Constraints and optimal behaviour in plankton and fish

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http://www.bio.uib.no/modelling/pages/publications.php

Outline

- The Holling disk equation
  - Phytoplankton
  - Fish
- Some applications and lessons from a simple mechanistic model
- Optimal behaviour and dynamic programming
  - Daphnia in experiments
  - Larval fish and food abundance
  - Planktovore fish in hypoxia

The Holling disk equation (Holling type II)

The predator has two alternative activities, *searching* or *handling*:

$$T = t_s + t_h$$

Time spent handling prey:

$$t_h = P_e T_h$$

Number of prey encountered in t:

$$P_e = aNt_s$$

a: search rate [m^3 $predator^{-1}$ sec^{-1}]
N: prey density [prey m^{-3}]
T_h: handling time of one prey [sec $prey^{-1}$]
P_e: prey encountered while searching [prey $predator^{-1}$]
t: time spent on various activities [sec $predator^{-1}$]

Time available to search for prey:

$$P_e = aN t_s \Leftrightarrow$$

$$t_s = \frac{P_e}{aN}$$

We want an expression for *feeding rate* P_e/T as a function of prey density N:

$$T = t_h + t_s = P_e T_h + \frac{P_e}{aN} =$$

$$P_e(T_h + \frac{1}{aN}) = P_e(\frac{T_h aN + 1}{aN})$$

$$\frac{T}{P_e} = \frac{T_h aN + 1}{aN} \Leftrightarrow$$

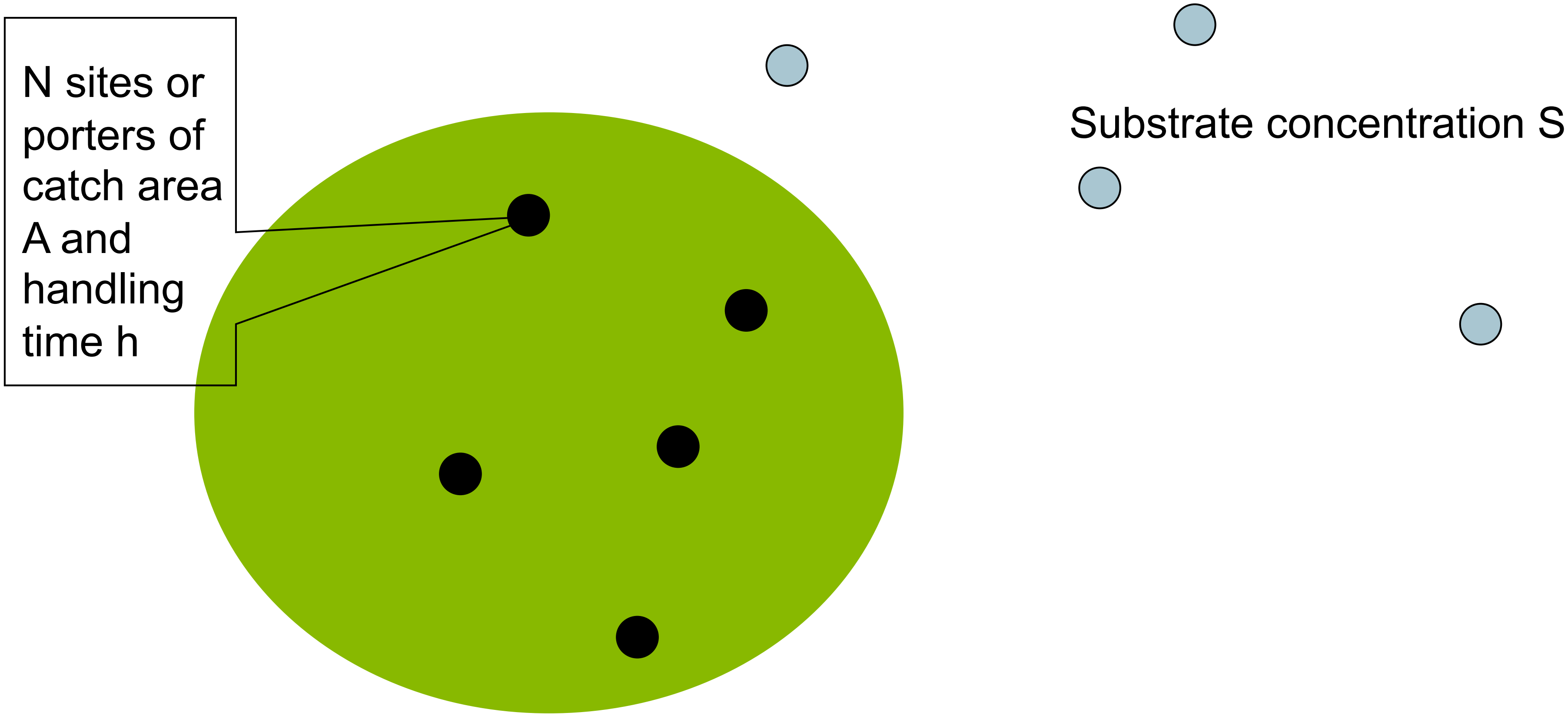
$$\frac{P_e}{T} = \frac{aN}{1 + T_h aN} \Leftrightarrow$$

The Holling disk equation:

$$P_e = \frac{aNT}{1 + T_h aN}$$

Phytoplankton

- Mechanisms of nutrient uptake in osmotrophs



Aksnes & Egge 1991 A theoretical model for nutrient uptake in phytoplankton. MEPS 70: 65-72

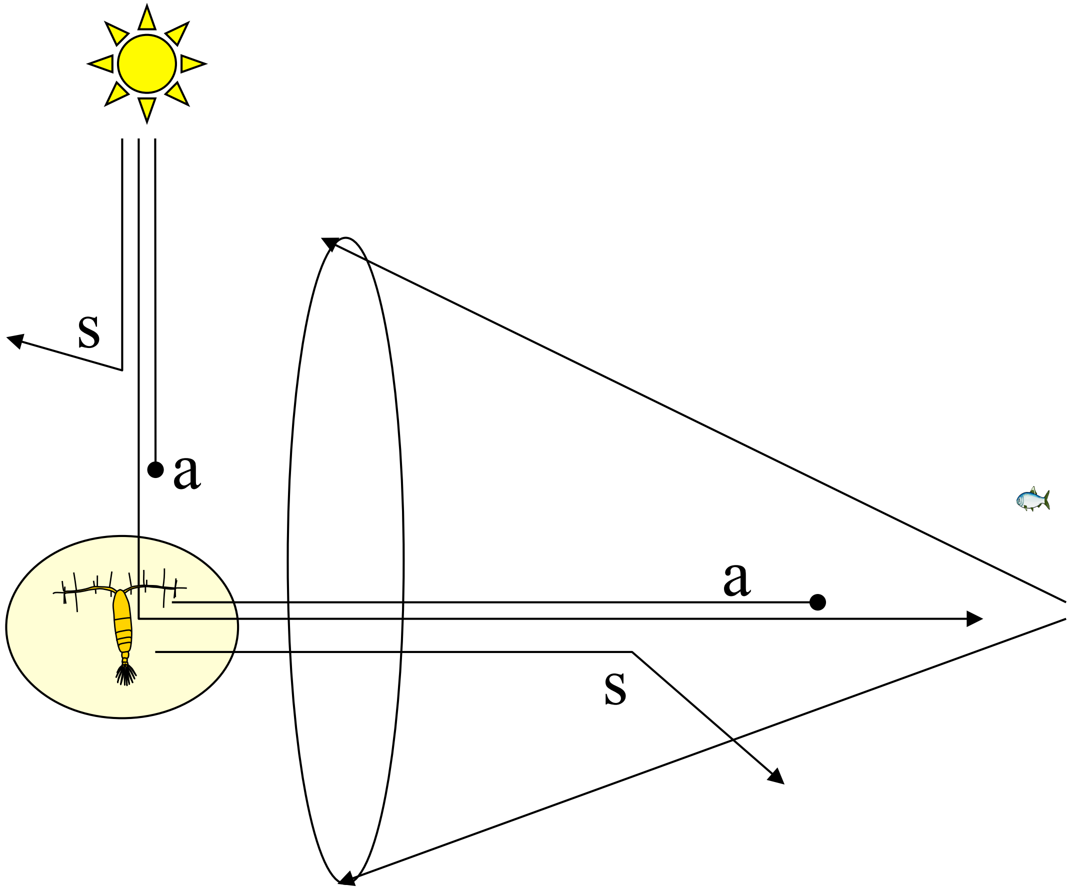
Holling disk model for nutrient uptake

Nutrient encounters at one site:

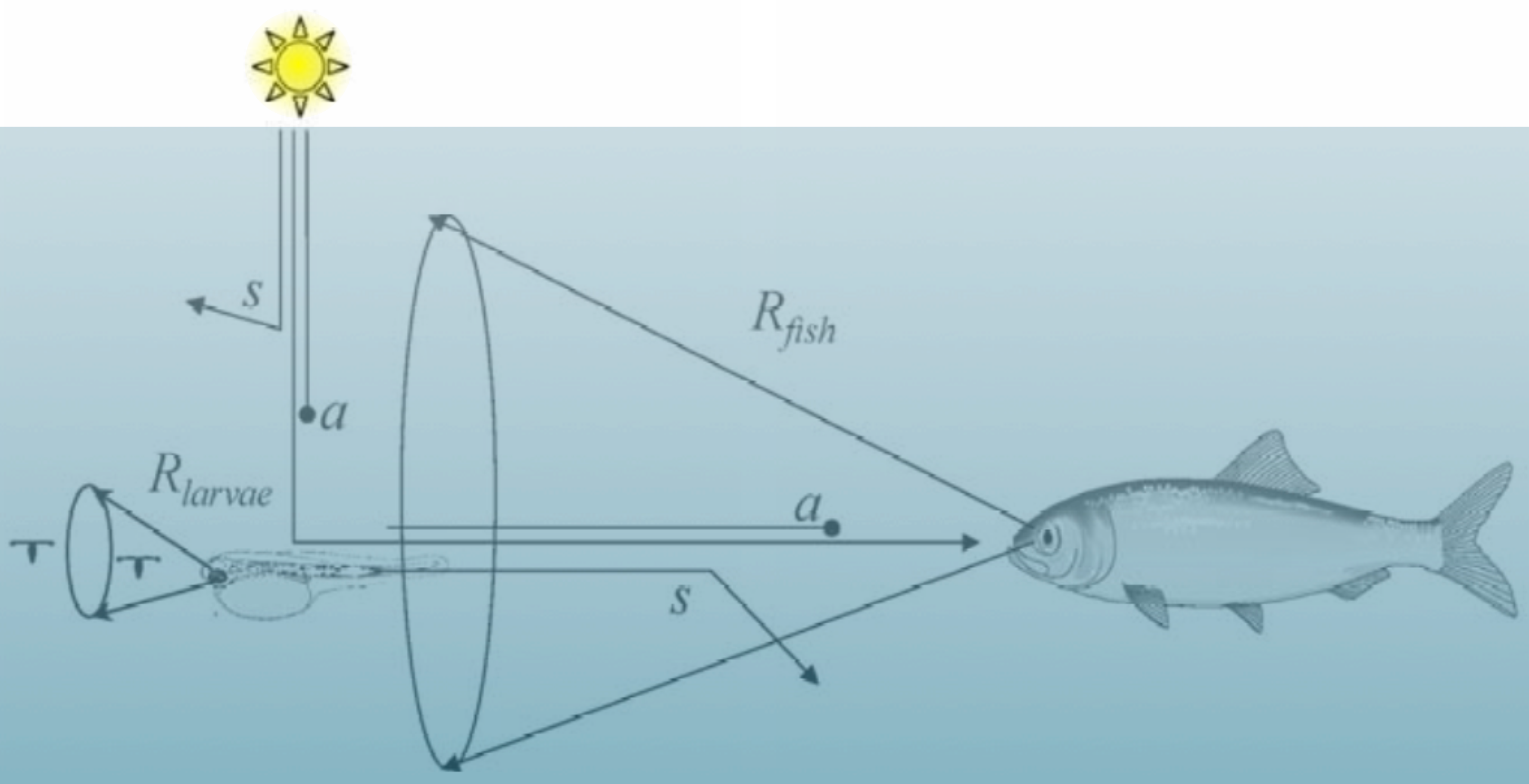
$$V = n\frac{t_s AvS}{t_s + t_h} = \frac{nAvS}{t_s + hAvS}$$

Aksnes & Egge 1991

What determines detection distance R in fish?

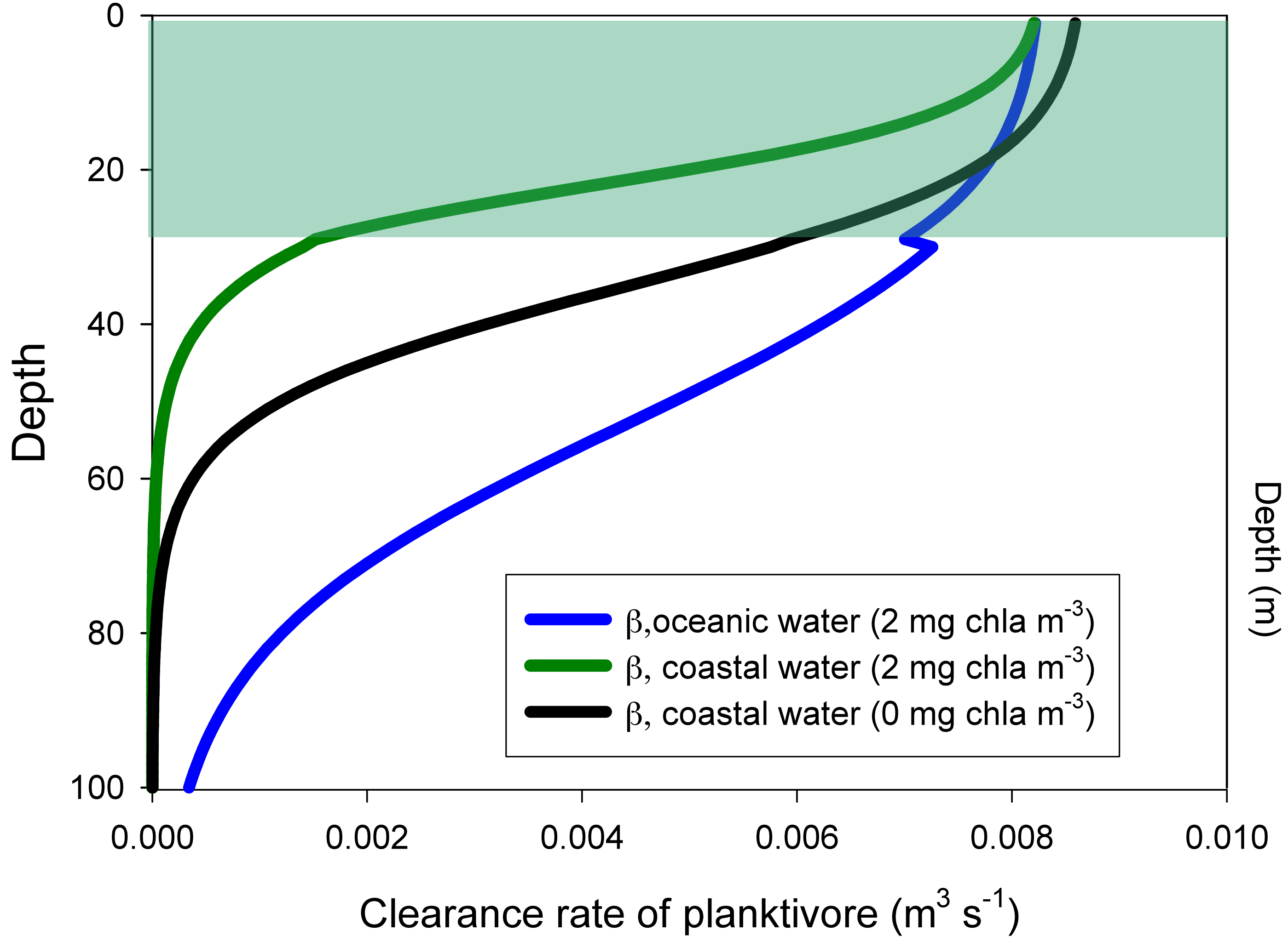


Light, vision, encounters, and predation



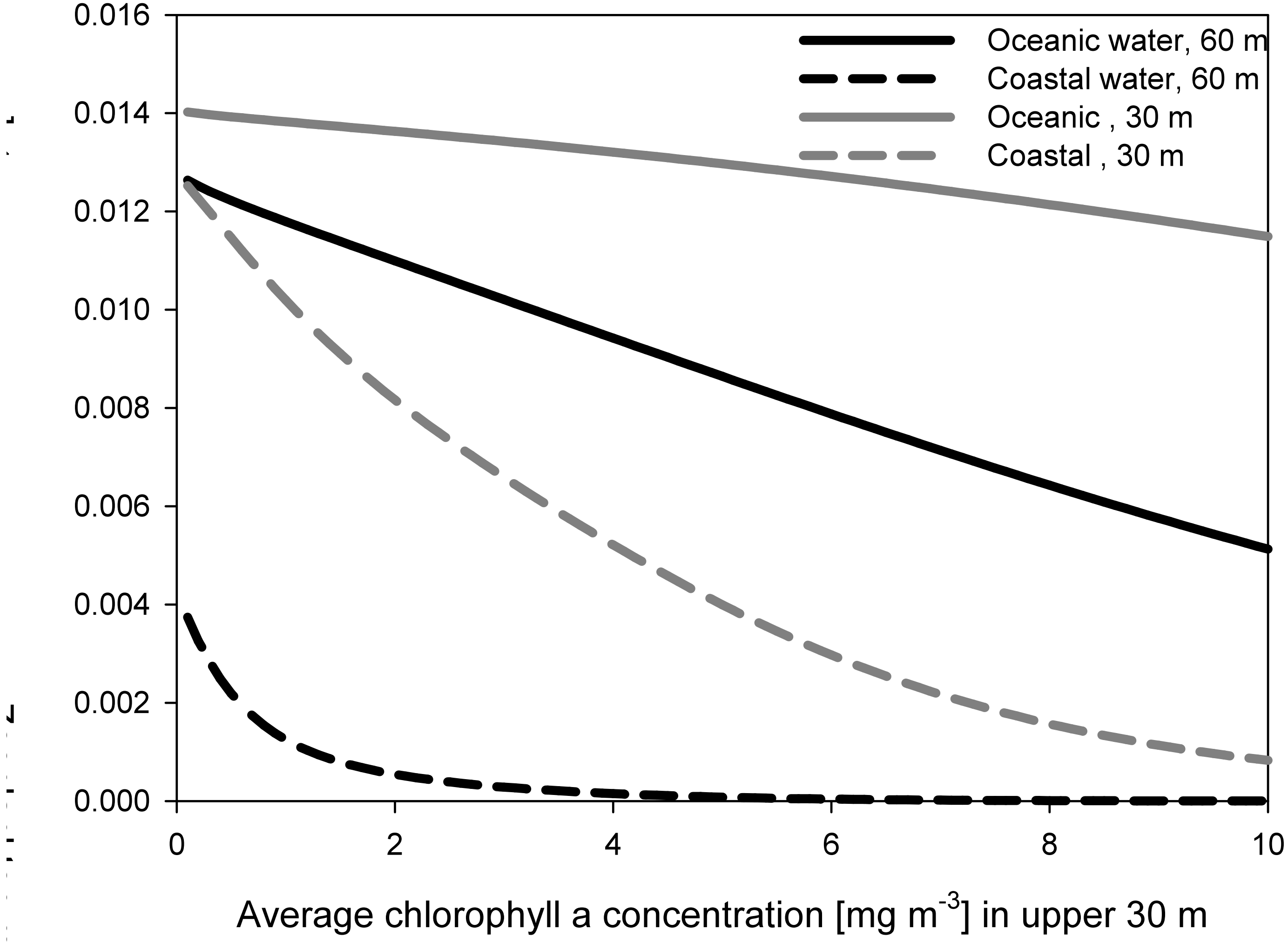
Fiksen Ø, Aksnes DL, Flyum MH, Giske J. 2002. *Hydrobiologia*, **484**: 49-59.

