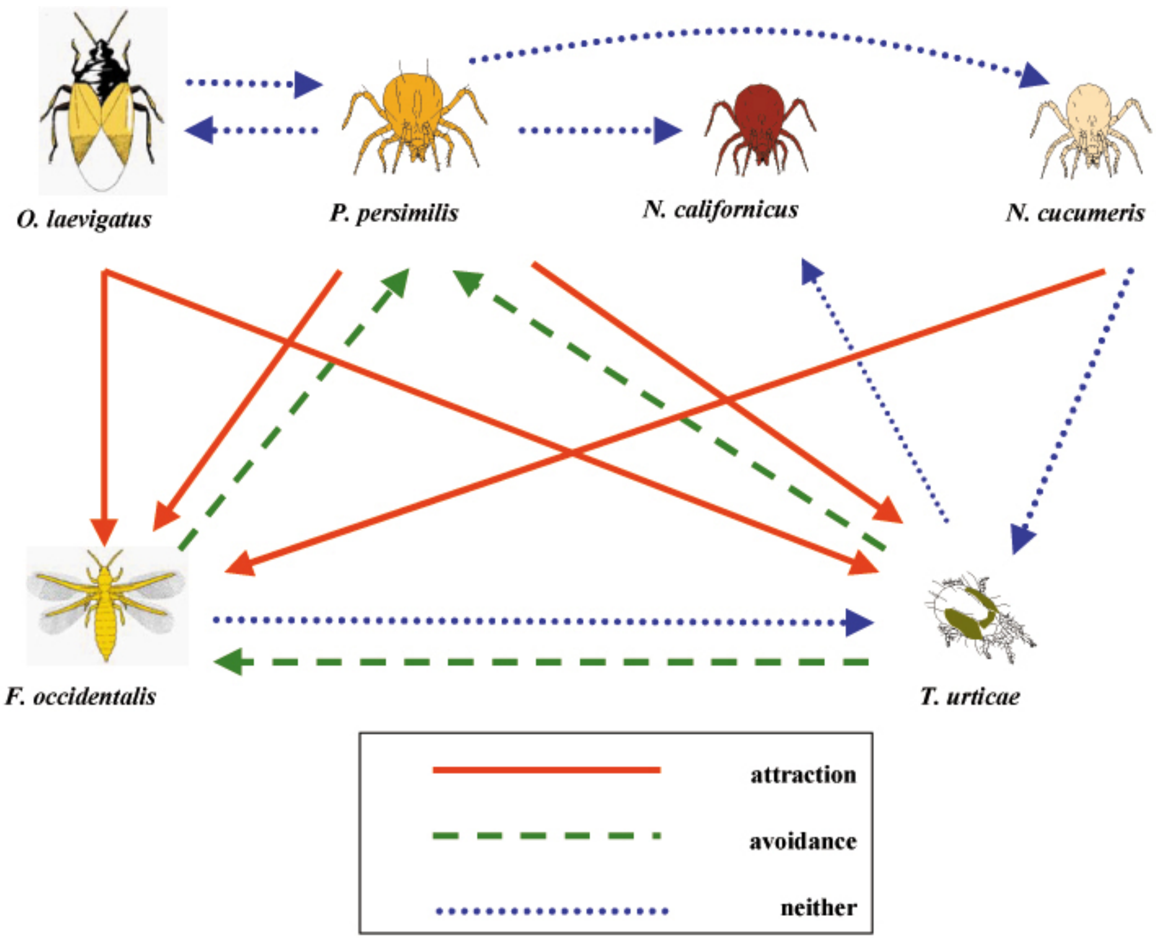
mortality rate influence by the abundance of prey



