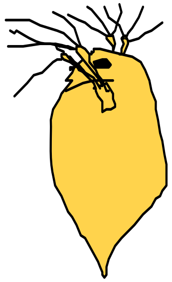
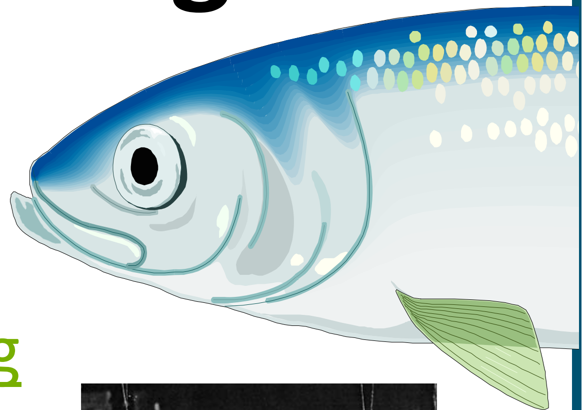
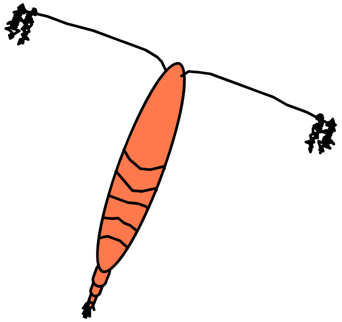


Optimality models of behaviour and life strategies





Øyvind Fiksen

University of Bergen

www.bio.uib.no/modelling

Øystein Varpe
Norwegian Polar Centre
Svalbard

Christian Jørgensen
Uni Research, Bergen

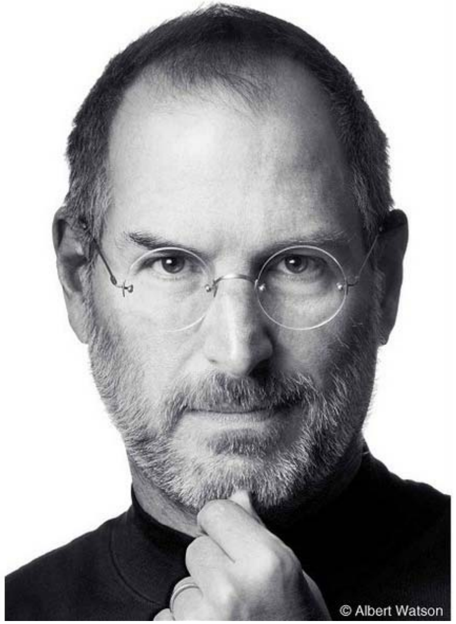
Anders F Opdal
Uni Research, Bergen

www.bio.uib.no/te

Computers..

"So we used them in our work, but...much more importantly... it had nothing to do with using them for anything practical. It had to do with...to be a mirror of your thought process, to actually learn how to think..
I think everybody in this country should learn how to program a computer, should learn a computer language, because it teaches you how to think."