Fish foraging, depth and turbidity



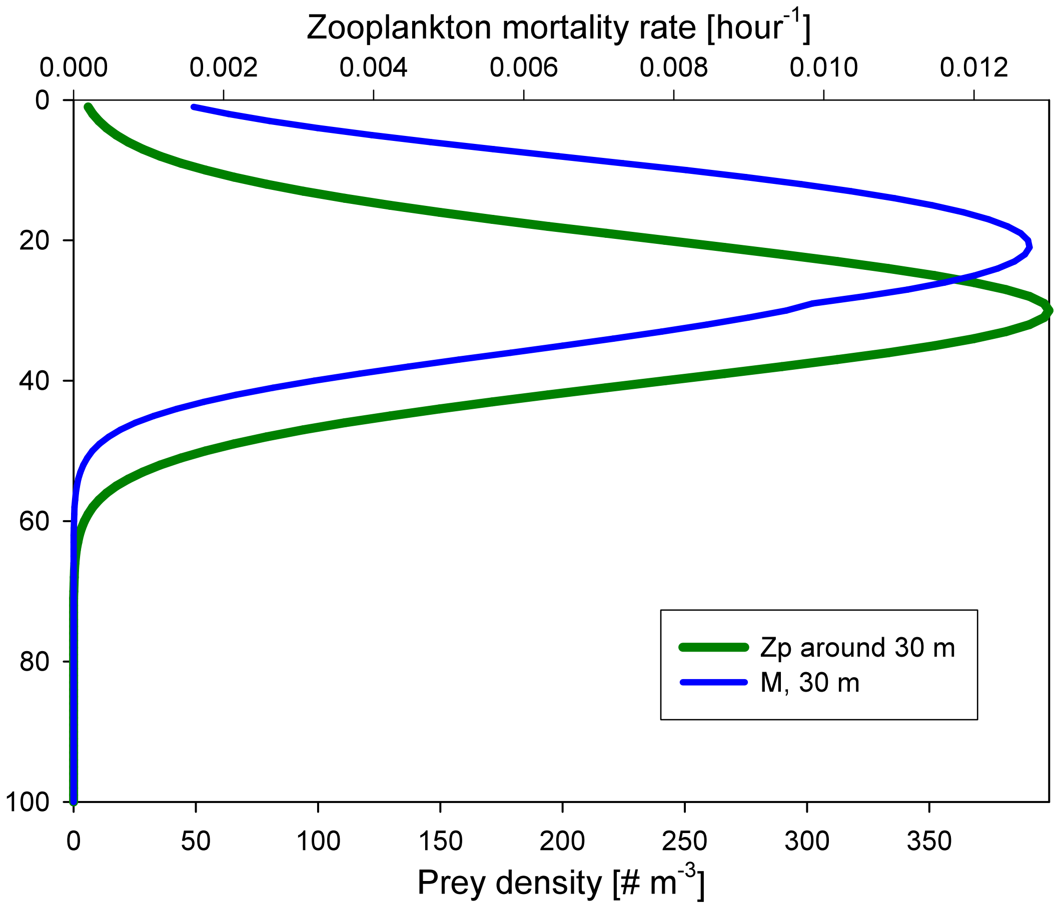
Fiksen & al 2002

Zooplankton mortality, phytoplankton and water type

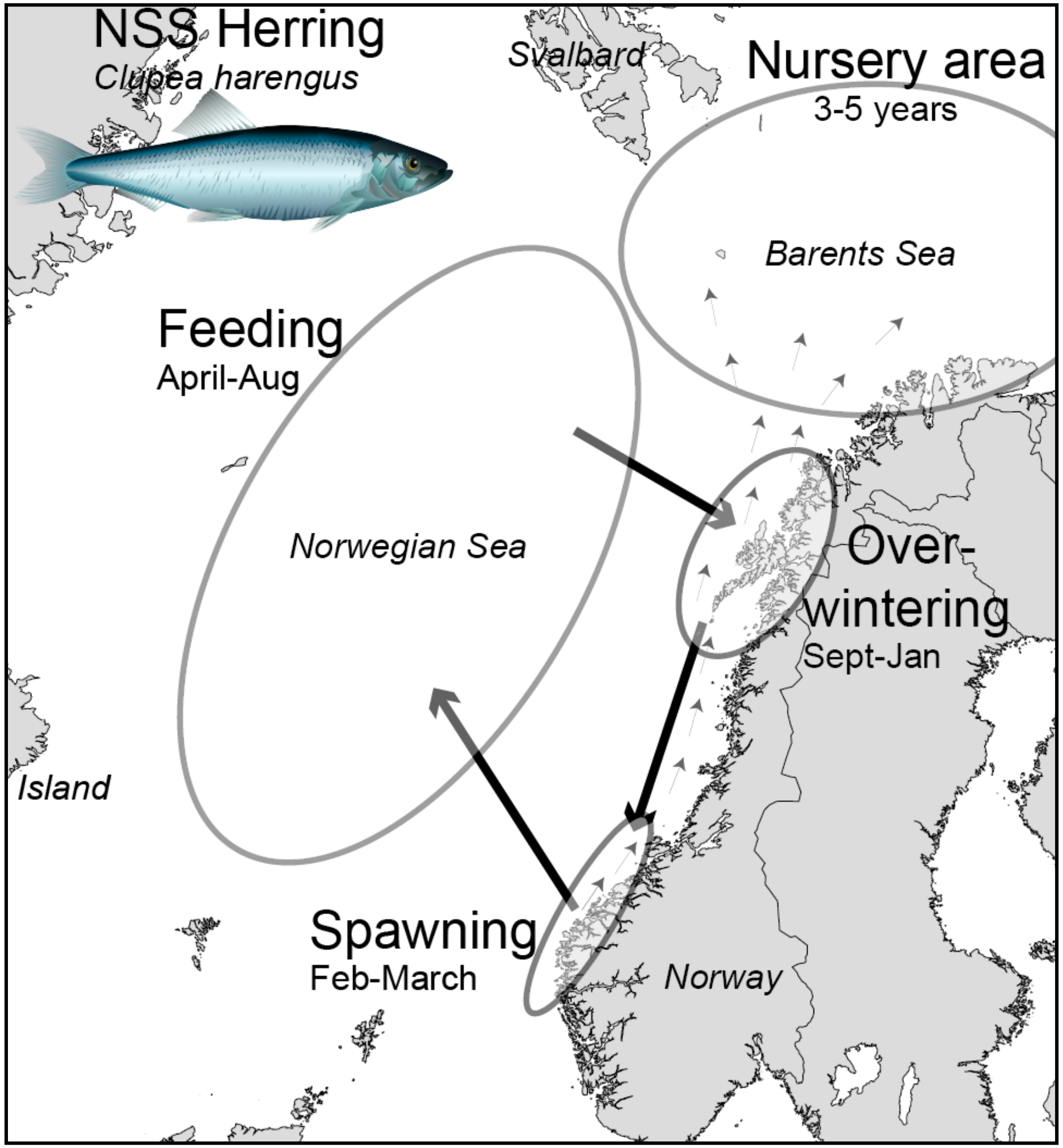


Huse & Fiksen 2010

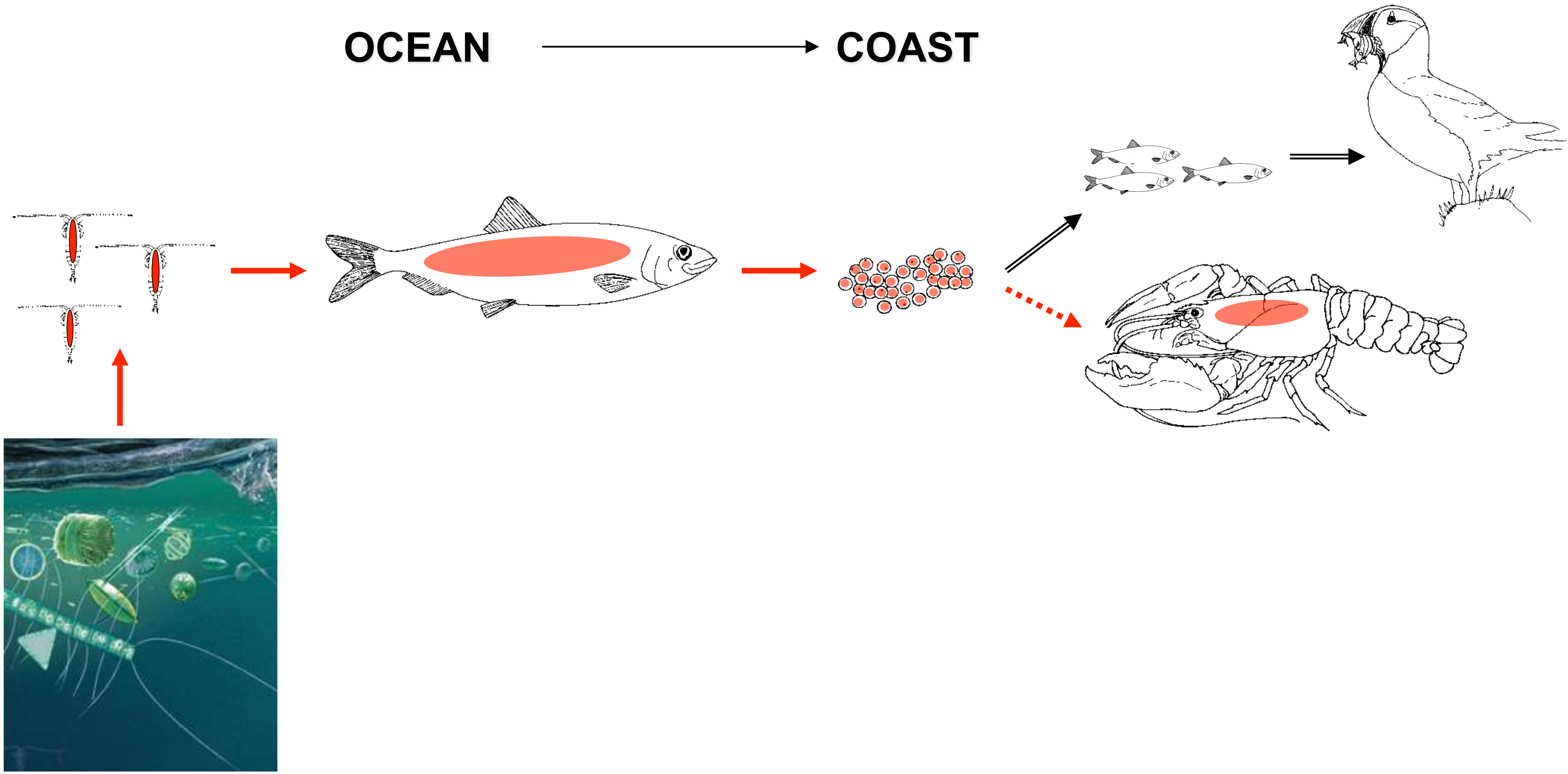
Prey distribution and fish foraging efficiency



Huse & Fiksen 2010

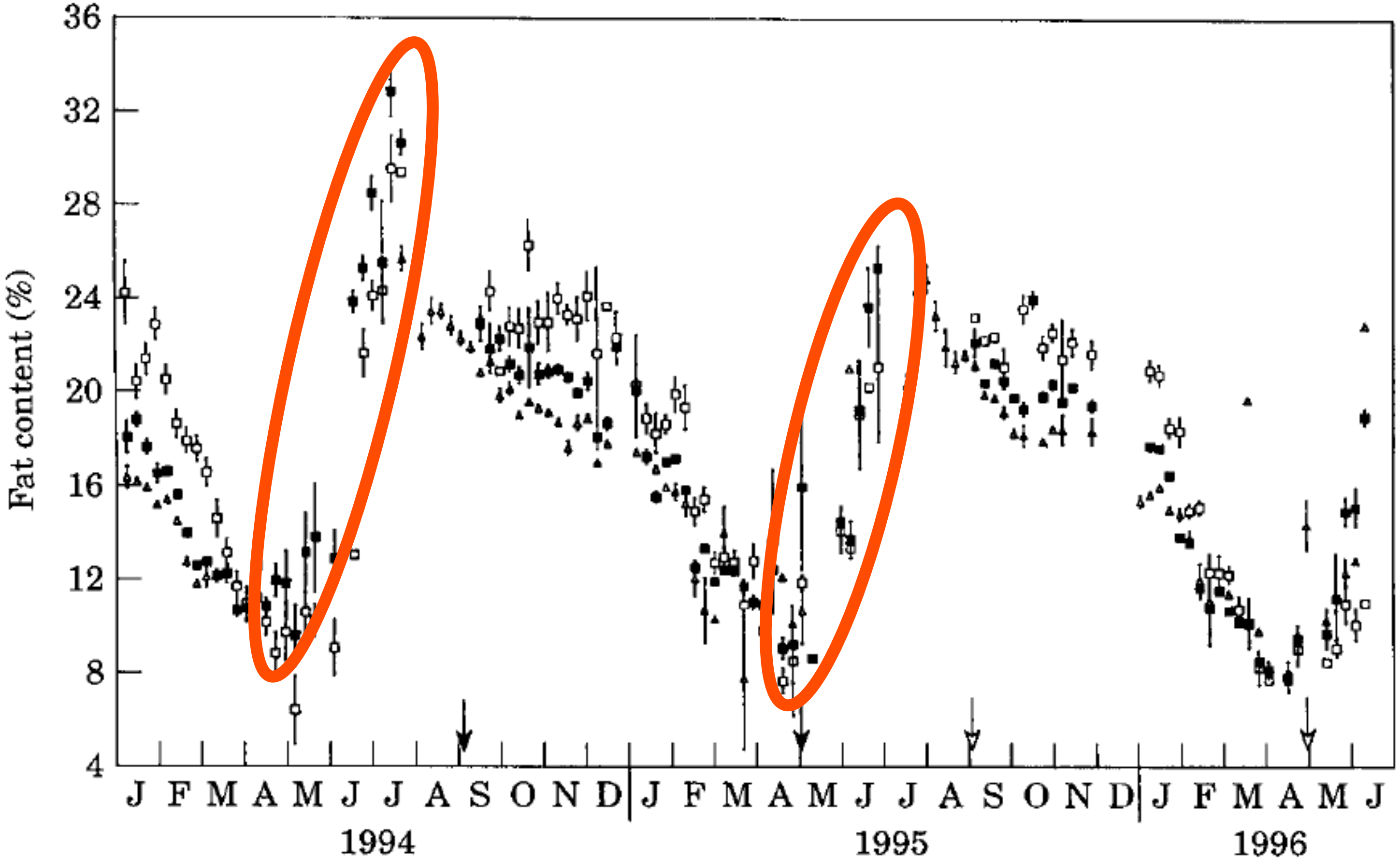

NSS Herring
Clupea harengus
Svalbard
Nursery area
3-5 years
Barents Sea
Feeding
April-Aug
Norwegian Sea
Over-
wintering
Sept-Jan
Island
Spawning
Feb-March
Norway

The fat conveyor belt



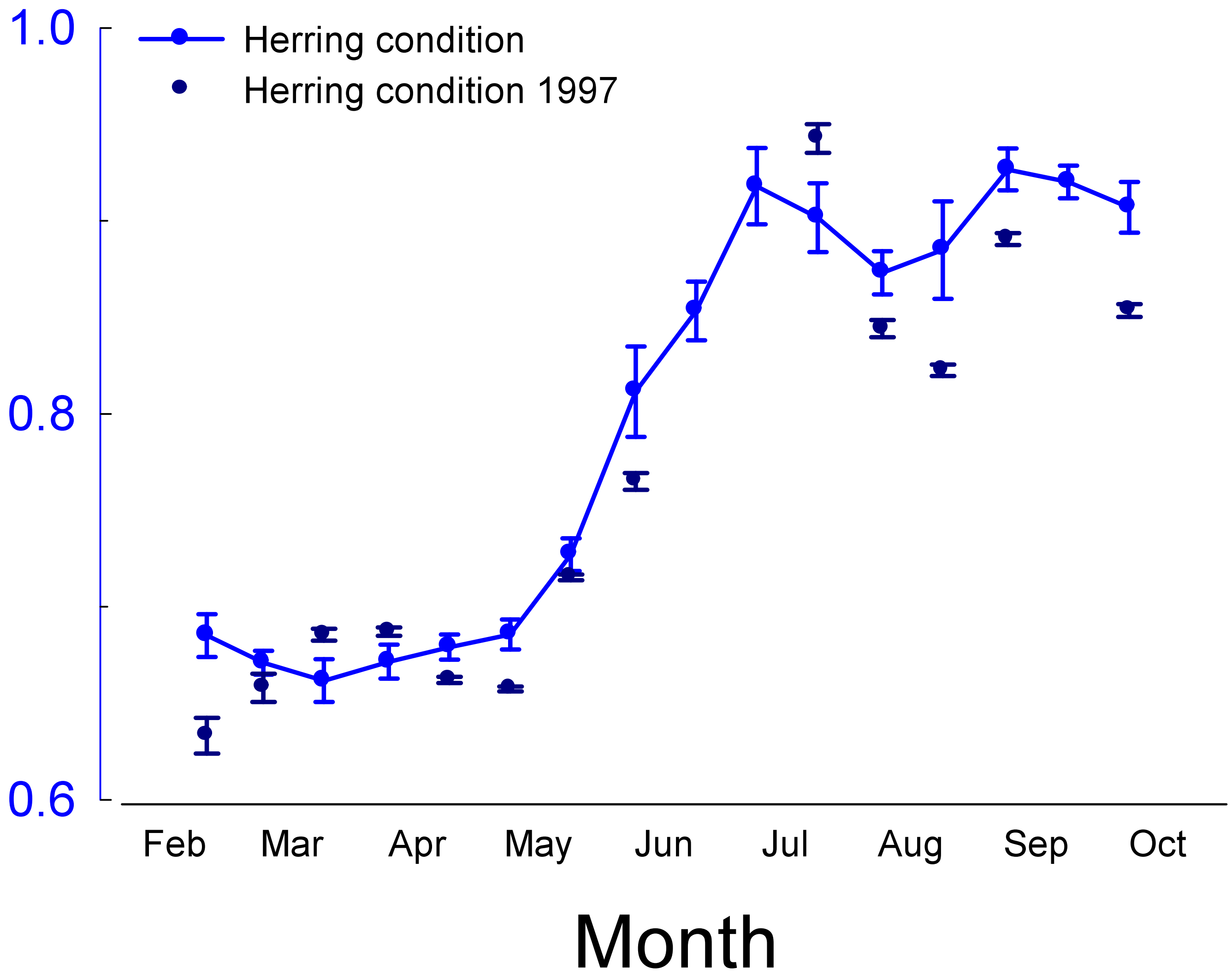
Varpe, Slotte & Fiksen (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. Oecologia 146:443-451.

Herring get fat in a few weeks

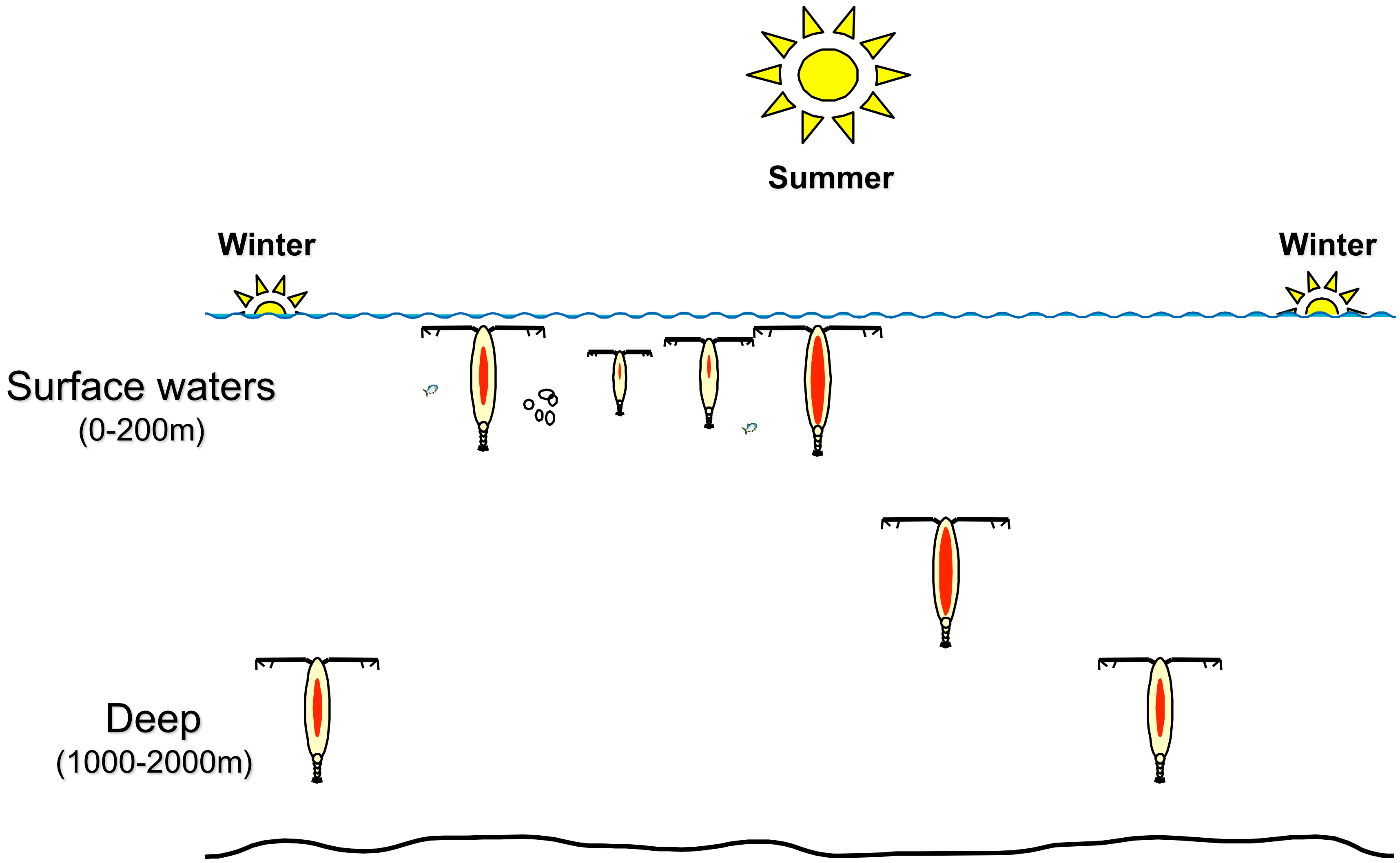


Slotte 1999

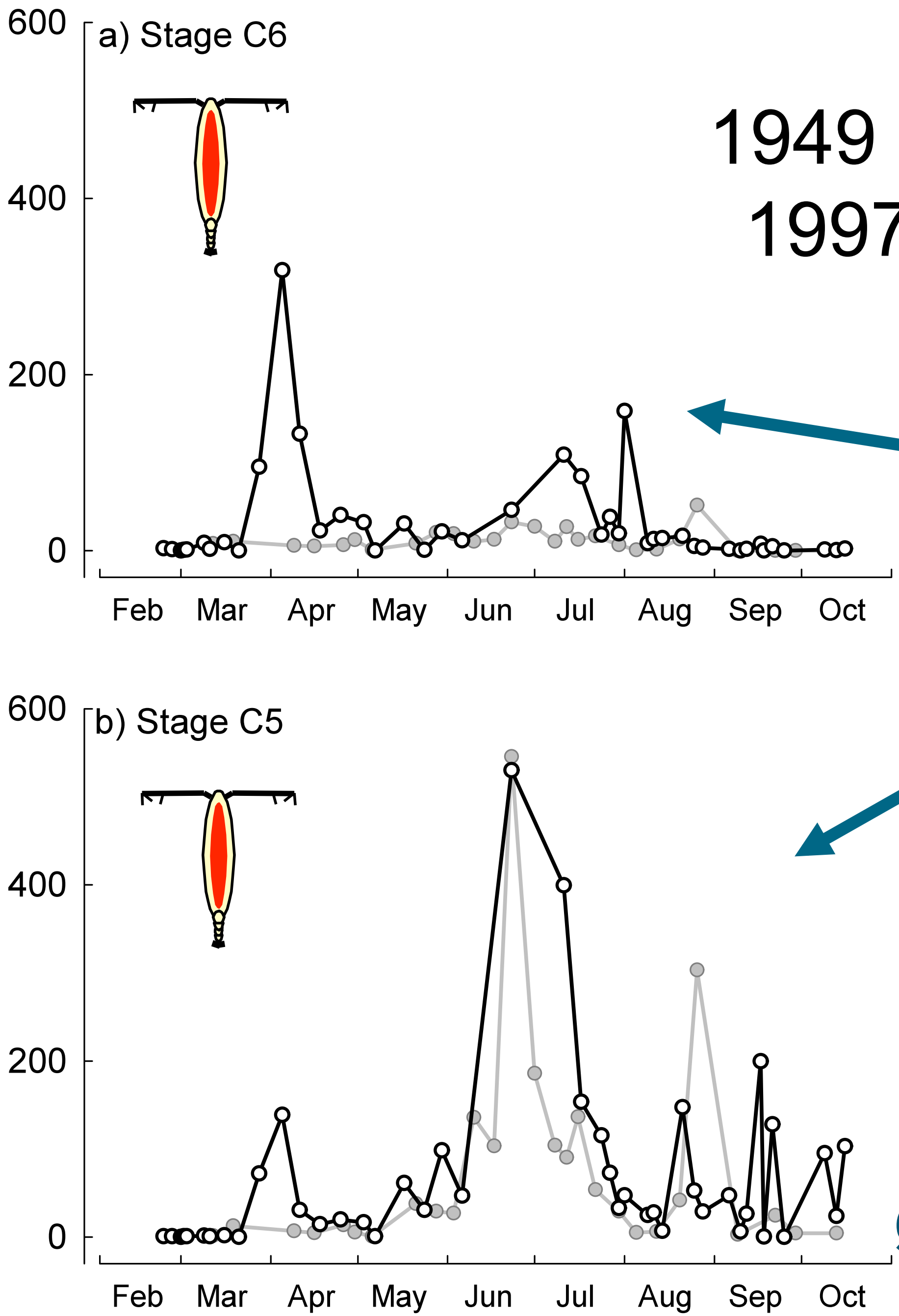
Condition 1990-2003



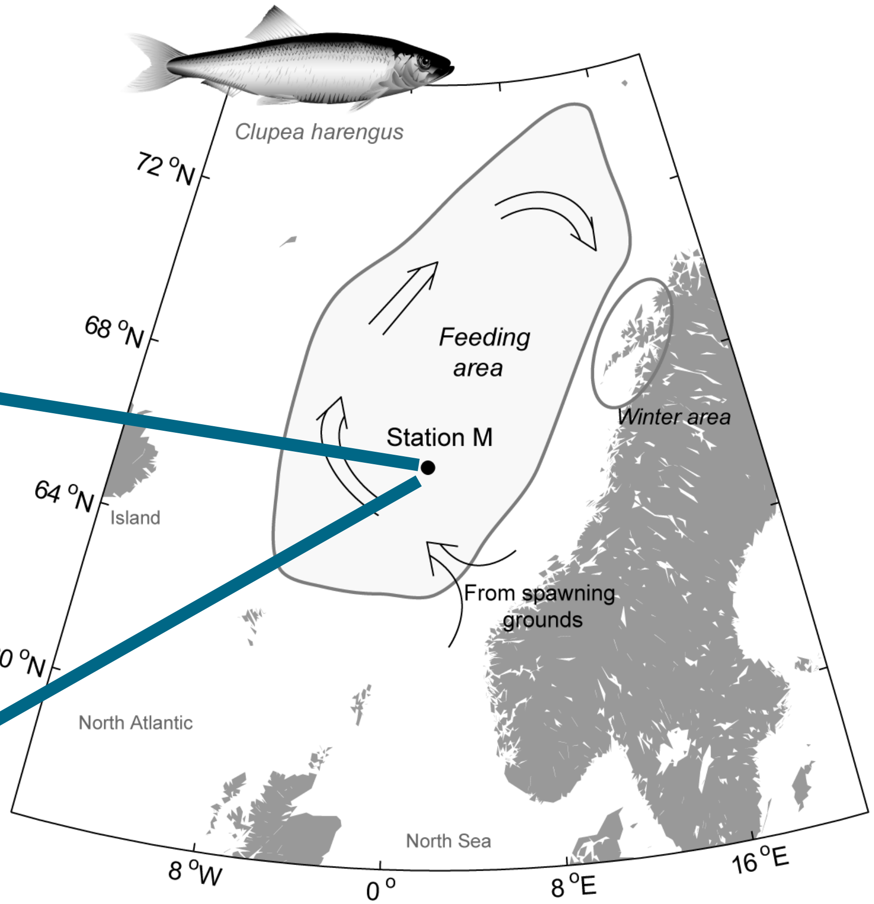
Life cycle of main prey, *Calanus finmarchicus*