Behaviourally mediated indirect interactions

My enemy's enemy is my protector

My prey's prey is bait



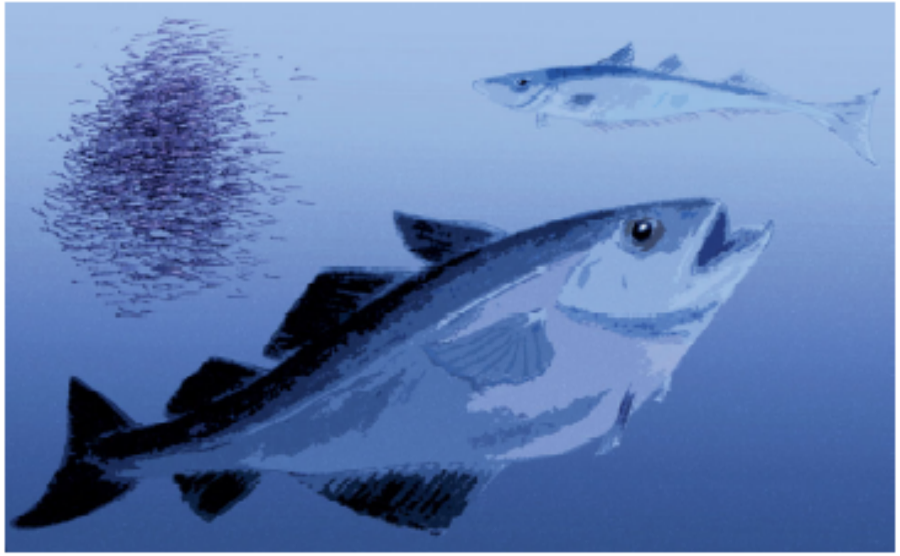
Behaviourally mediated indirect interactions

Vol. 299: 1–5, 2005	MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser	Published September 1

FEATURE ARTICLE: NOTE

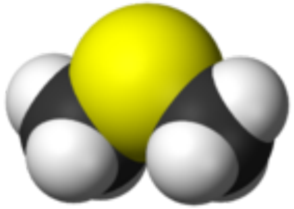
Piscivorous fish patrol krill swarms

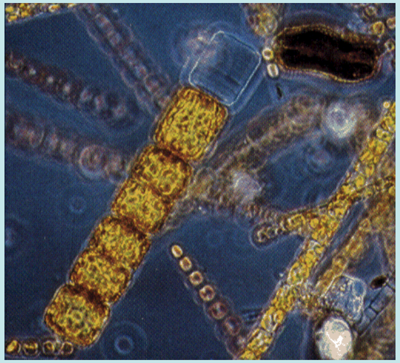
Stein Kaartvedt[1,*], Anders Røstad[1], Øyvind Fiksen[2], Webjørn Melle[3], Thomas Torgersen[2], Mari Tiseth Breien[3], Thor A. Klevjer[1]

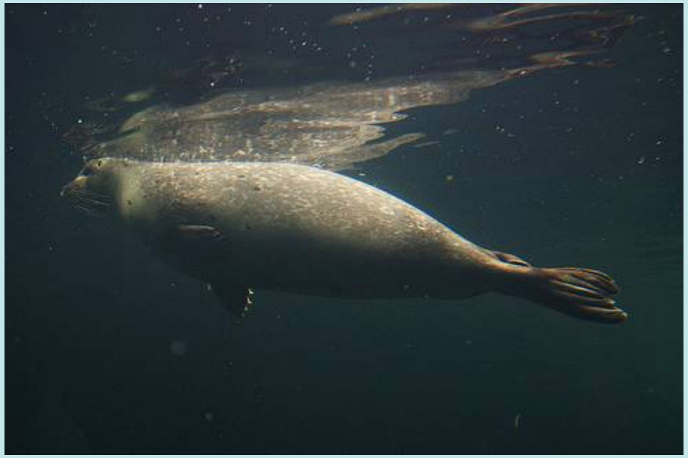


Behaviourally mediated indirect interactions

Dimethylsulphides







Behaviourally mediated indirect interactions