Calanus-data from Ocean Weathership Station M



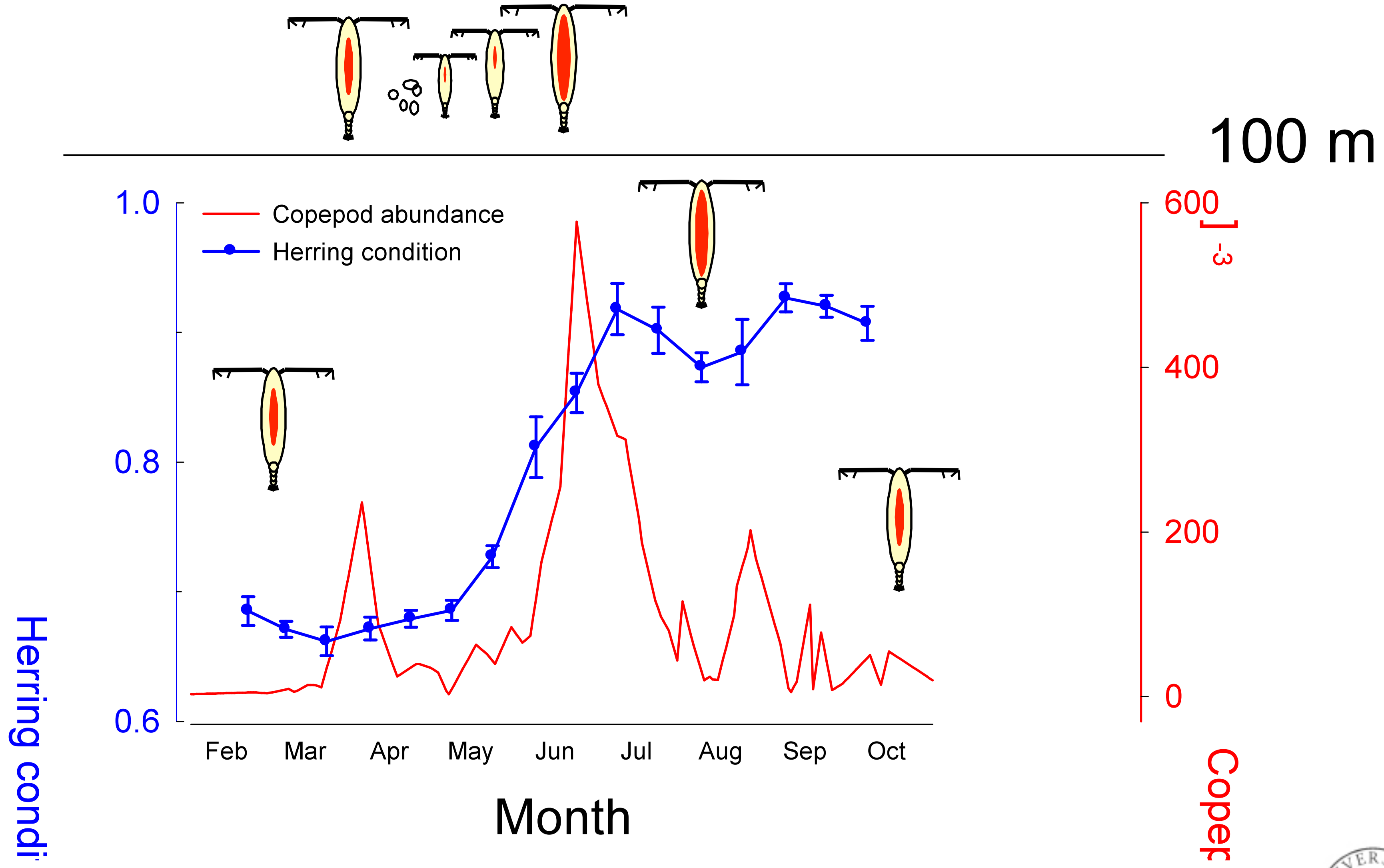
1949 &
1997



Østvedt 1955, TASC 1997

www.uib.no

Do prey abundance cause the fattening?



What really determines prey intake?

Search rate

Prey density

Prey consumption

$$i = \frac{\beta N}{1 + h\beta N}$$

Prey handling time

Seasonal herring foraging model

Search
rate

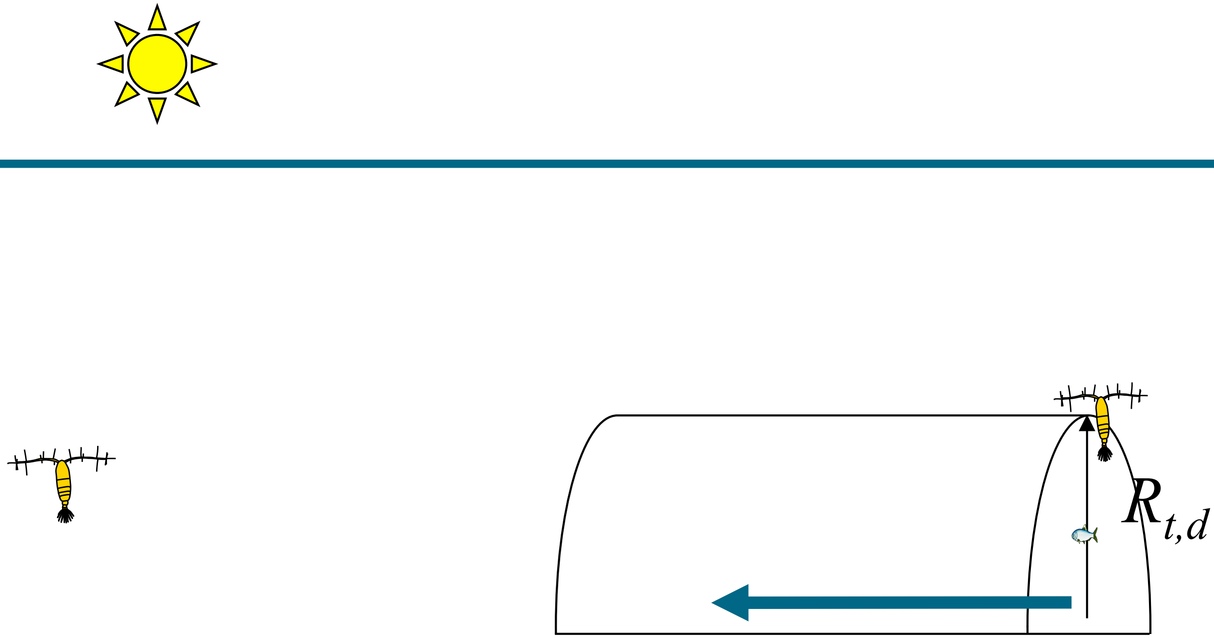
Daily prey
consumption

Prey density

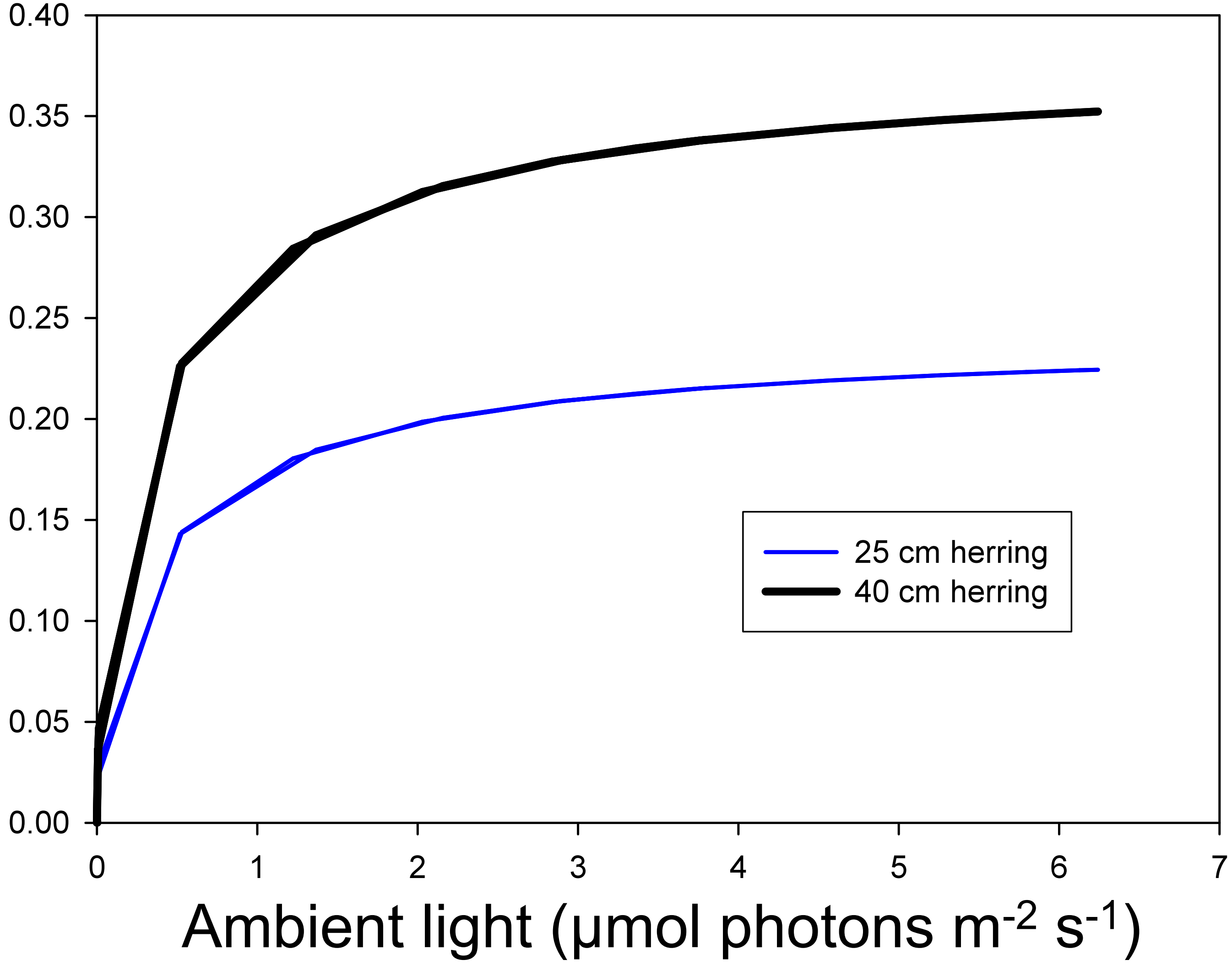
$$i_d = \sum_{t=1}^{24} \frac{\beta_{t,d} N_d}{1 + h\beta_{t,d} N_d}$$

Prey handling
time

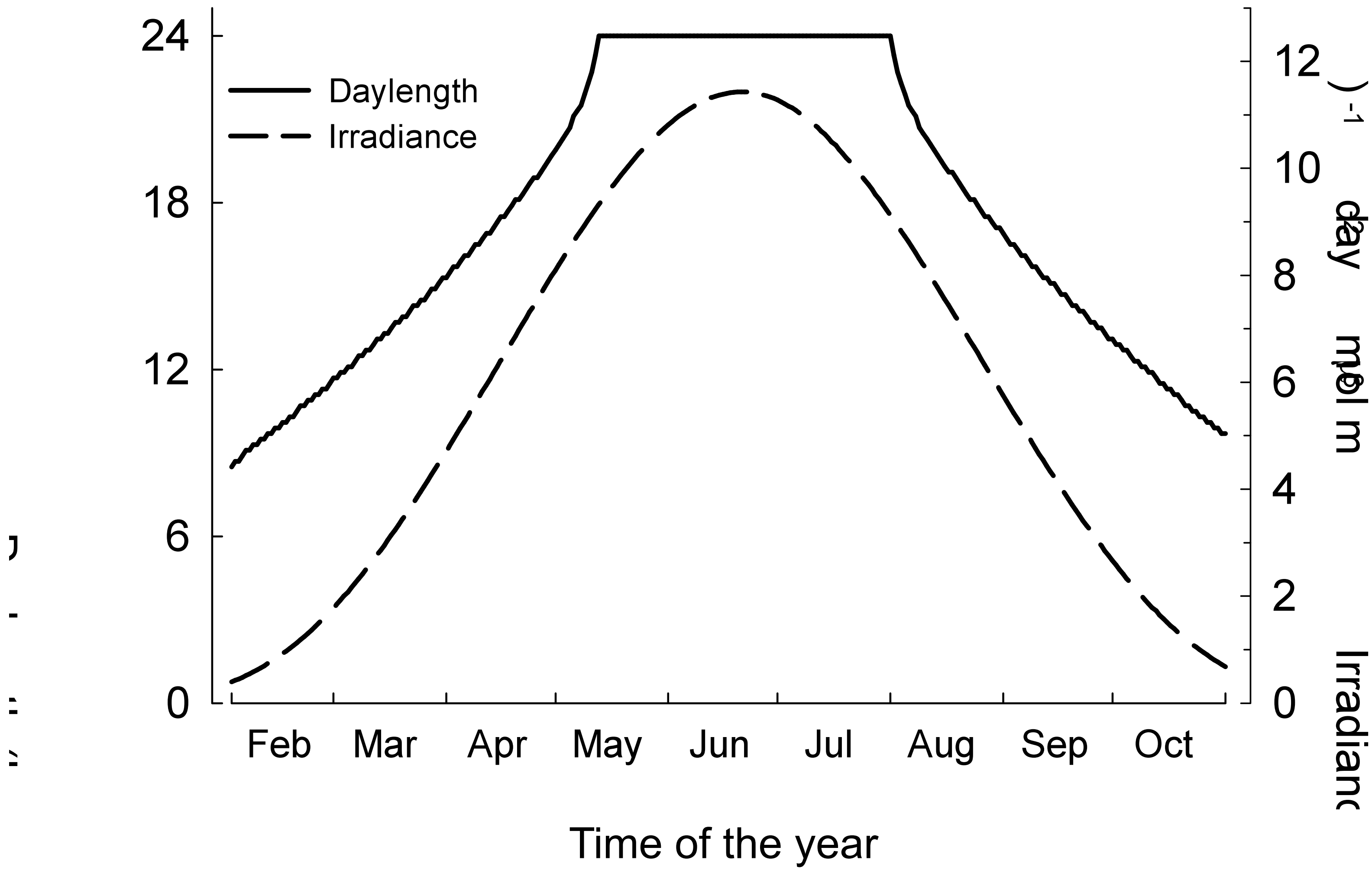
Particulate visual feeding



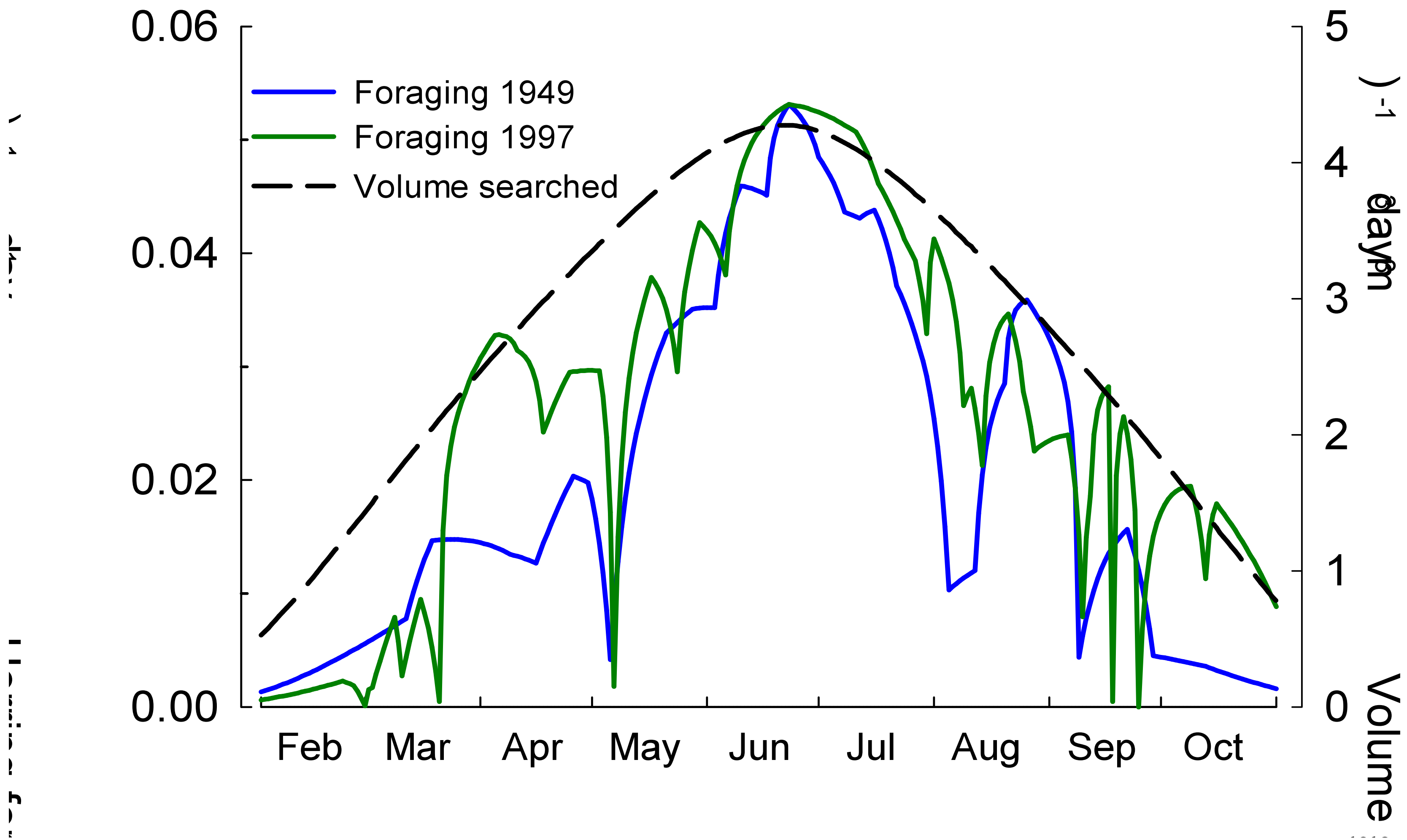
Prey detection distance



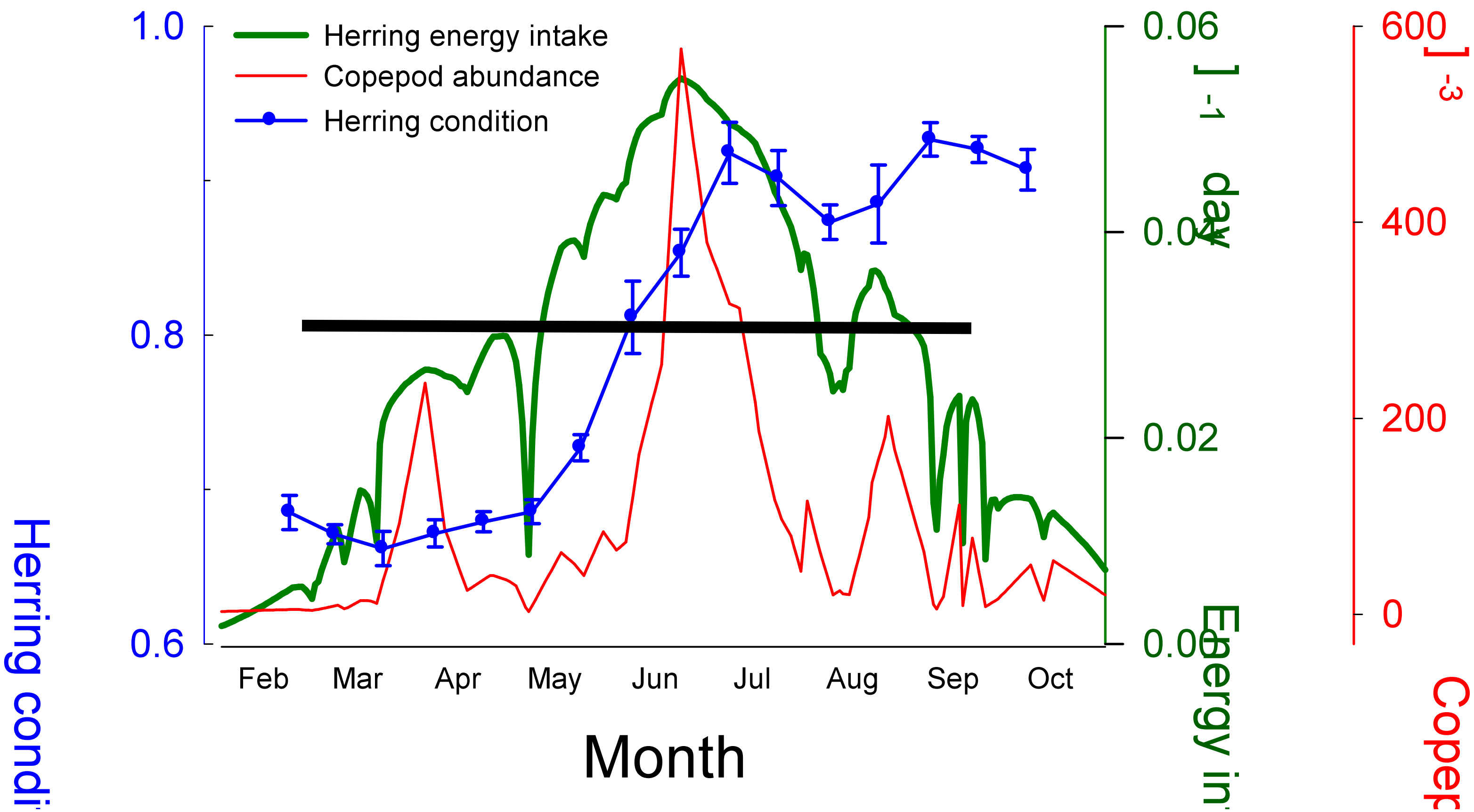
Seasonal irradiance & daylength



Search- and feeding rate



Conclusion



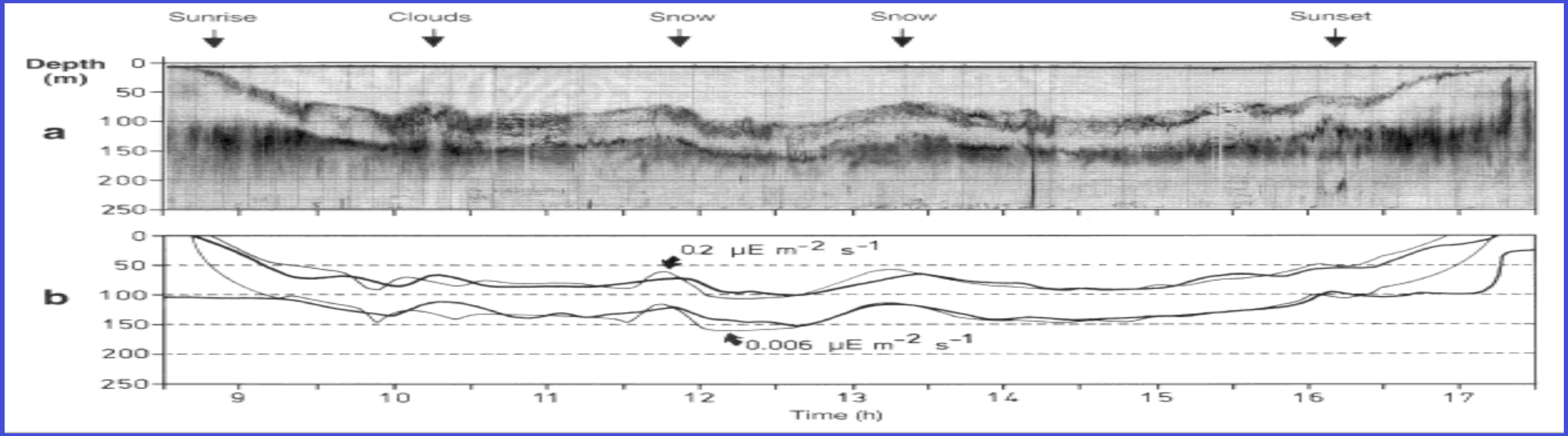
Varpe Ø & Fiksen Ø 2010 Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. Ecology 91:311-318

Light Controls Predation and Marine Food Web Structure

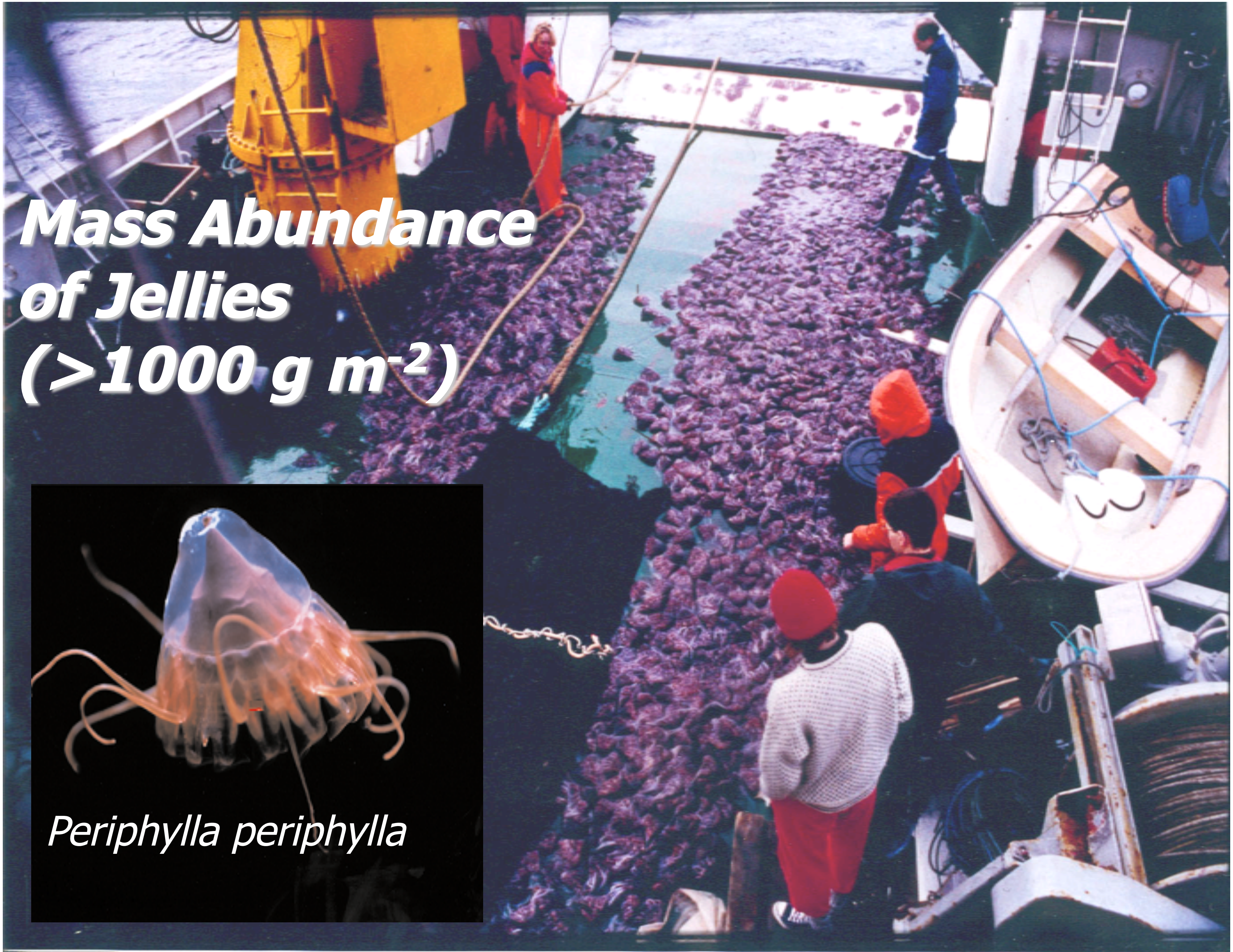
Dag L. Aksnes

University of Bergen
Norway

Light dependent behavior in a mesopelagic fish (*Maurolicus muelleri*)



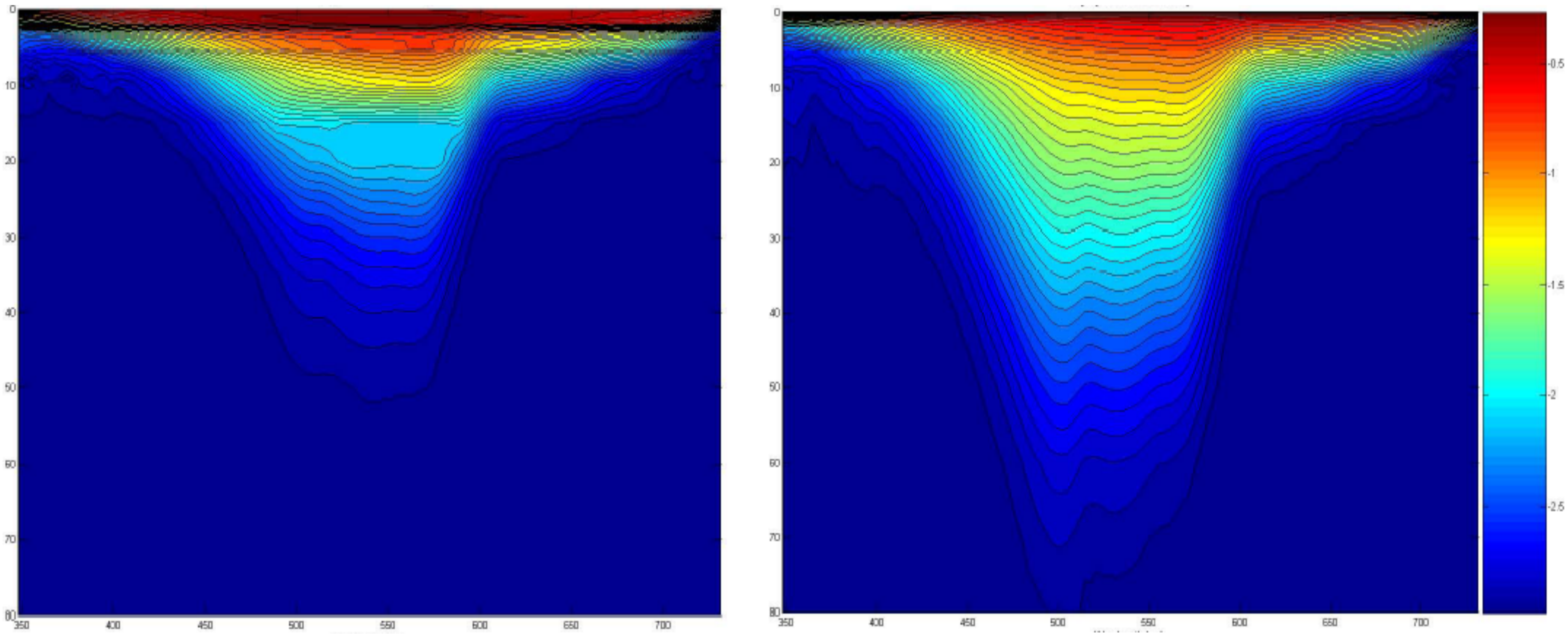
Baliño & Aksnes, 1993


Mass Abundance
of Jellies
(>1000 g m^{-2})
Periphylla periphylla

Light extinction in two different fjords

Lurefjorden

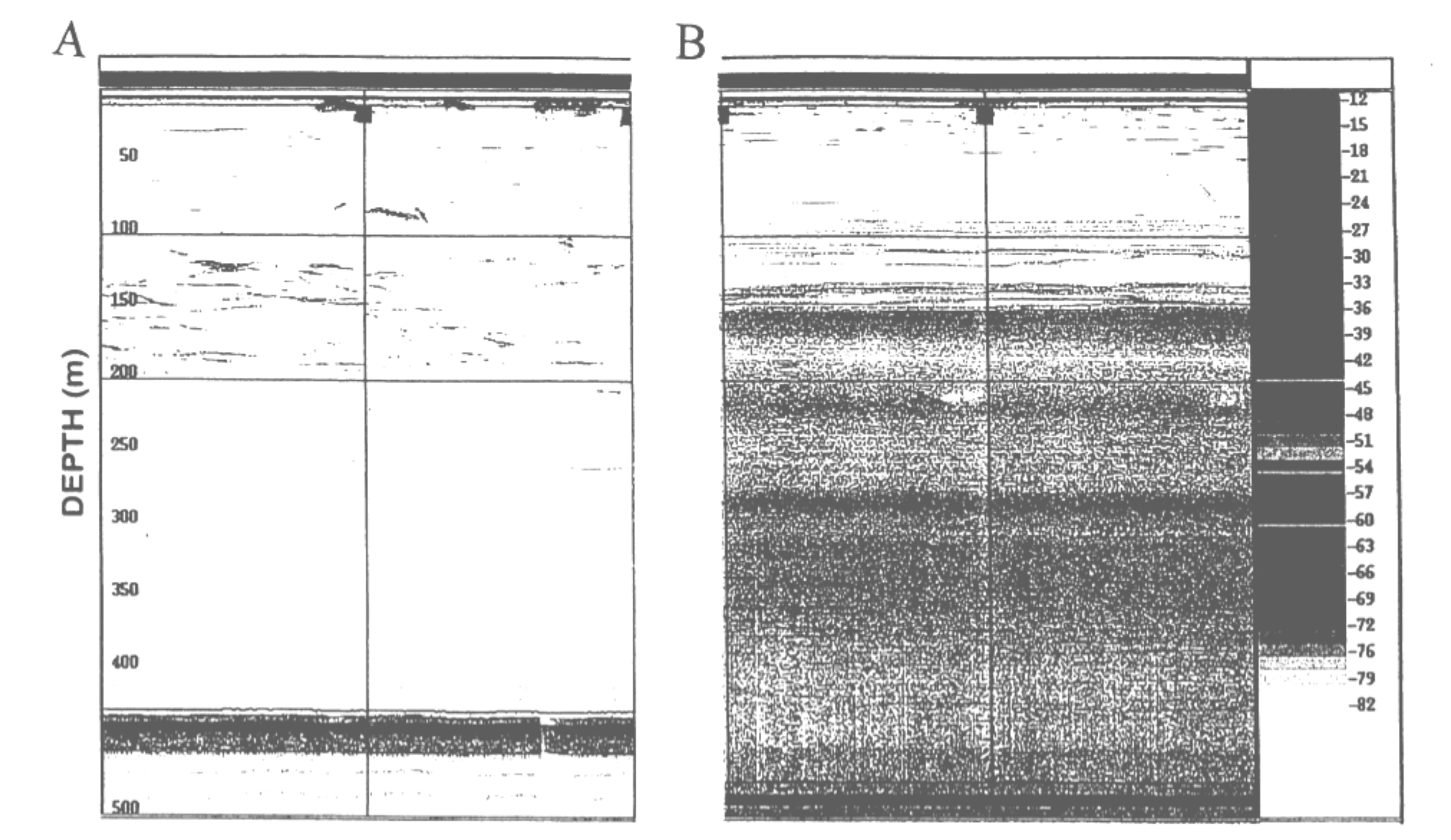
Masfjorden



Wavelenght

Observations made 10/10 2006
by Stein Kaartvedt

Fish or Jellies – a question of visibility? *Eiane et al. (1999), Limnol. Oceanogr.*



Jelly-fjord

Fish-fjord

Zooplankton is more abundant in the jelly-fjord (and larger in size)

Table 1. Biomass (mg C m^{-3}) of zooplankton, mesopelagic fish (*M. muelleri* and *B. glaciale*), and *P. periphylla* (modified from Salvanes et al. 1995).

	Zooplankton		Mesopelagic fish		*P. periphylla*	
	Autumn	Spring	Autumn	Spring	Autumn	Spring
Masfjorden	3.92	2.66	1.32	2.63	0.00	0.00
Lurefjorden	31.60	7.92	0.00	0.00	10.4	26.4

Eiane et al 1999

Visual Feeding Rate at Depth z

$$f = \frac{h^{-1}N}{(h\pi(r\sin\theta)^2 v)^{-1} + N}$$

Prey density	N
Handling time	h
Cruising speed	v
Reaction field half angle	θ

Visual Range

$$r^2 e^{cr} = |C| A V \frac{E}{K + E}$$

Background light level	E
Light saturation parameter	K
Prey size	A
Prey inherent contrast	C
Visual capacity	V

Light Level

$$E = E_0 e^{-kz}$$

Surface light level	E_0
Light attenuation	k
Depth	z

Feeding rate integrated for a light limited water column

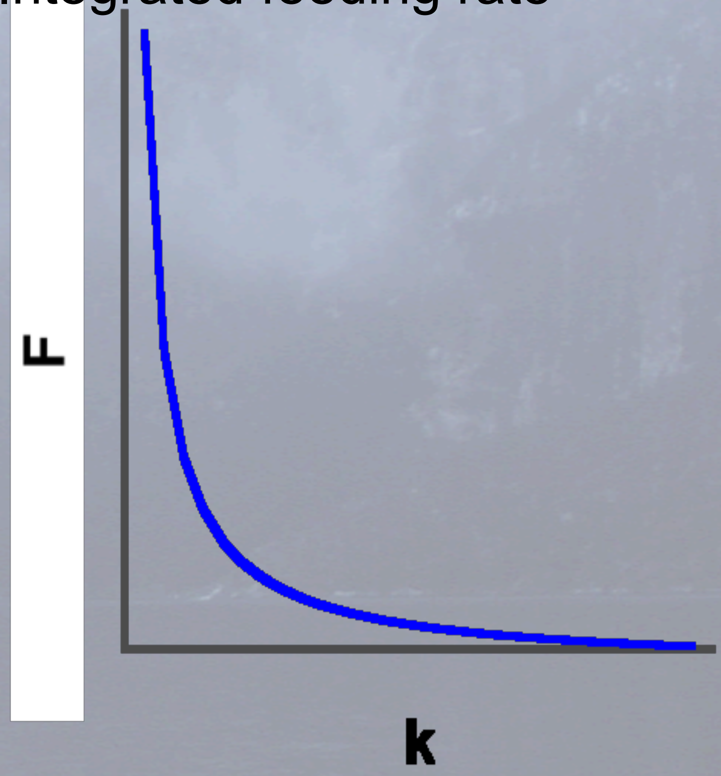
Assumption 1: Prey density is low

Assumption 2: Light intensity is low

Integration leads to:

$$F = A\frac{1}{k} + B$$

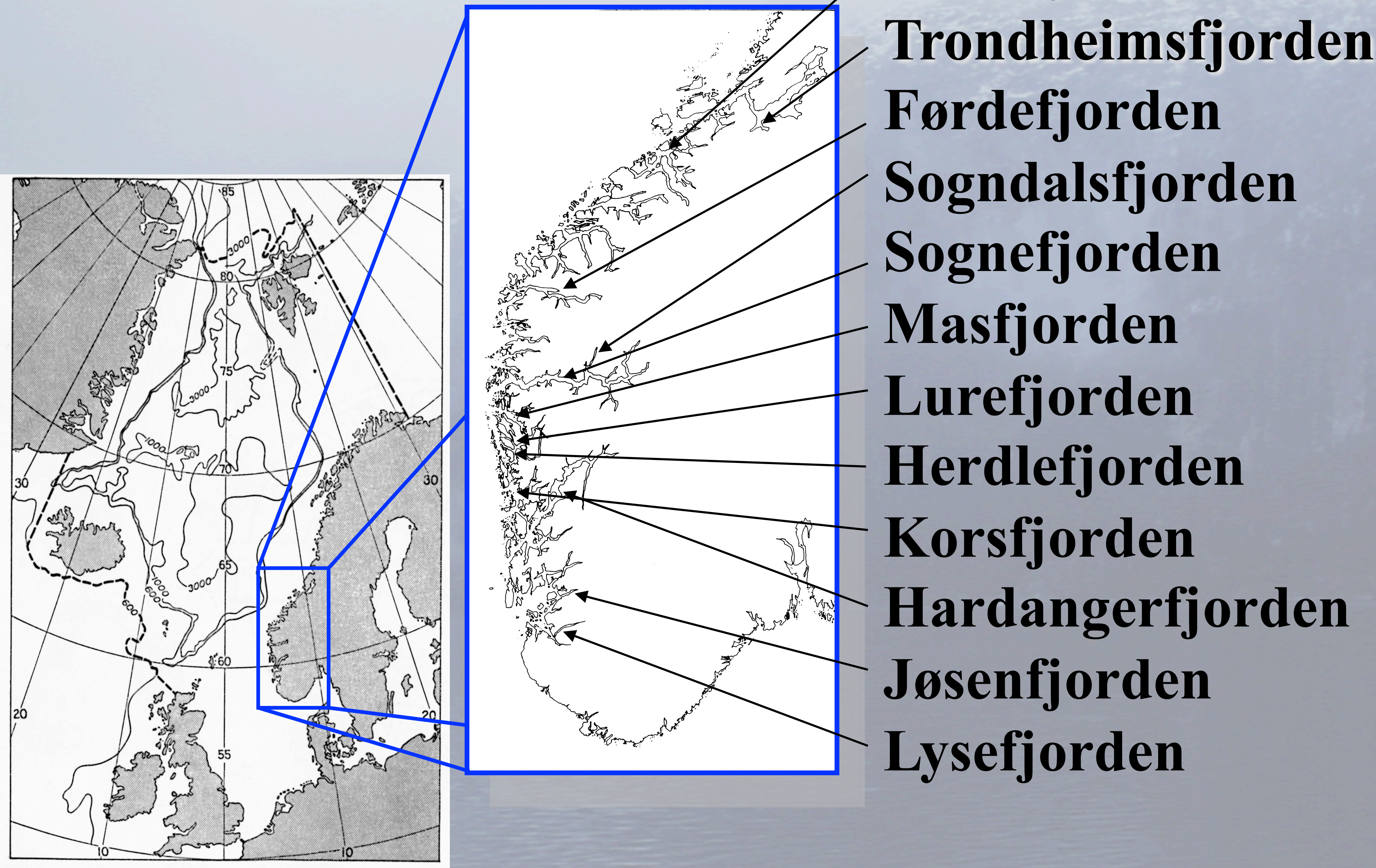
Integrated feeding rate



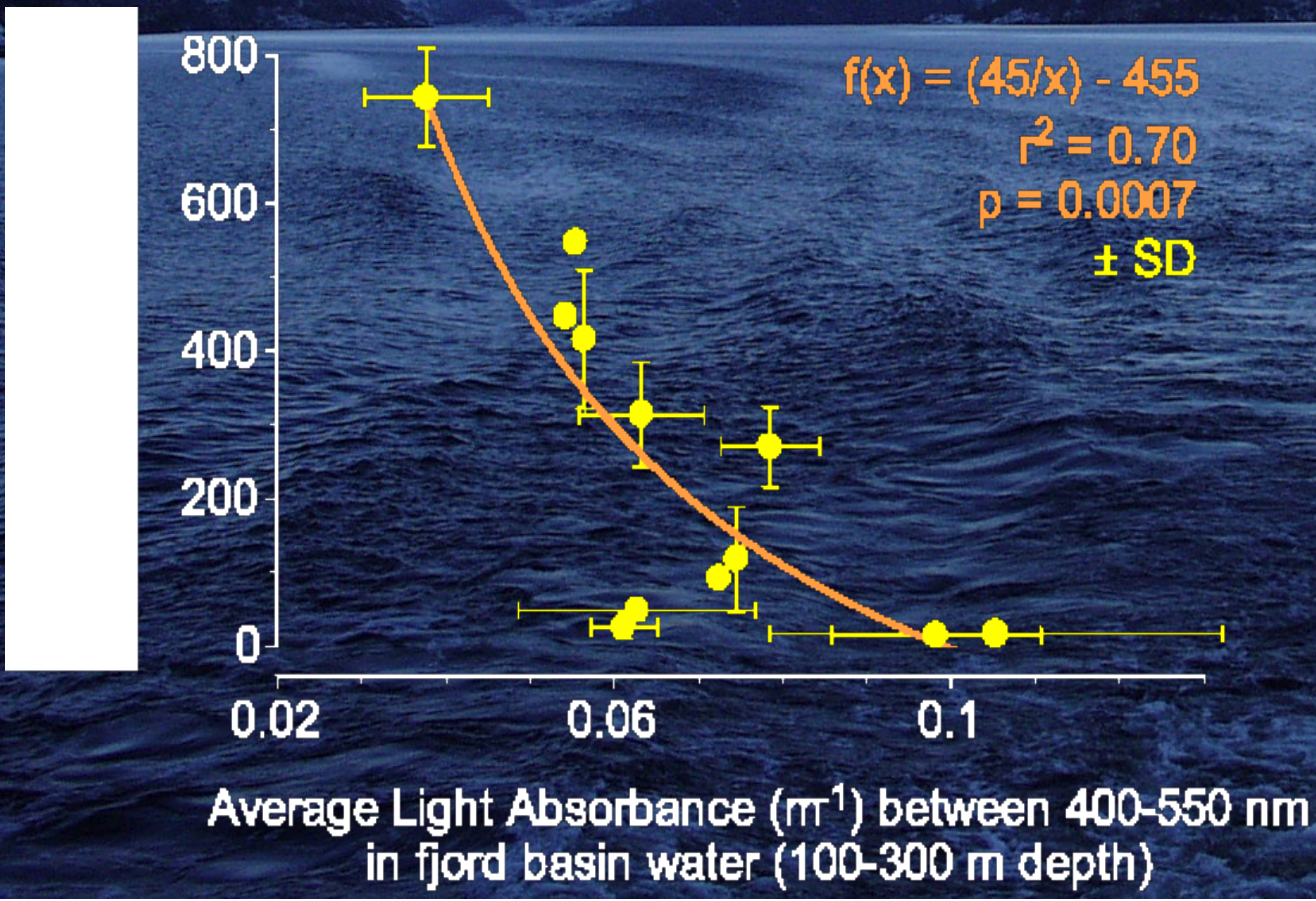
Light extinction

Aksnes & al. 2004; Aksnes 2007

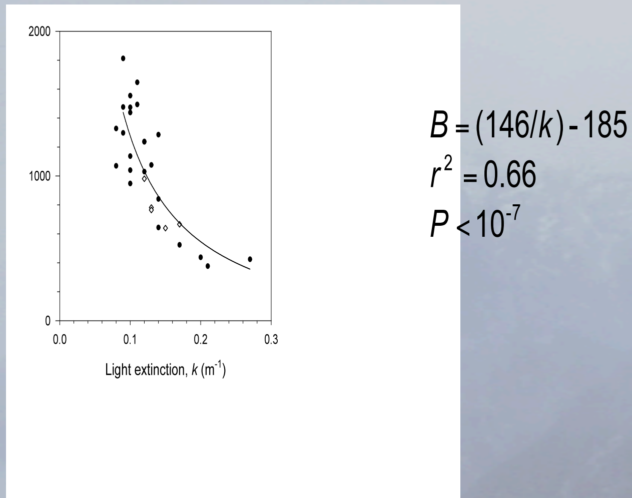
12 Fjords on the Norwegian West Coast were sampled



Fish Abundance vs. Light Environment



Planktivorous fish versus light extinction in the Black Sea



Fish data: Black Sea sprat and anchovy biomass (Prodanov *et al* 1997 and FAO fishery statistics)

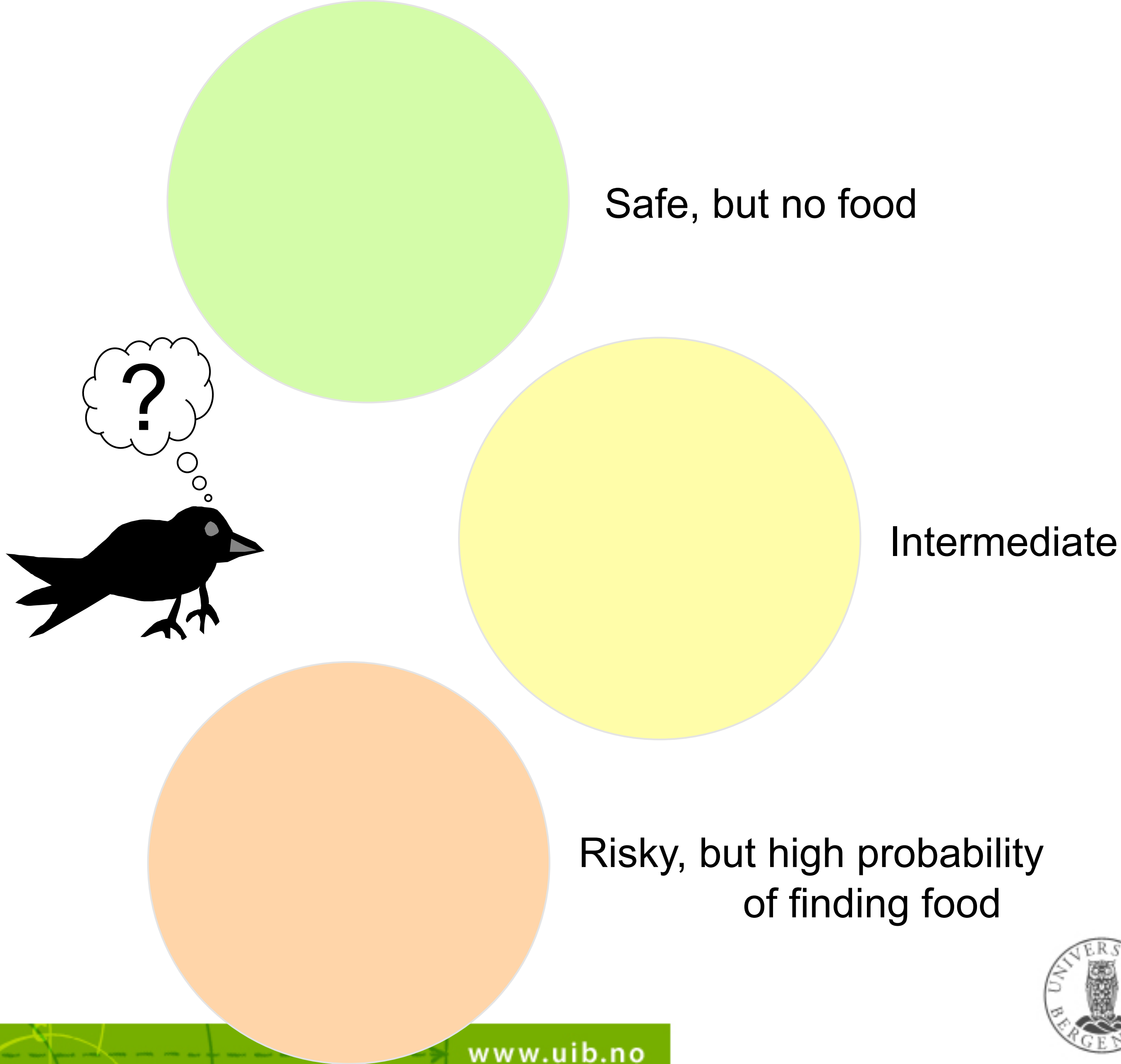
Light extinction: Data are transformed ($k = 1.7/Z_w$) Secchi-disc measurements (Z_w) that are annually and spatially integrated for the Black Sea. (Vladimirov *et al* 1997)

Aksnes & al. 2004; Aksnes 2007

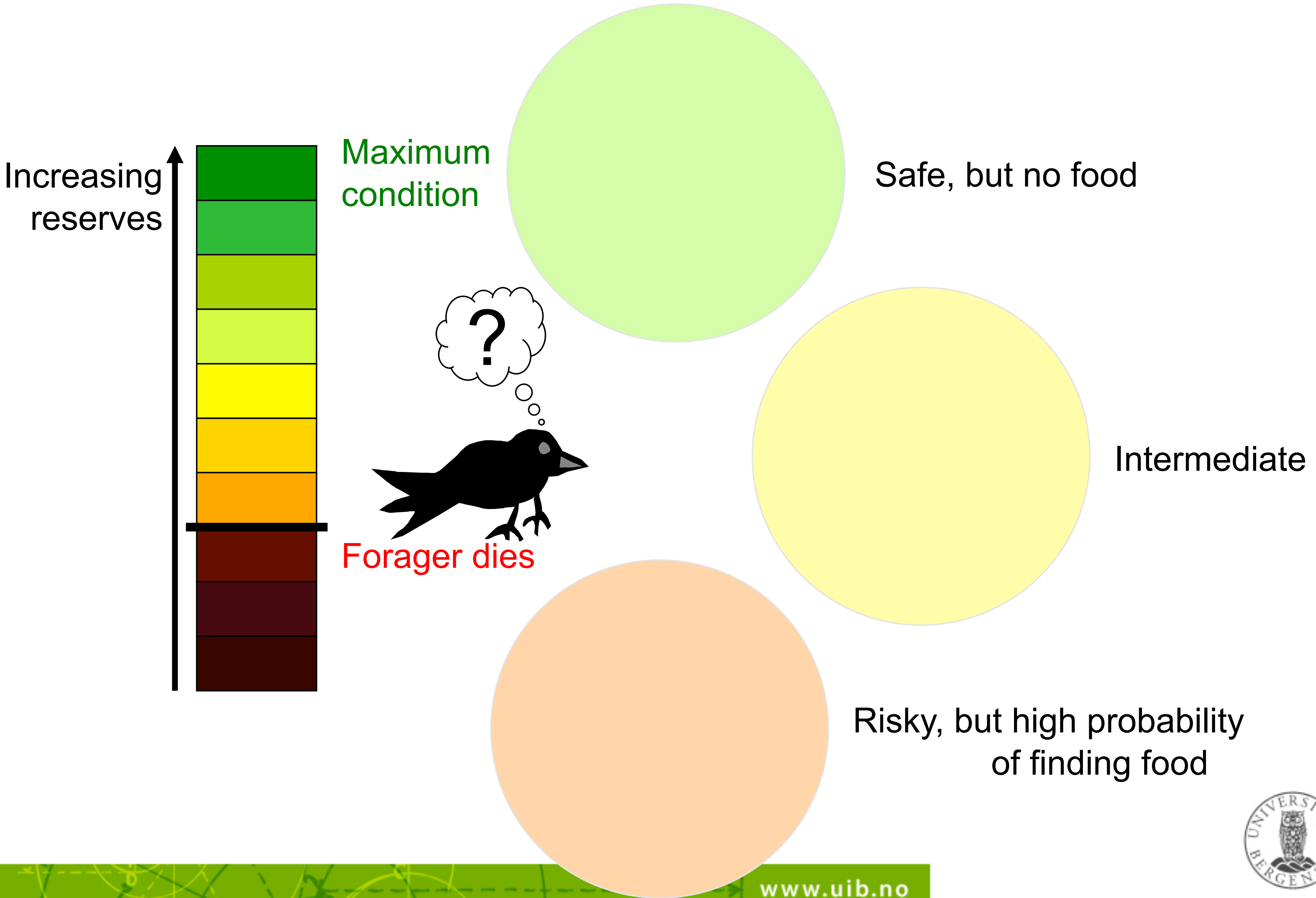
Optimal behaviour – some examples using stochastic dynamic programming

Optimal patch choice

Mangel & Clark 1988 Dynamic modeling in behavioural ecology. Princeton Univ Press



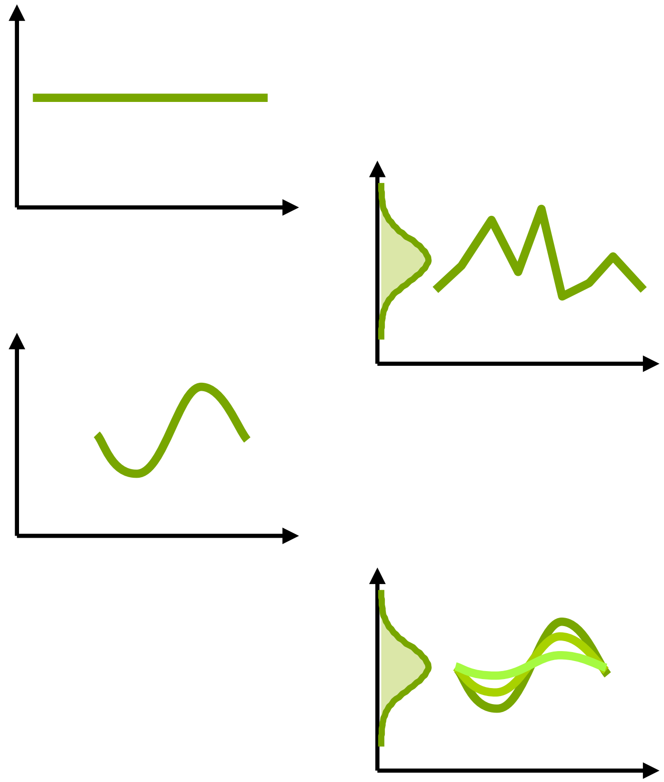
Individual state: energy reserves



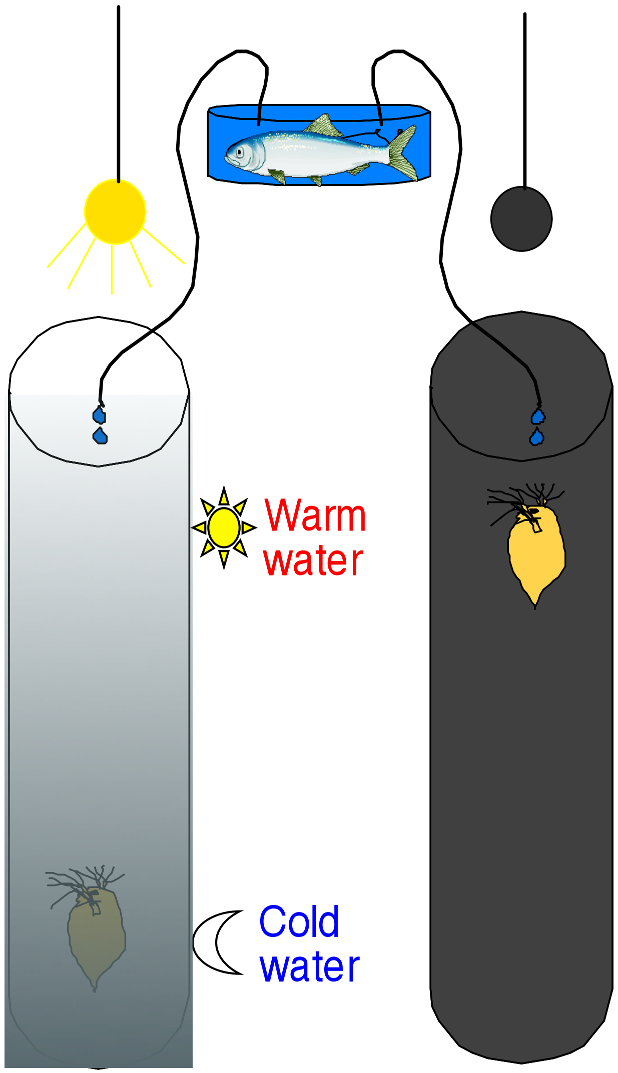
Individual state influences patch choice

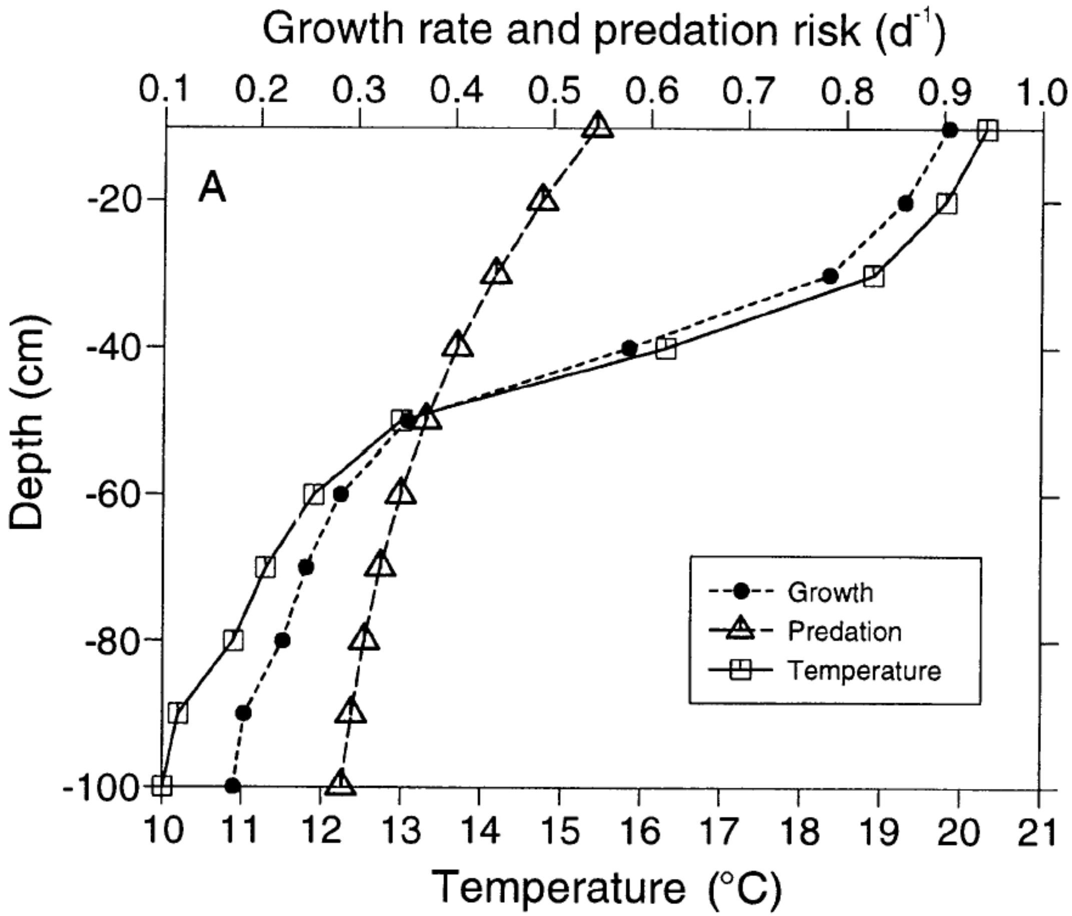
Environment

- Optimization requires that fitness can be described by a fixed function
  - A constant environment
  - A stochastic environment with constant variability
  - A repetitive seasonal environment
  - A repetitive seasonal environment with years drawn from a distribution with constant variability

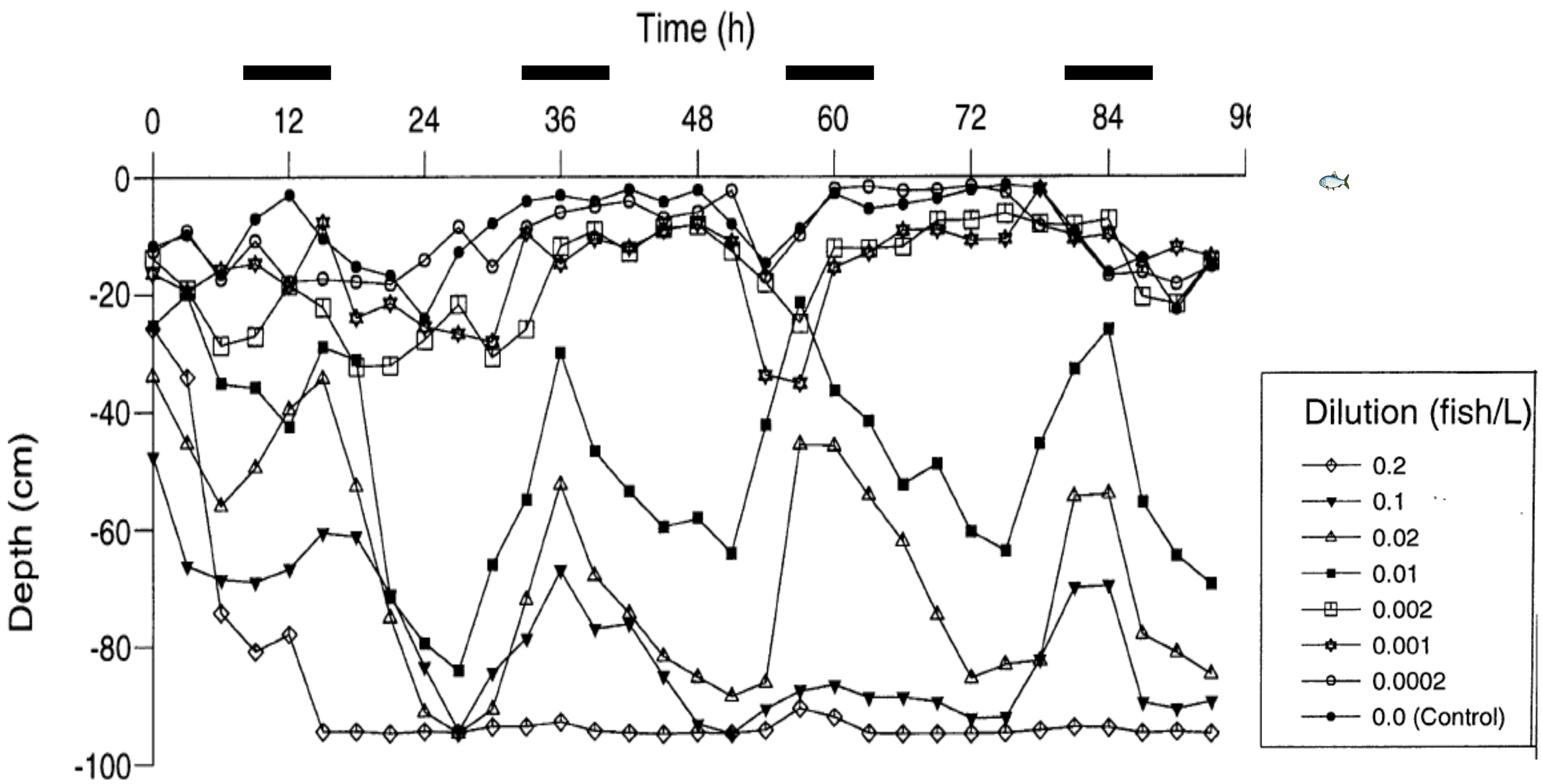


An experiment with *Daphnia magna*



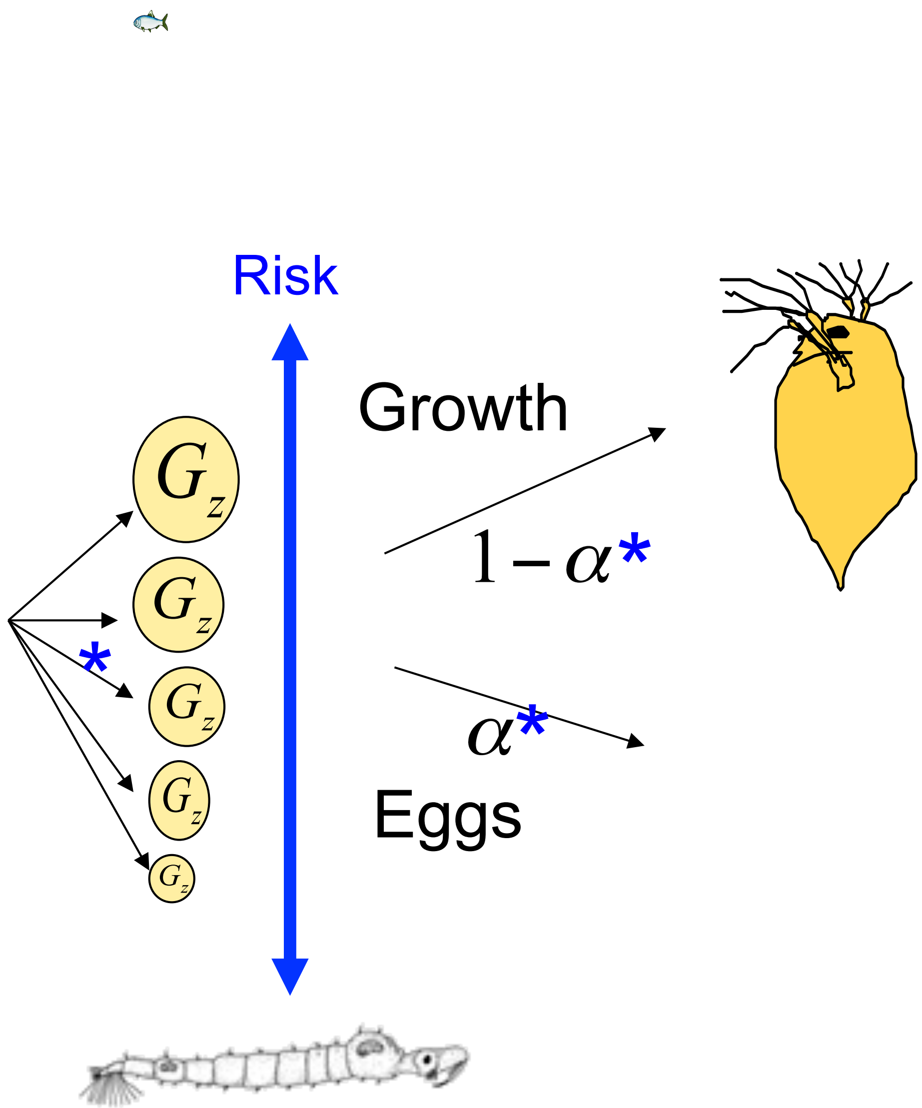


Loose & Dawidowicz 1994



Loose & Dawidowicz 1994

Optimal habitat selection and allocation of energy



The dynamic programming equation

Maximise fitness = find the behavioural and life history decision that maximises (current + expected future reproduction)

$$\Phi(w, t = T) = 0$$

Fitness (size, time)

$$\Phi(w,t) =$$

Survival

Eggs

Future fitness (new state, next time)

$$\max_{z,\alpha} P_s(w,z)\left\{R(w,z,\alpha) + \Phi\left[w'(w,z,\alpha), t+1\right]\right\}$$

Computer pseudo-code

```
Program SDP

DEFINE TERMINAL FITNESS(STATE,HORIZON)

DO TIME FROM HORIZON-1 TO 1 IN STEPS OF -1

  DO STATE = MINSTATE, MAXSTATE
    DO HABITAT = 1,N_HABITATS
      DO ALLOCATION = 1, N_ALLOCATION

            Find NEW_STATE(HABITAT, ALLOCATION)
            Find REPRODUCTION(HABITAT, ALLOCATION)
            Find SURVIVAL(HABITAT,ALLOCATION)

            Find FITNESS=SURVIVAL*[FITNESS(NEW_STATE,TIME+1) + REPRODUCTION]

            IF(FITNESS>MAX_FITNESS) THEN
              STORE HABITAT*(STATE,TIME)
              STORE ALLOCATION*(STATE,TIME)
            ENDIF

       ENDDO ALLOCATION
      ENDDO HABITAT
            MAX_FITNESS=0
    ENDDO STATE
  ENDDO TIME
```

Loops

State dynamics (physiology)
&
ecological mechanics

Evaluate consequences of actions
in terms of fitness – save best

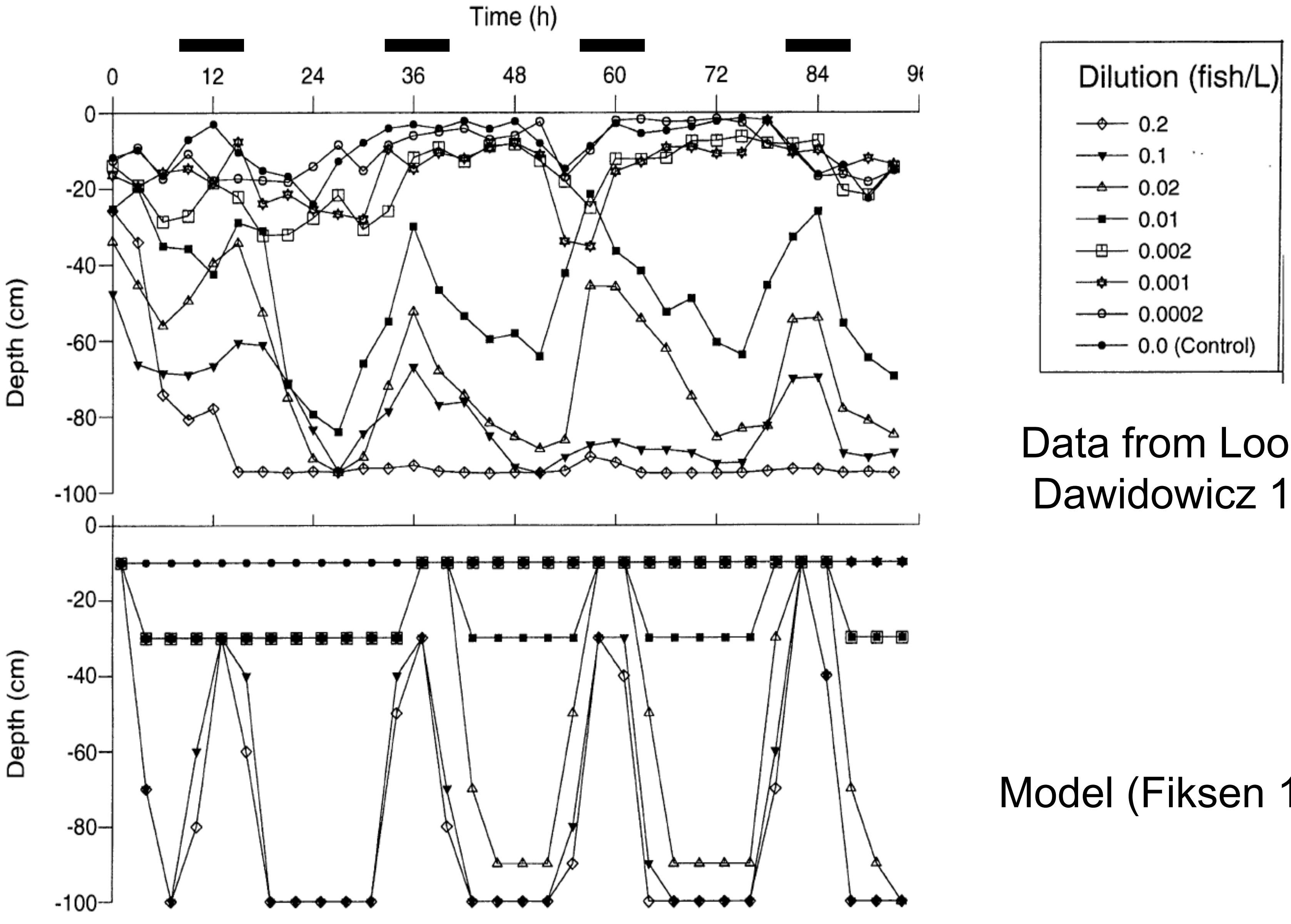
Optimal behaviour and life history

Optimal strategy depending on environment, body mass, time *and implicitly, expectations of future conditions*

$$z^*(w,t) \qquad \alpha^*(w,t)$$

These matrixes of the best strategy can be applied in forward projections with IBMs or state-structured population models

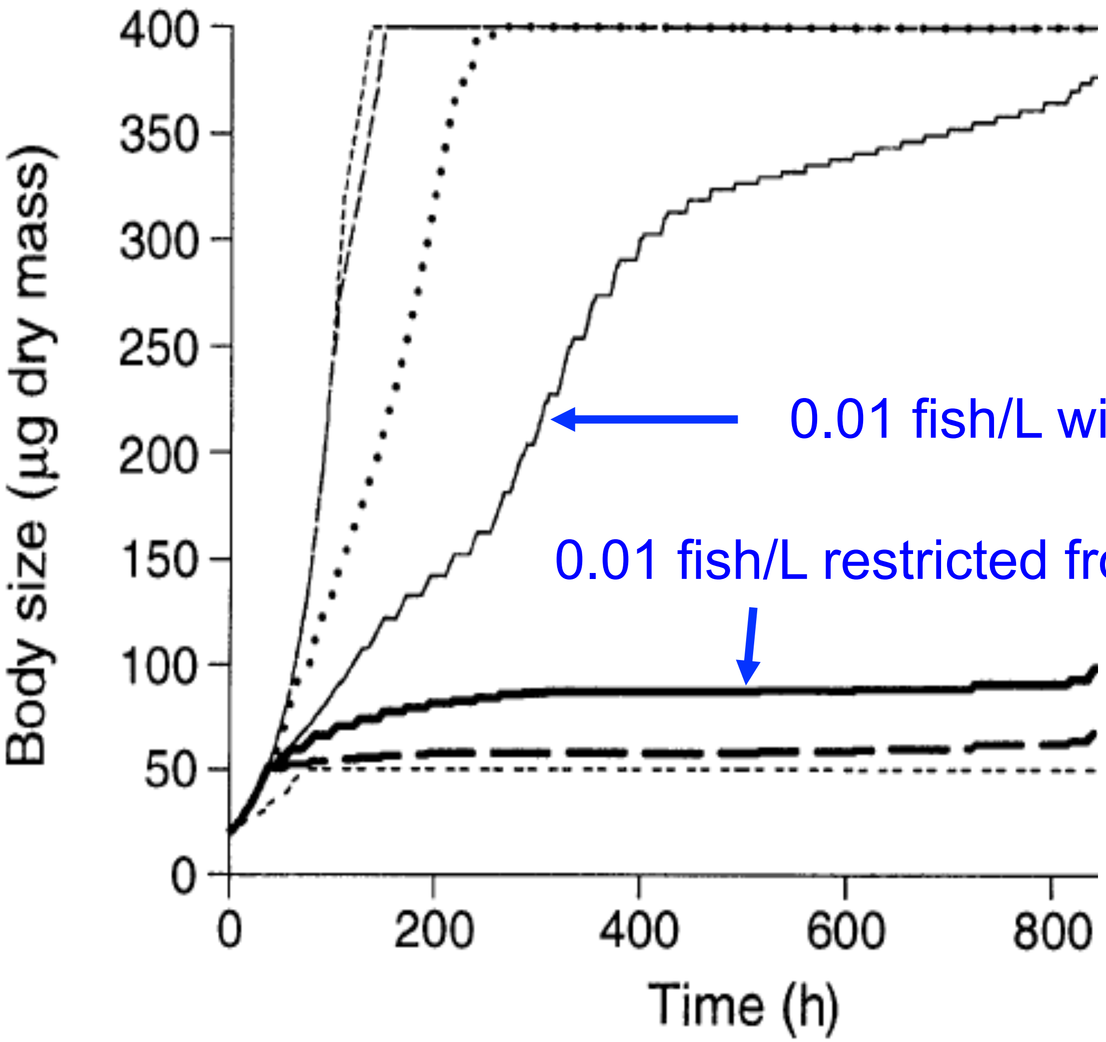
Optimal depth selection: data and model



Data from Loose & Dawidowicz 1994

Model (Fiksen 1997)

Behaviour and life-history decisions interact



Low fish density

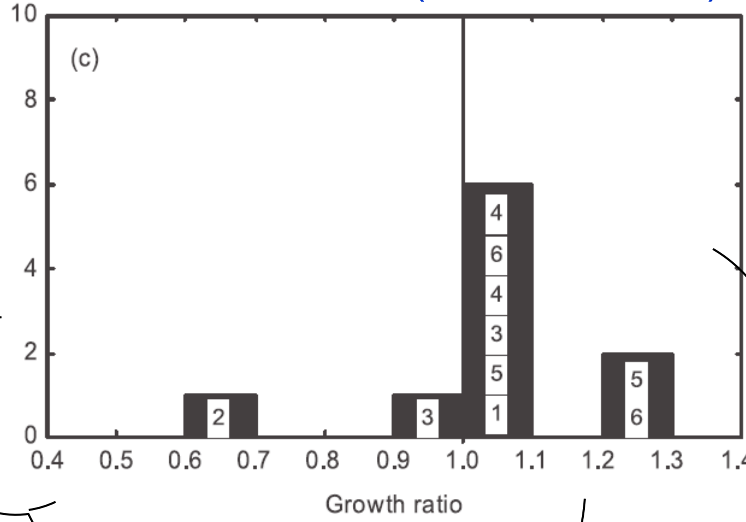
0.01 fish/L with DVM

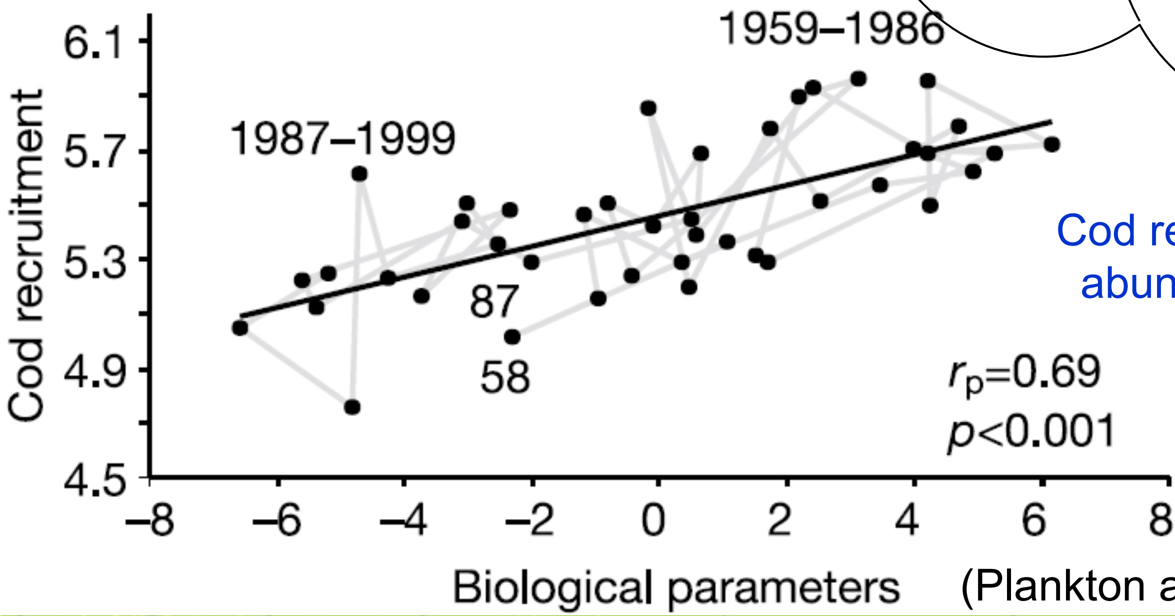
0.01 fish/L restricted from DVM

High fish density

Larval fish – and an apparent contradiction

Larval cod tend to grow at maximum rates in the field (Folkvord 2005)

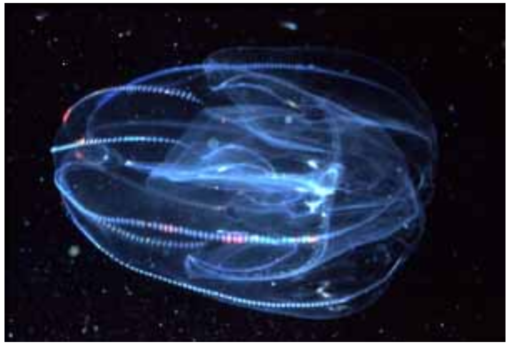




(Plankton abundance)

Cod recruitment depends on plankton abundance (Beaugrand & al. 2003)

Trade-offs and behaviour

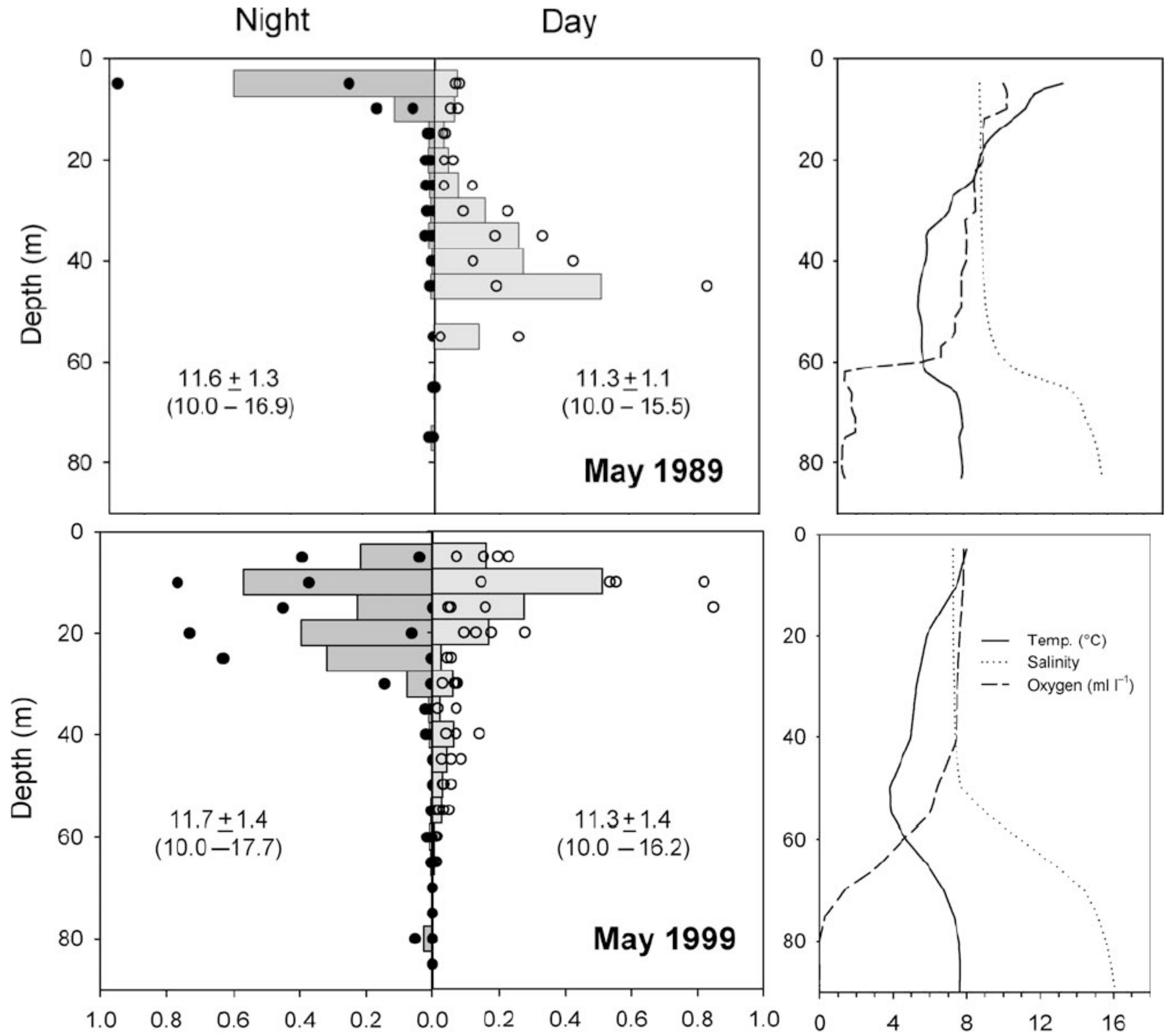


Risk depends on
depth position

Risk depends on
activity

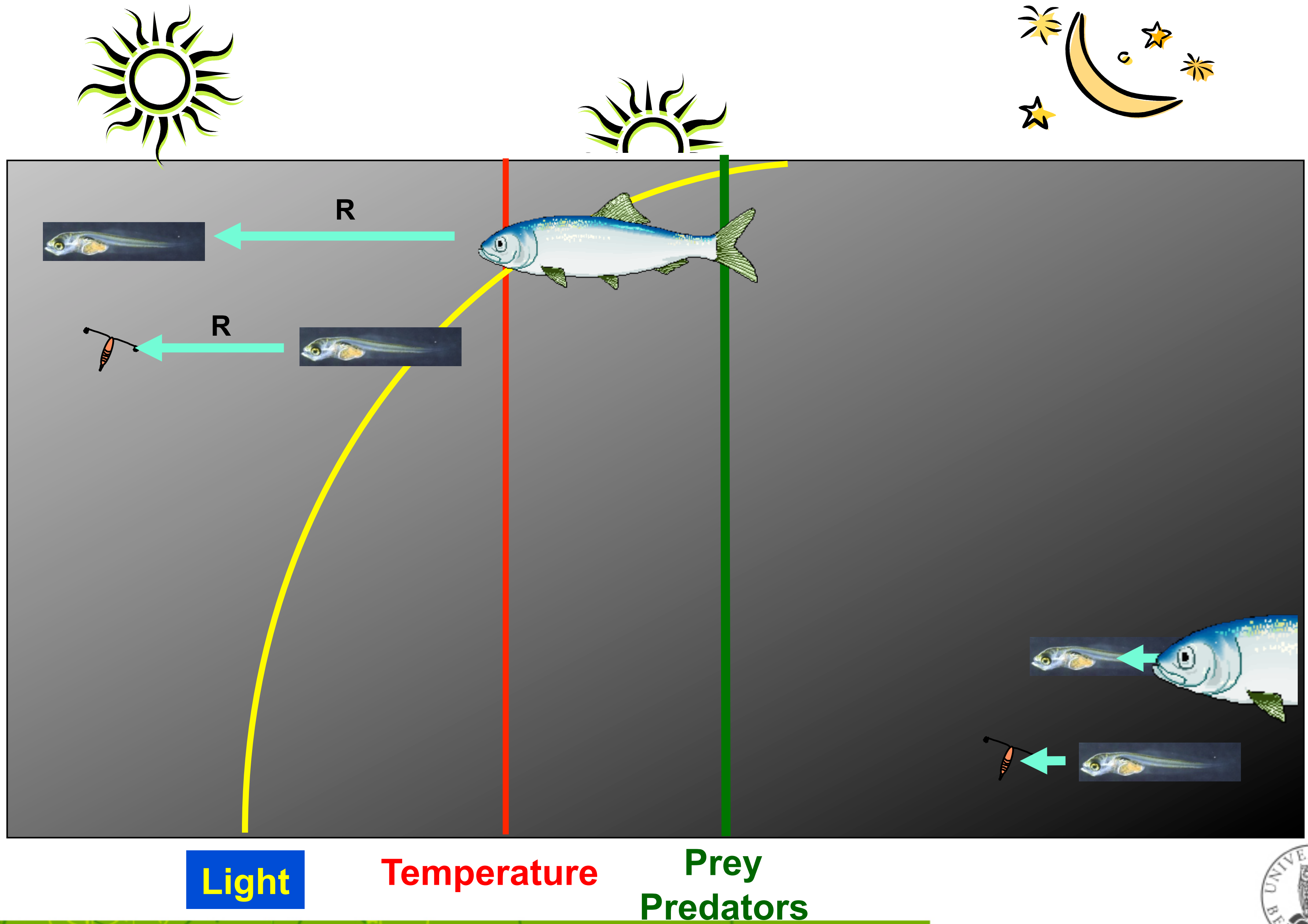
Larval feeding and
growth depend on both
depth and activity

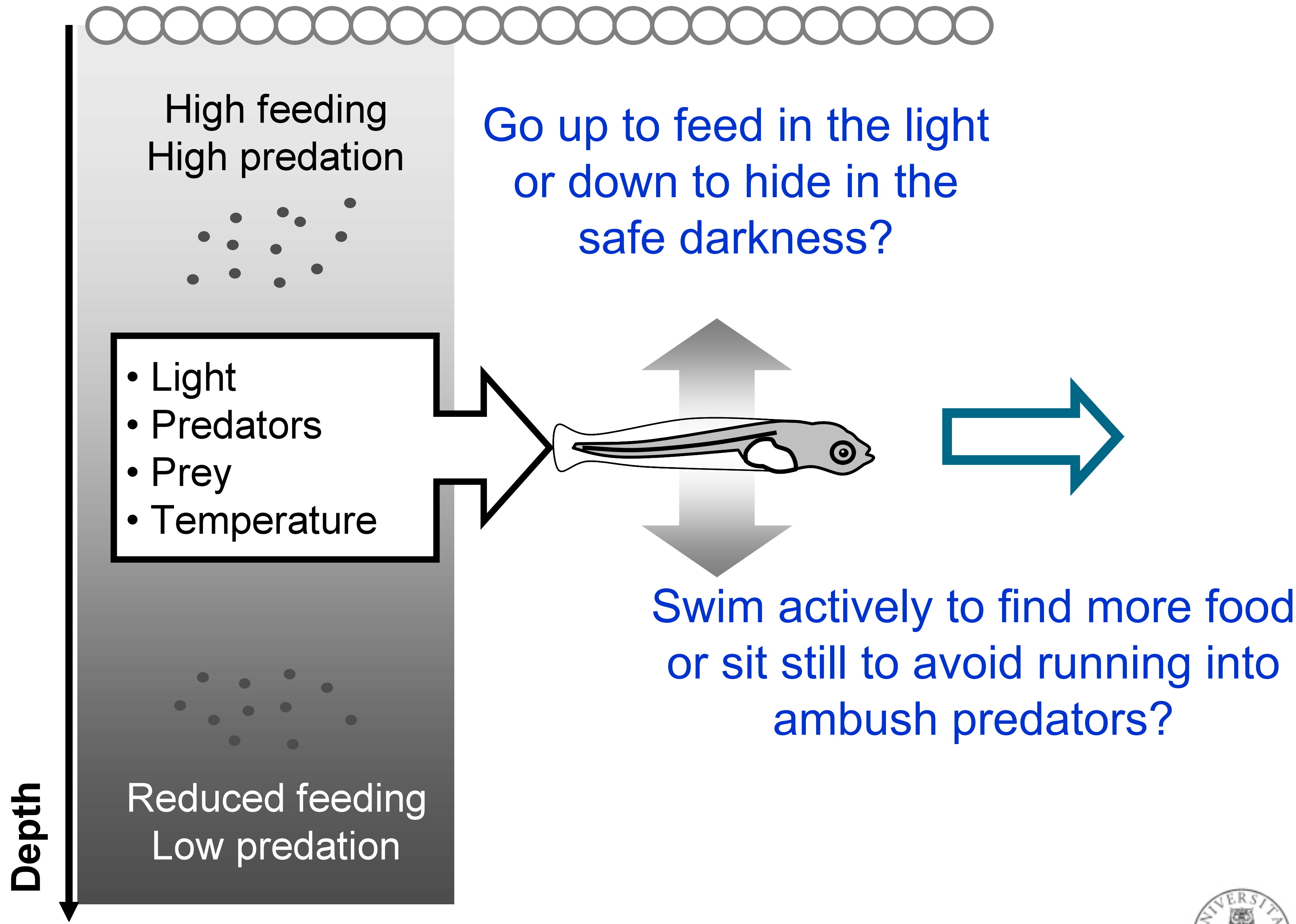
Sprat in the Baltic



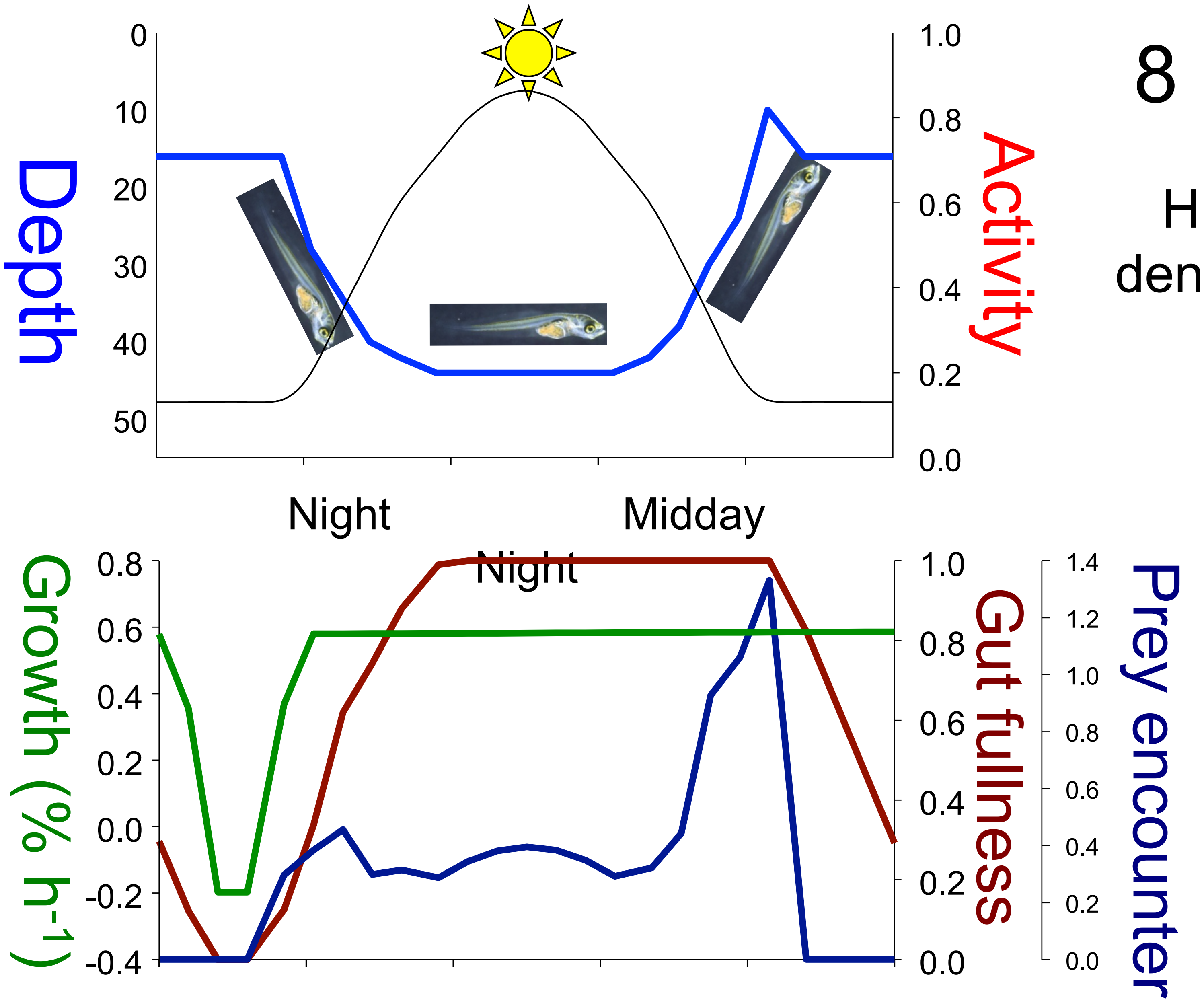
Voss & al 2007

Pelagic environments: vertical and diel gradients




High feeding
High predation
• Light
• Predators
• Prey
• Temperature
Reduced feeding
Low predation
Depth
Go up to feed in the light
or down to hide in the
safe darkness?
Swim actively to find more food
or sit still to avoid running into
ambush predators?

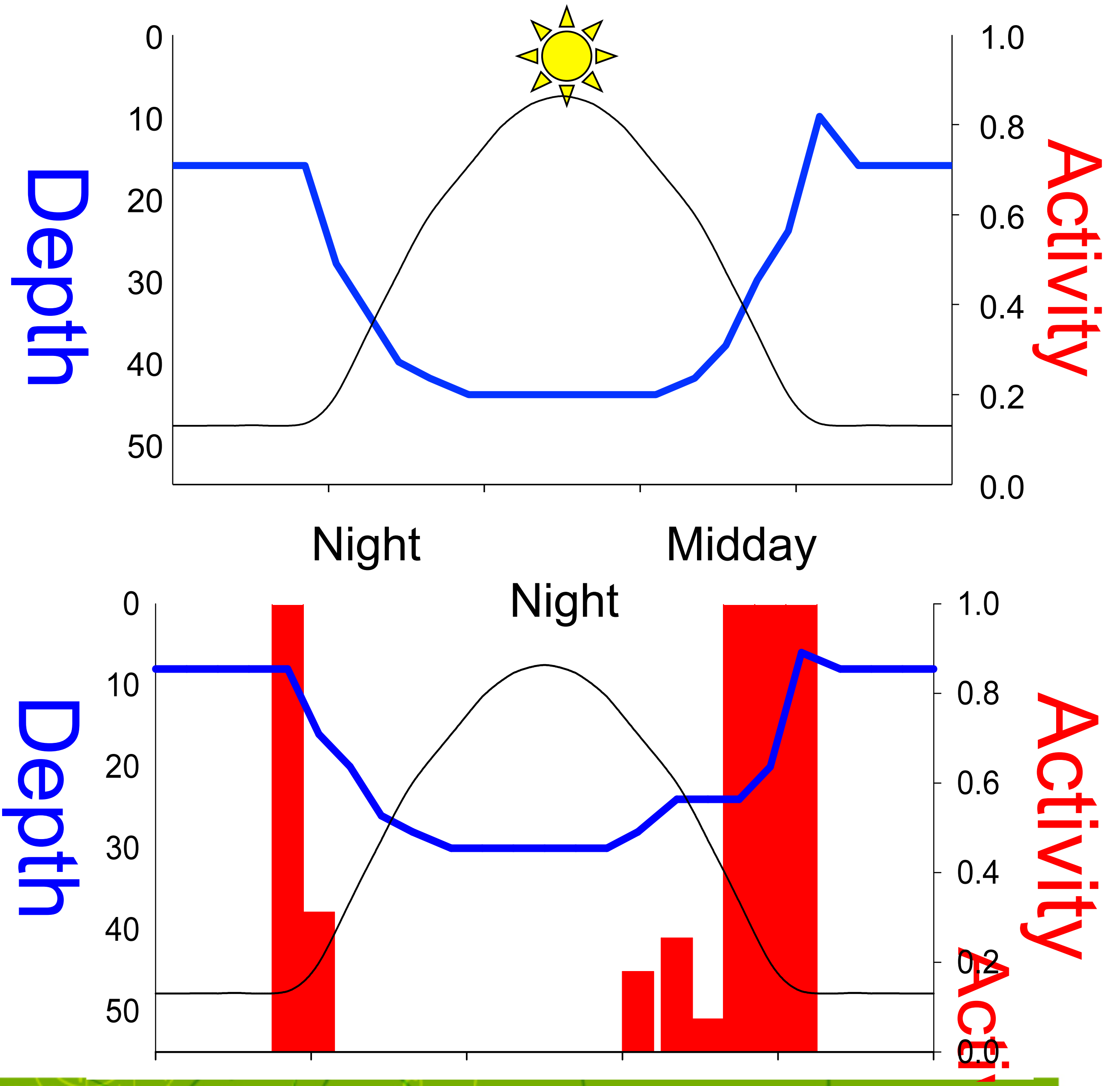
Optimal behaviour – maximize survival to given size



8 mm

High prey density (20/L)

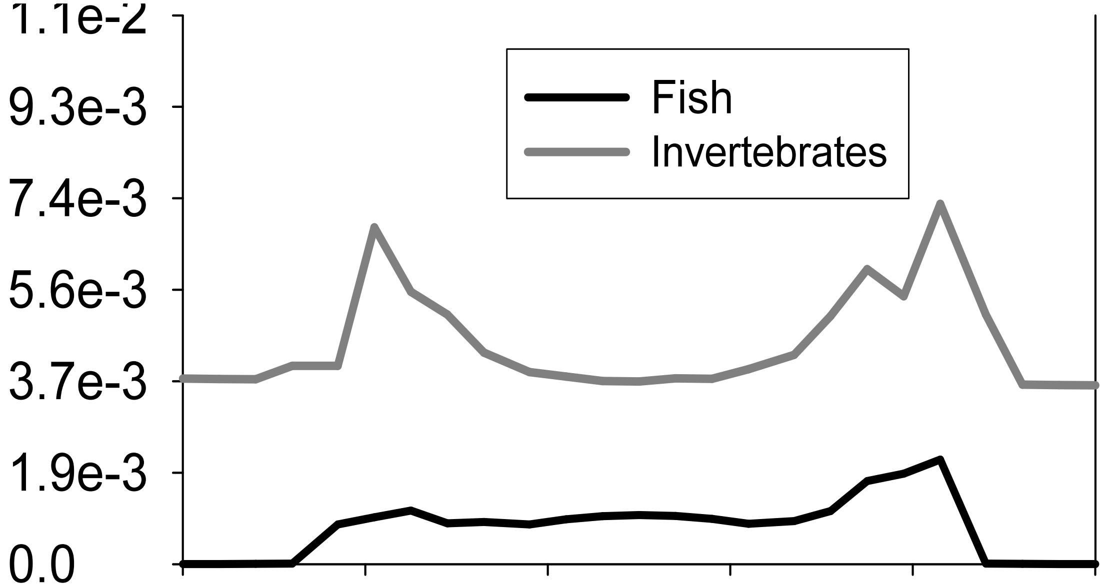
Optimal behaviour and prey availability



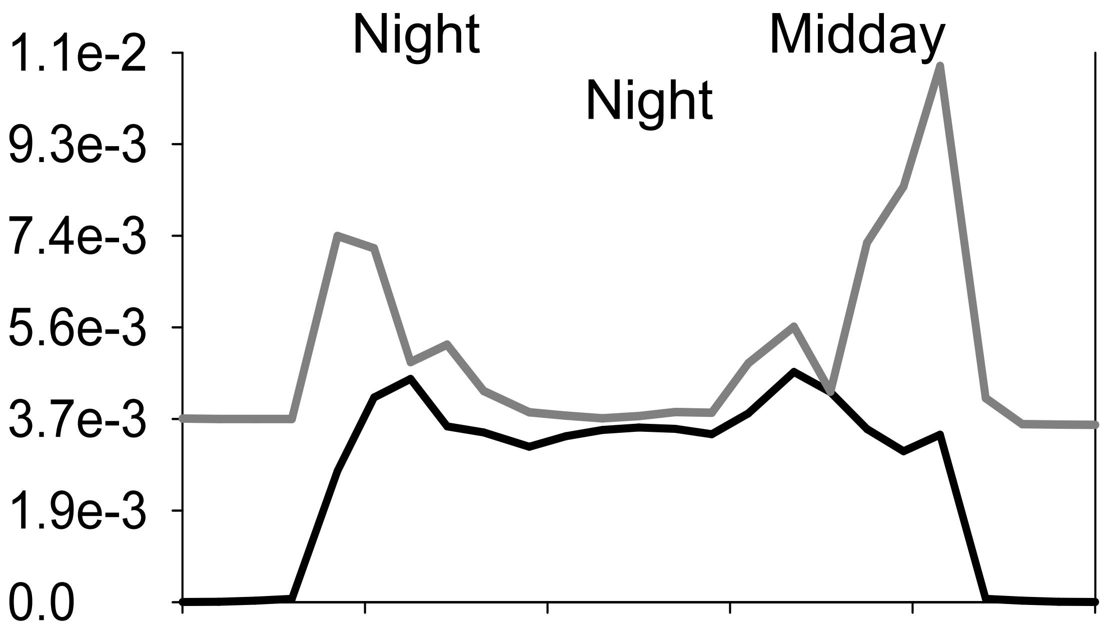
High prey density (20/L)

Low prey density (2/L)

Predation and prey availability

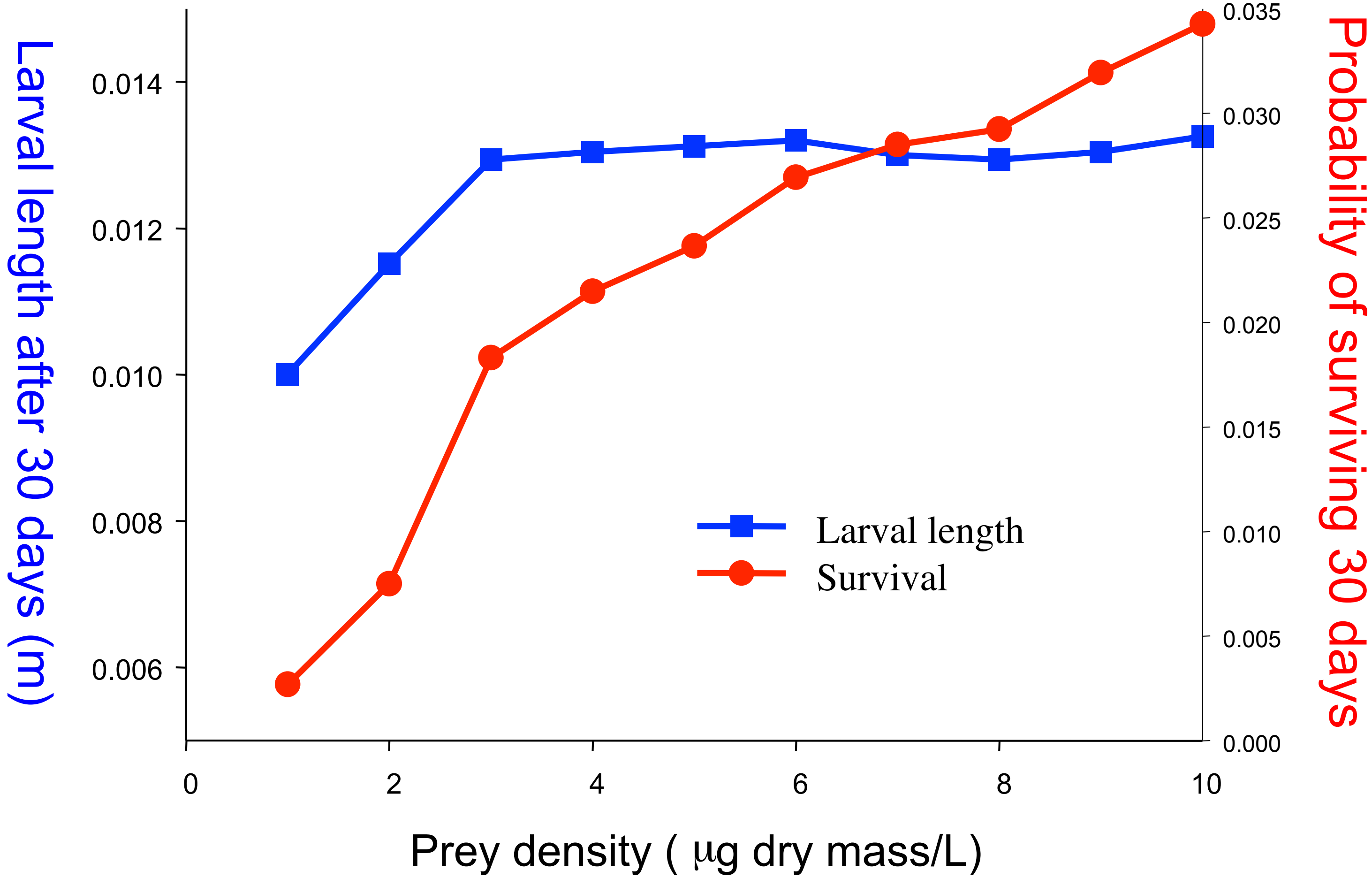


High prey density (20/L)

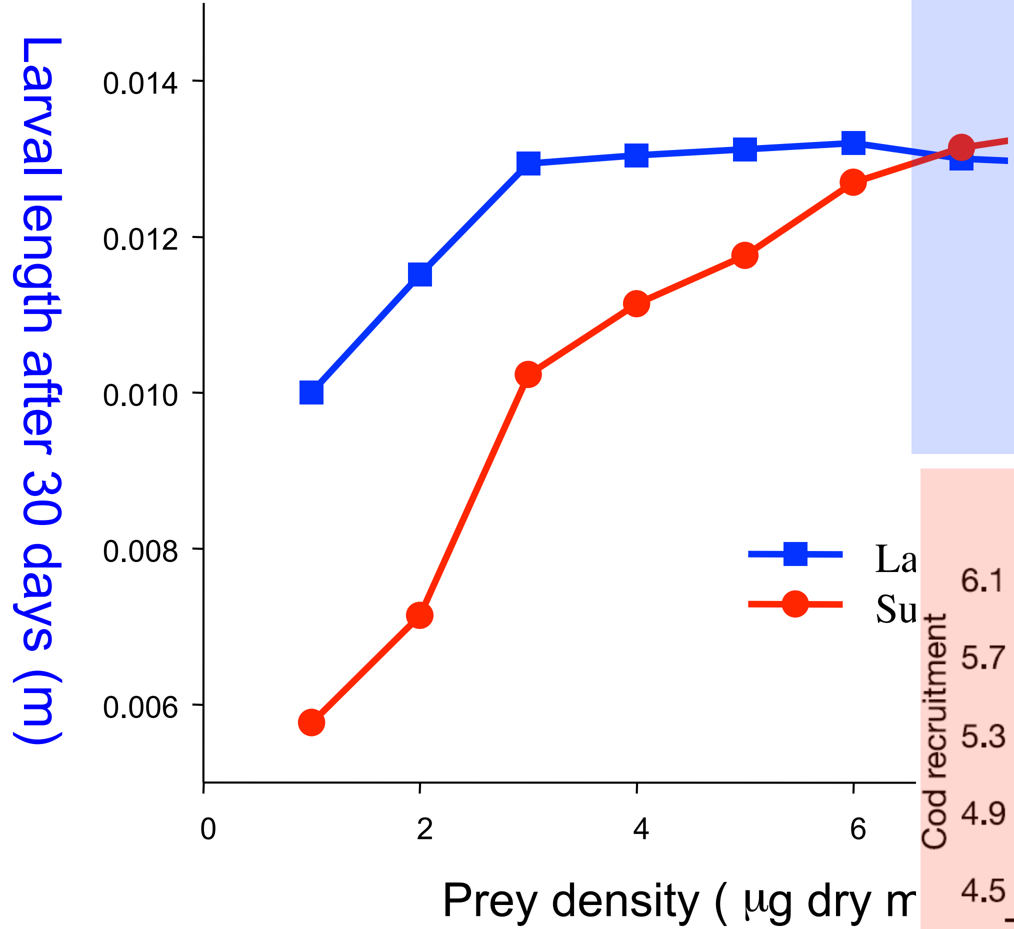


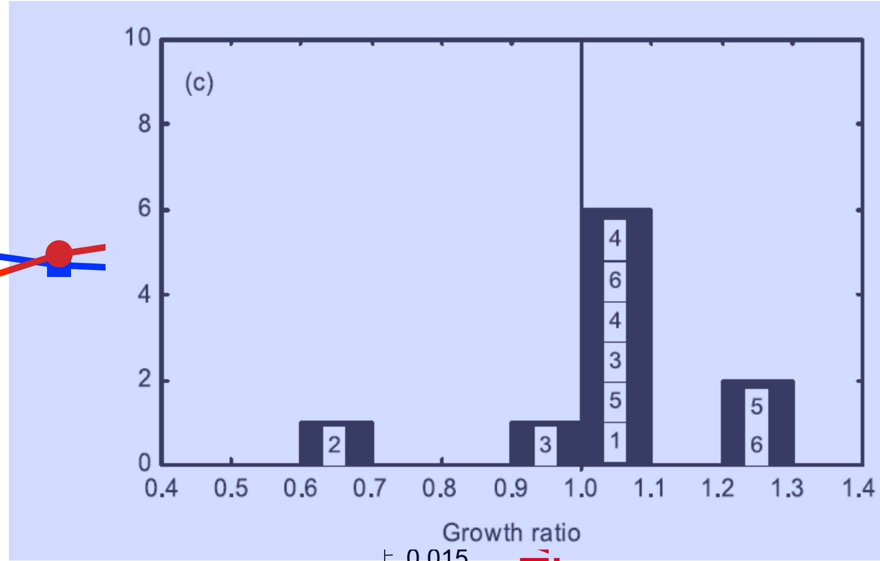
Low prey density (2/L)

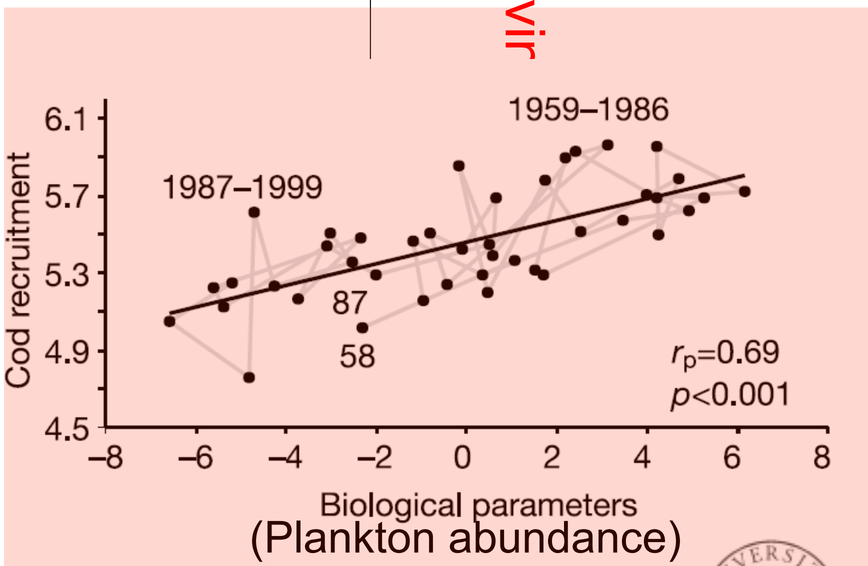
Prey density and recruitment success



Prey density and recruitment success







Fiksen & Jørgensen mscr

Fish deep in debt:
Fish behaviour in hypoxic gradients

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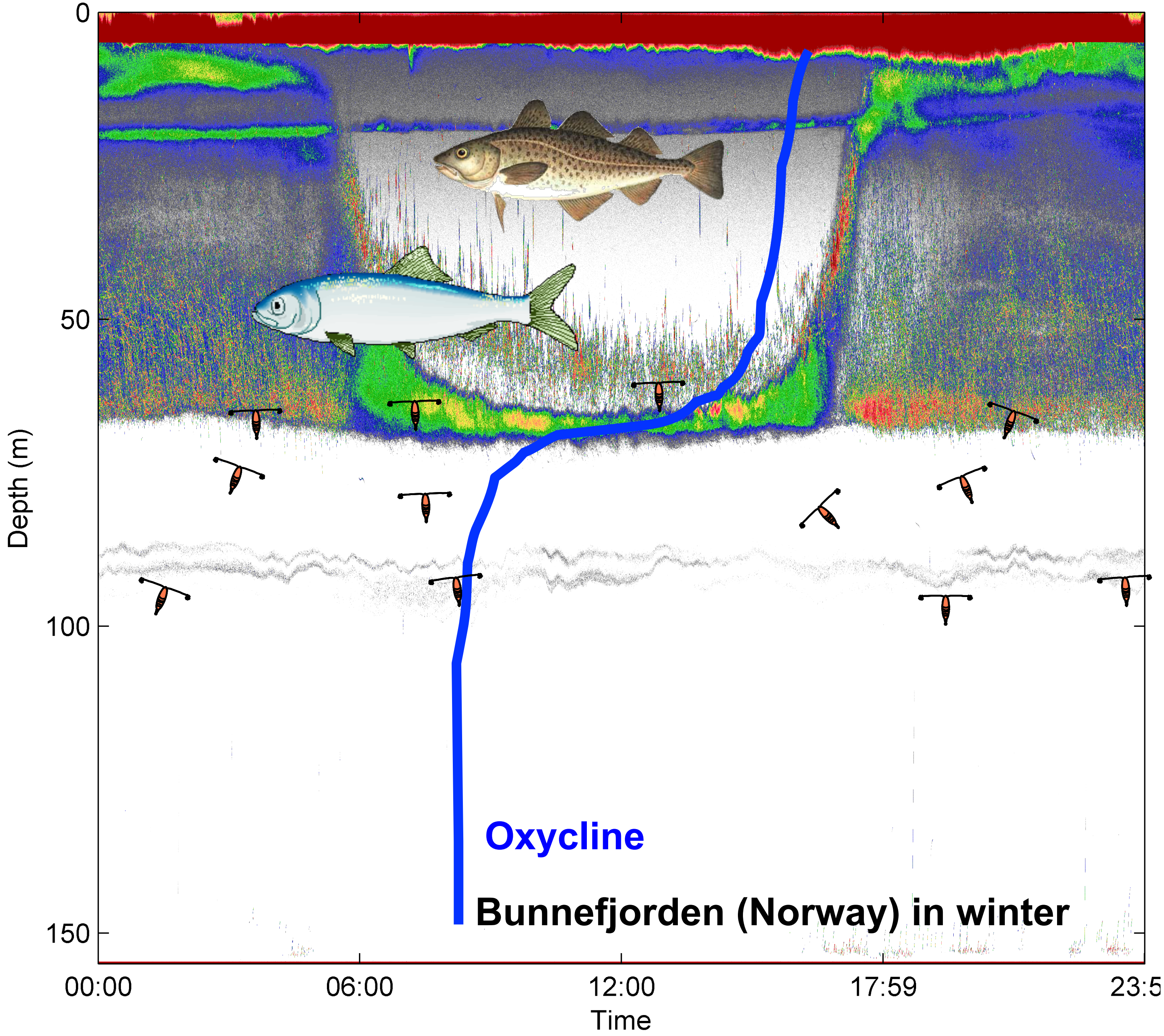
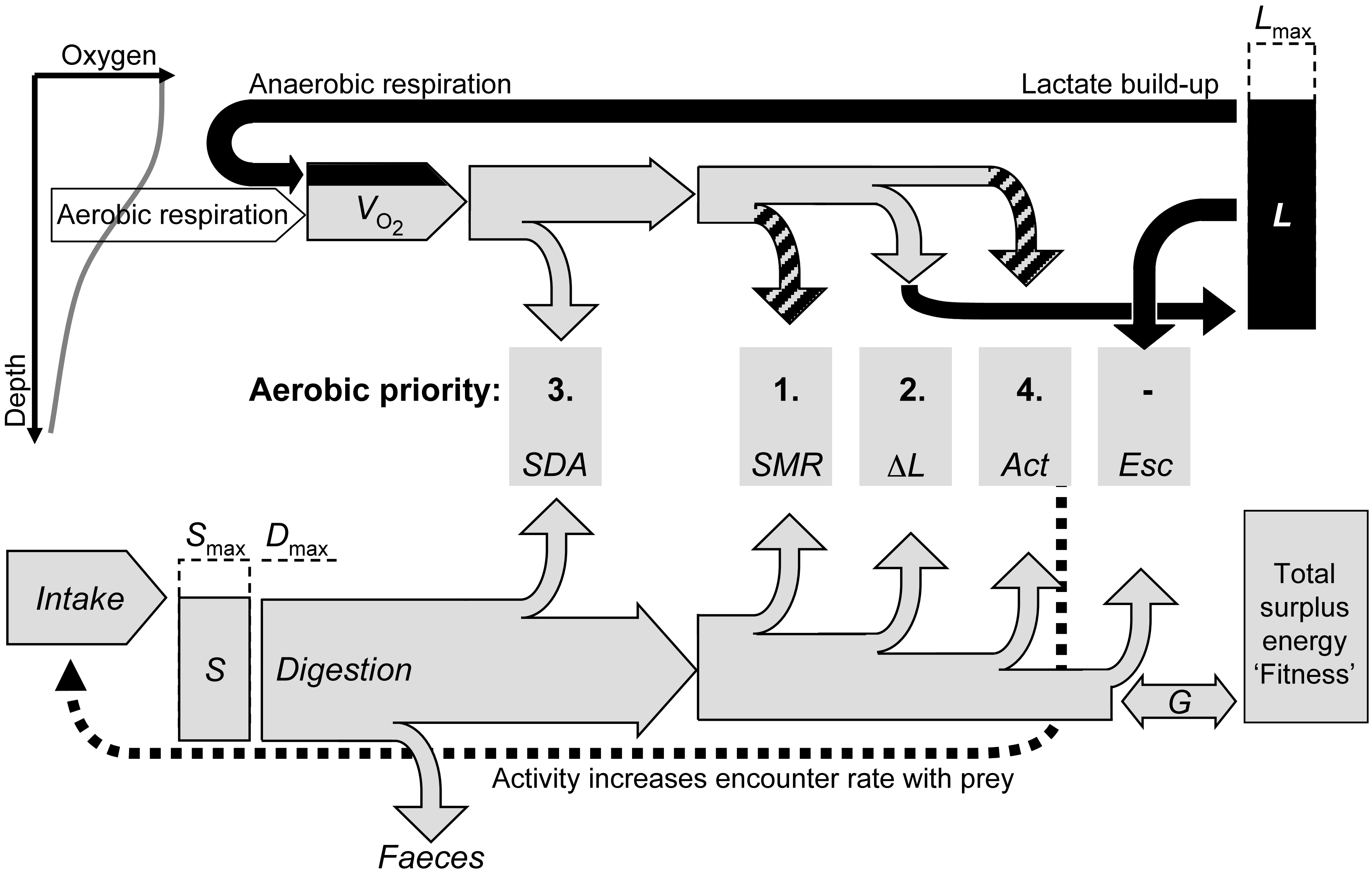
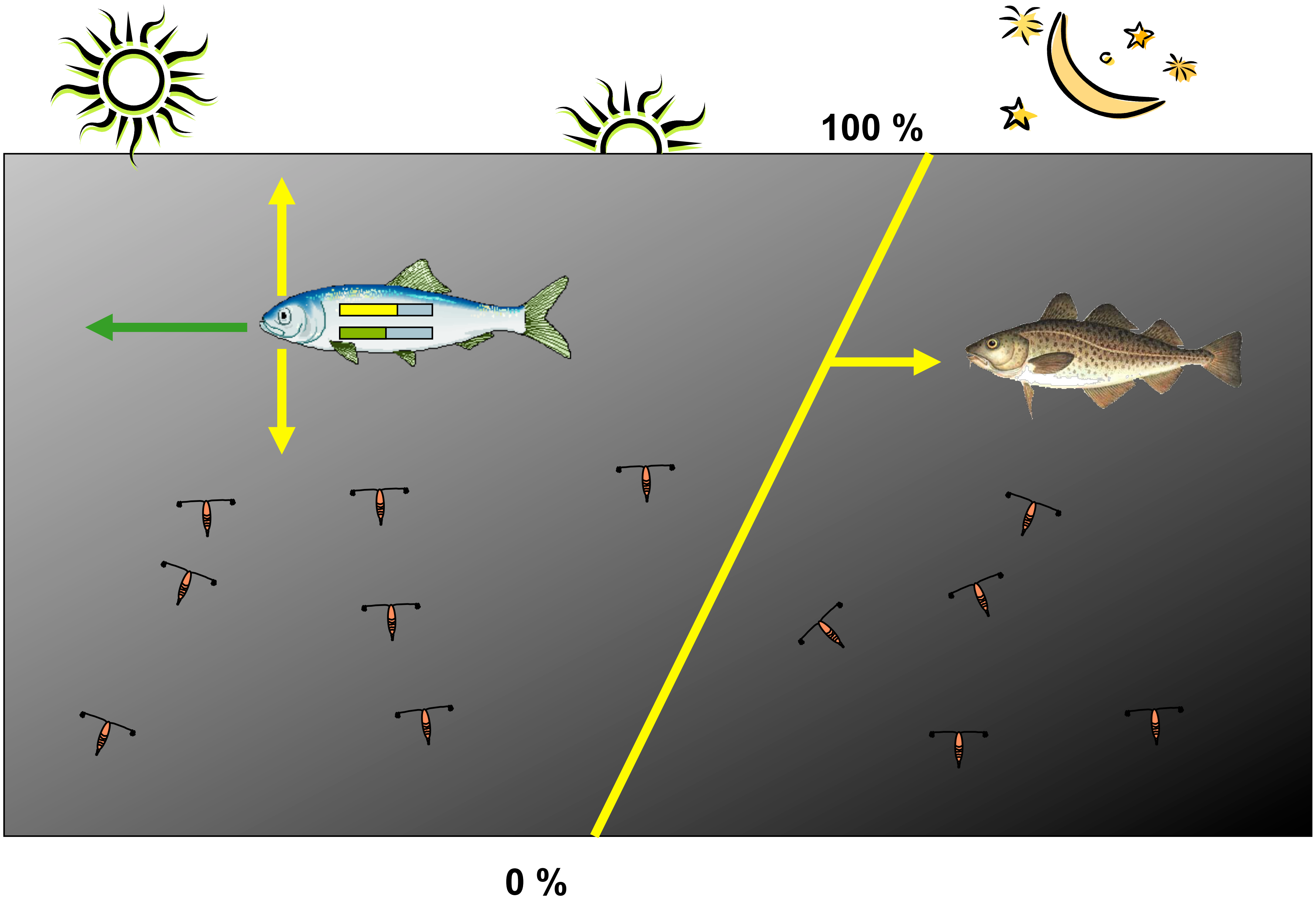


0
50
100
150
Depth (m)
00:00
06:00
12:00
17:59
23:5
Time
Oxycline
Bunnefjorden (Norway) in winter

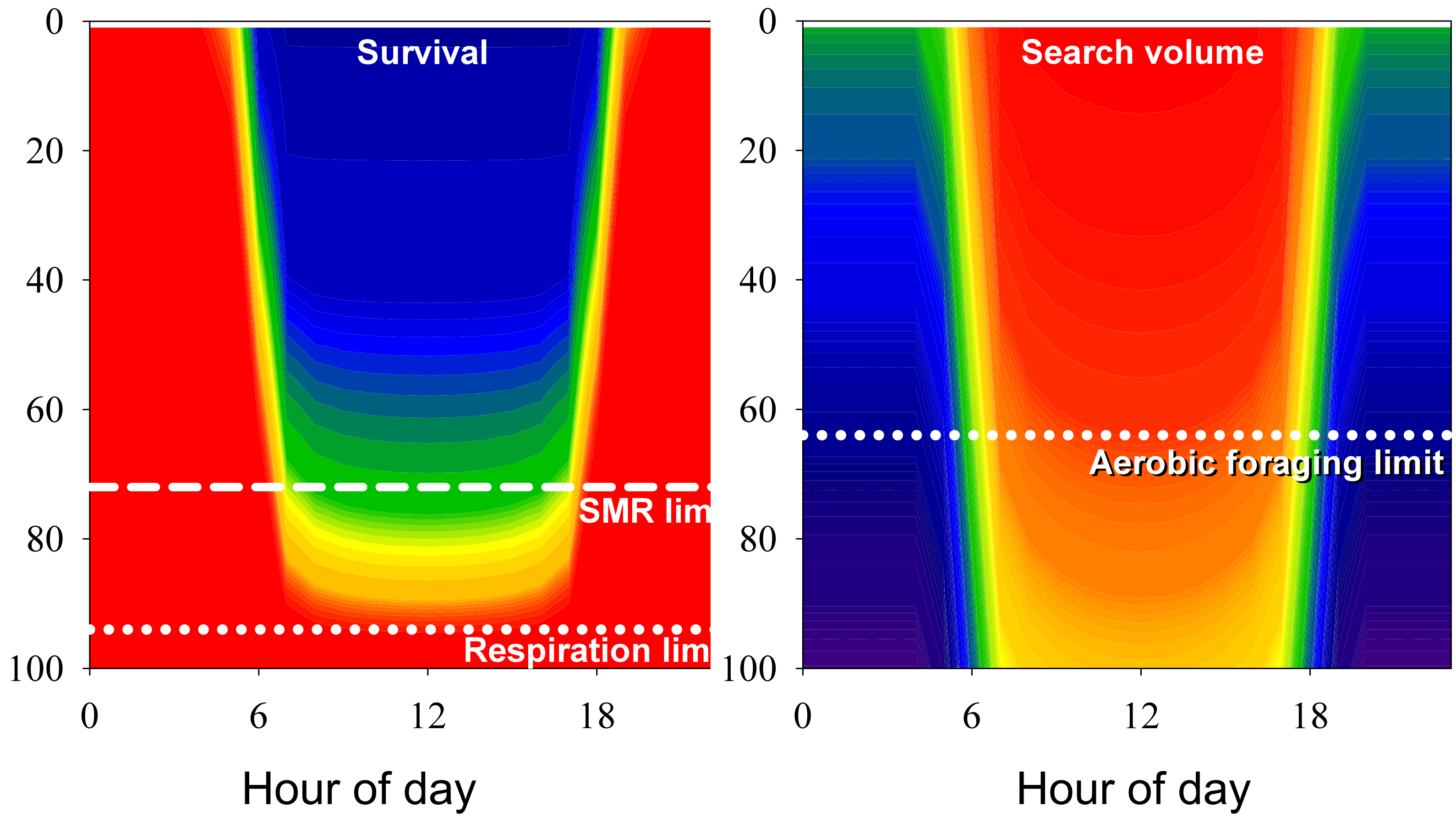
Energy and oxygen in bioenergetics



A model of fish in hypoxic gradients



Risk and foraging



Fitness and optimal behaviour

Fitness of state S, L in t

Fitness of new state in previous time-step given z and v

Energy gained in time-step

$$\Phi(S,L,t) = \max_{z,v} \sum_{k} P(k;z,v) P_e^k \left\{ \Phi[s',l',t+1] + d \cdot G(k,z,v) \right\}$$

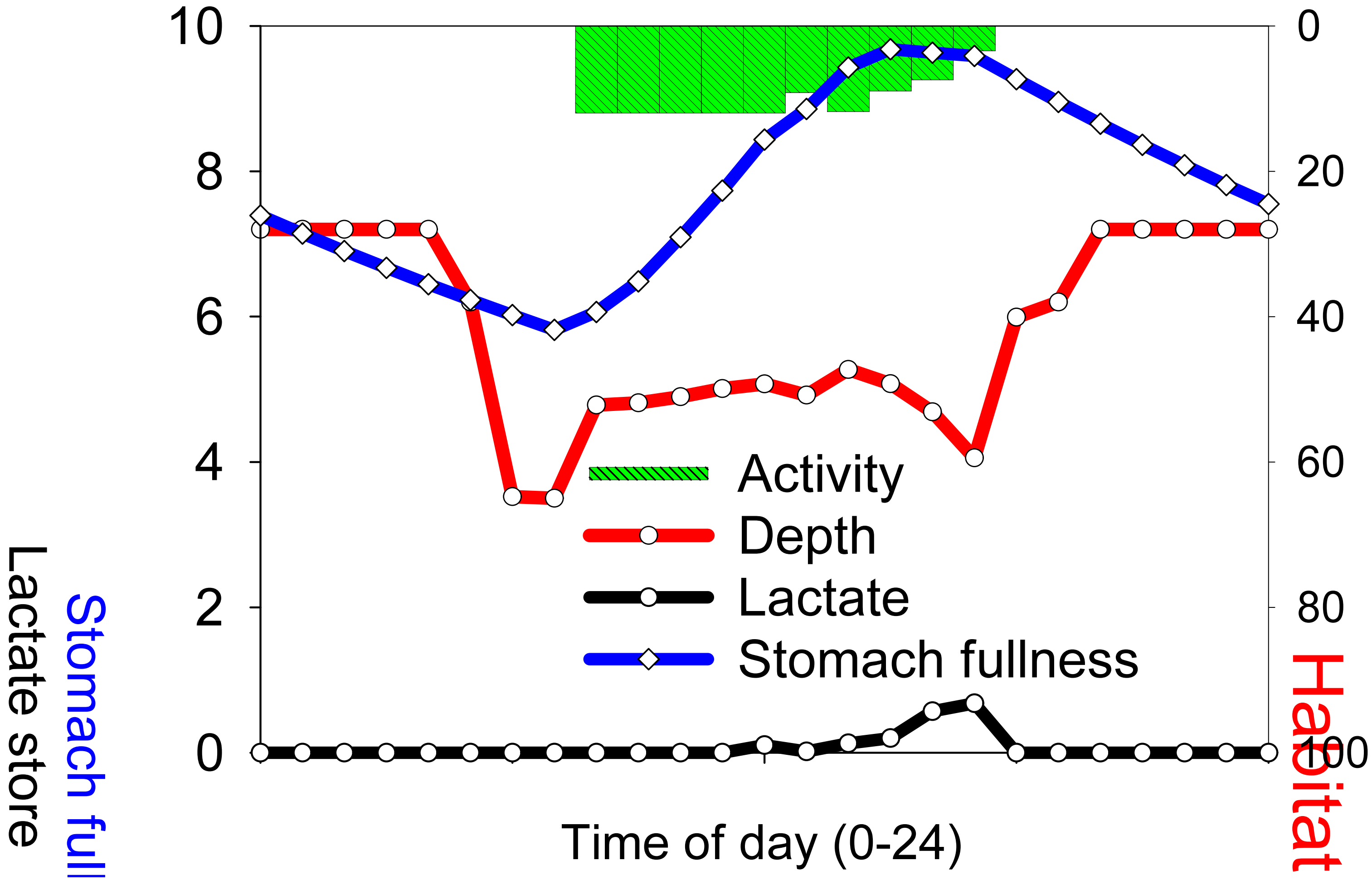
Probability of encountering k predators in unit time

Probability of surviving k predator encounter events

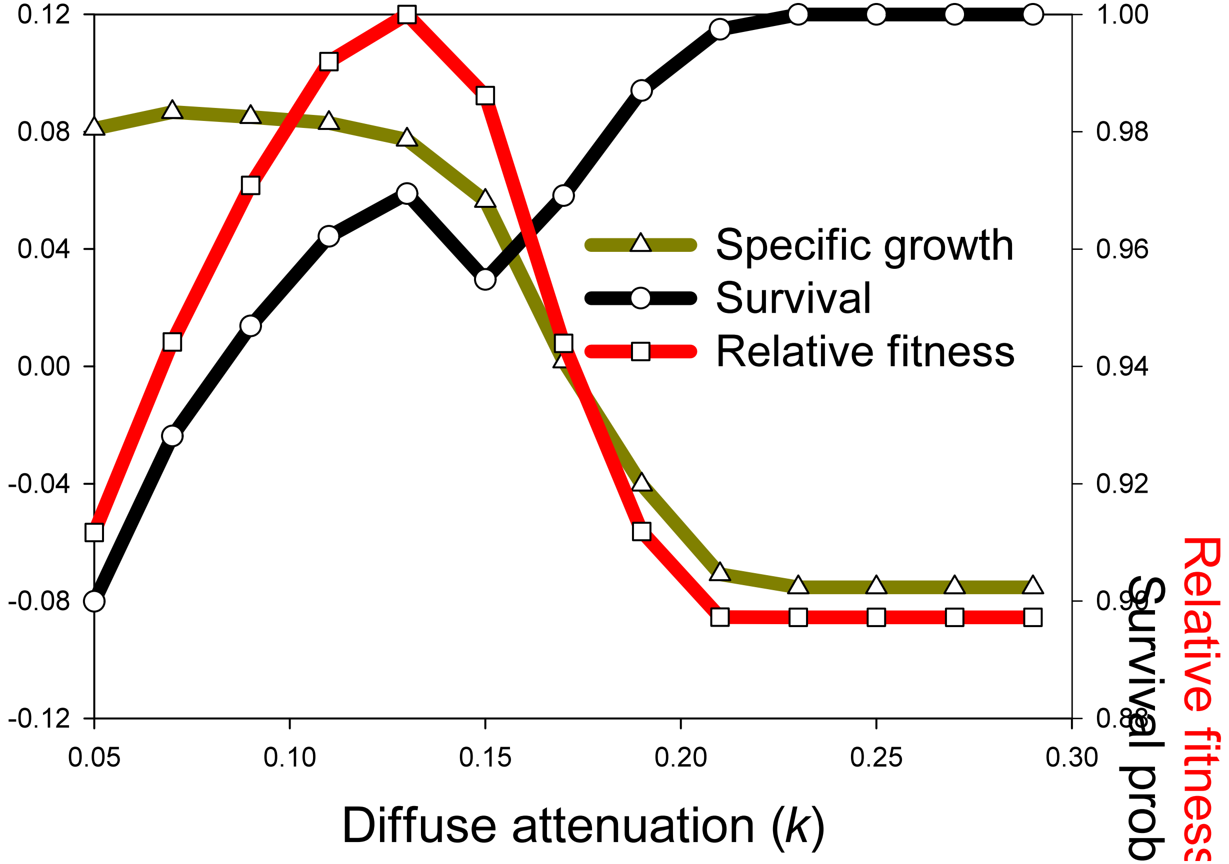
z*(S, L, t)

v*(S, L, t)

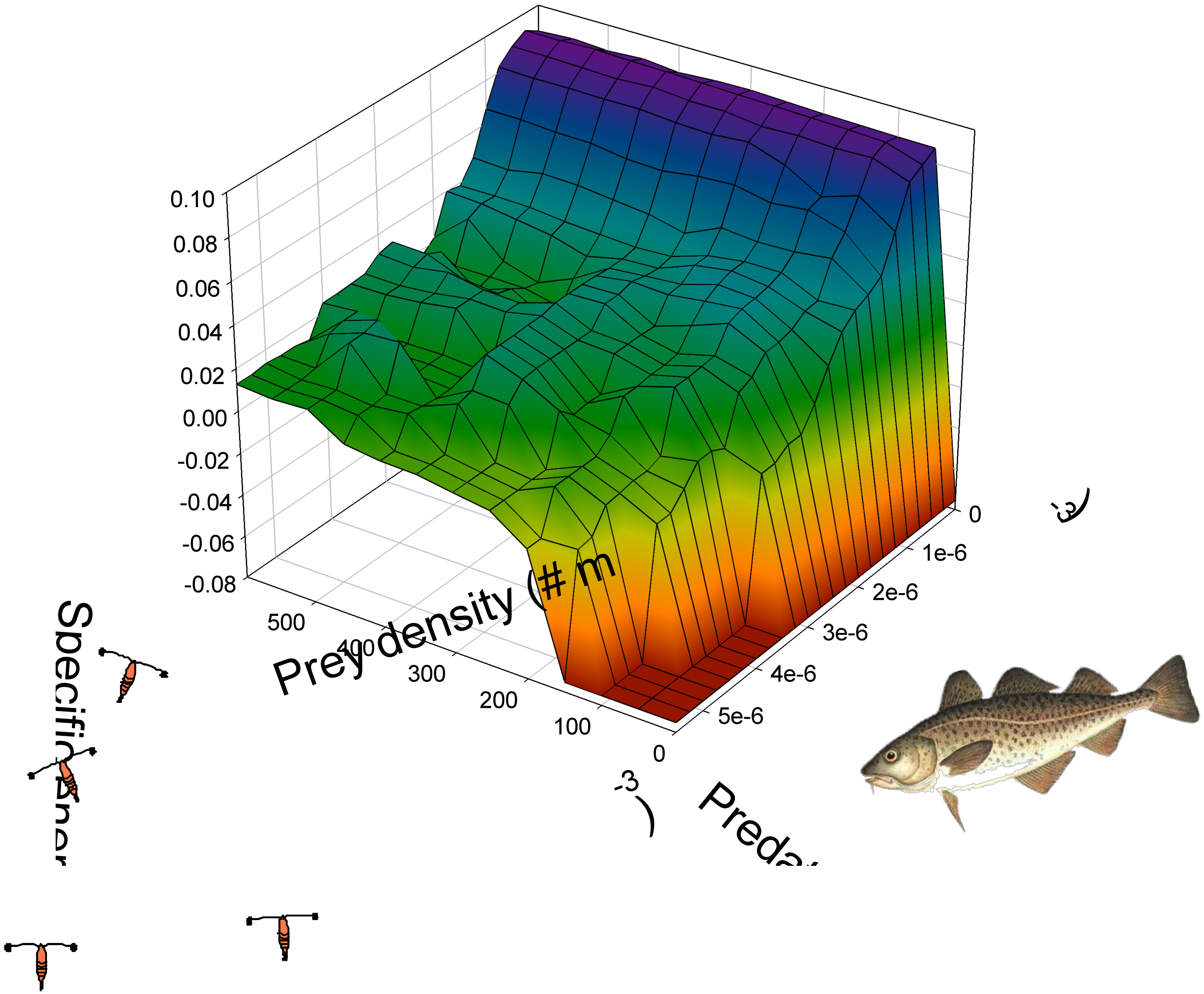
Optimal behaviour and states



Water clarity and fitness



Piscivores and zooplankton prey



Take home

- Mechanistic models
  - make trade-offs apparent
  - drive or guide experimental work
  - are useful to make sense of observations

- Optimality models
  - make clear predictions
  - suggests solutions to trade-offs
  - are particularly useful under state-dependence

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