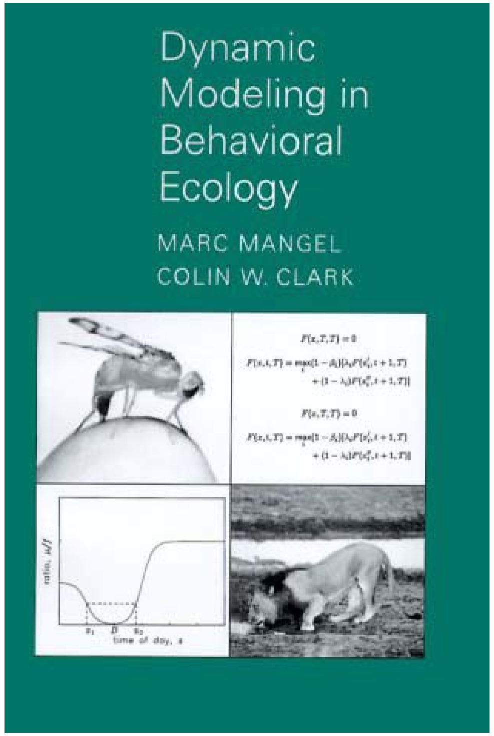
- Steve Jobs, 1995

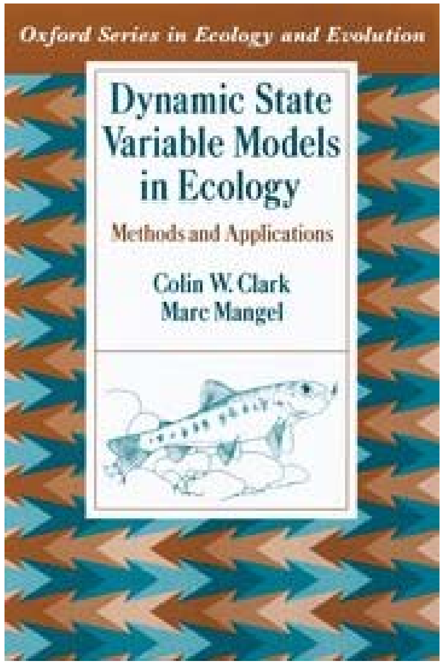


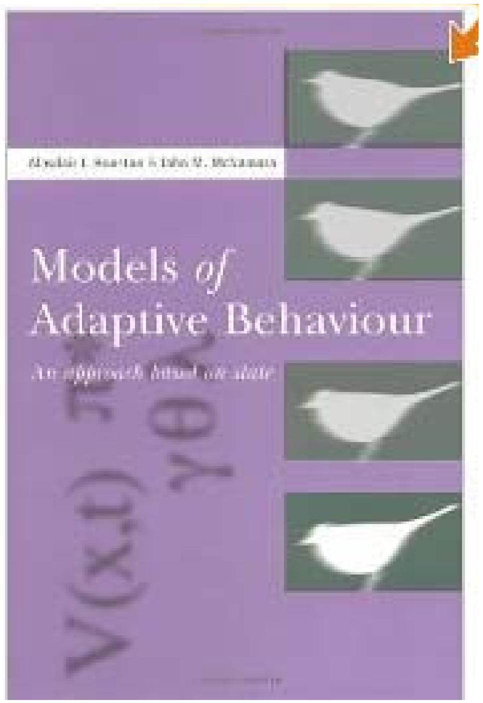
Optimality theory

- Strategy or decision – which traits are optimized
- Currency – what is maximized, or ‘fitness’ measure
- Constraints – what are the limits and trade-offs
- States – what are the relevant attributes

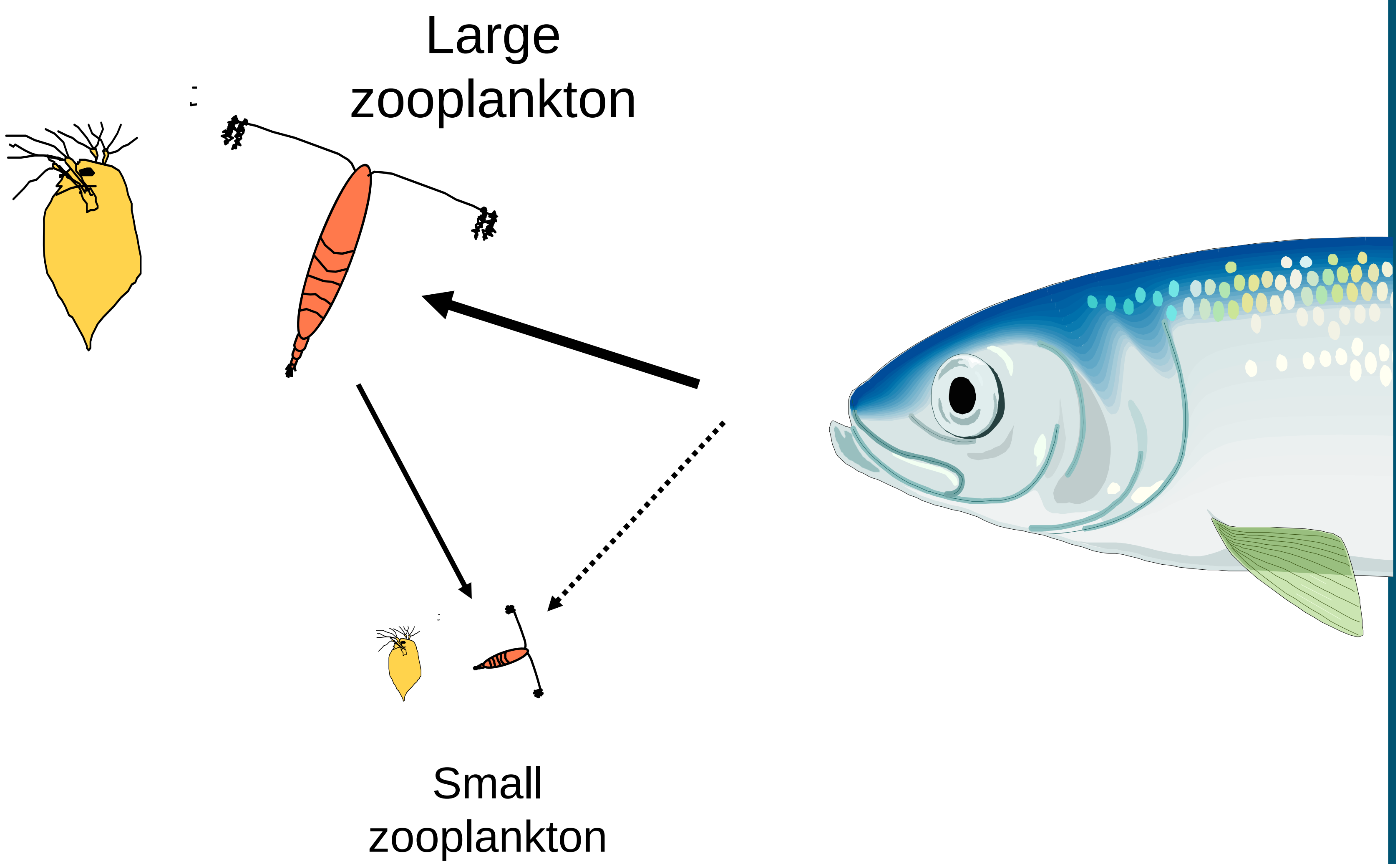
Dynamic programming
State-variable models



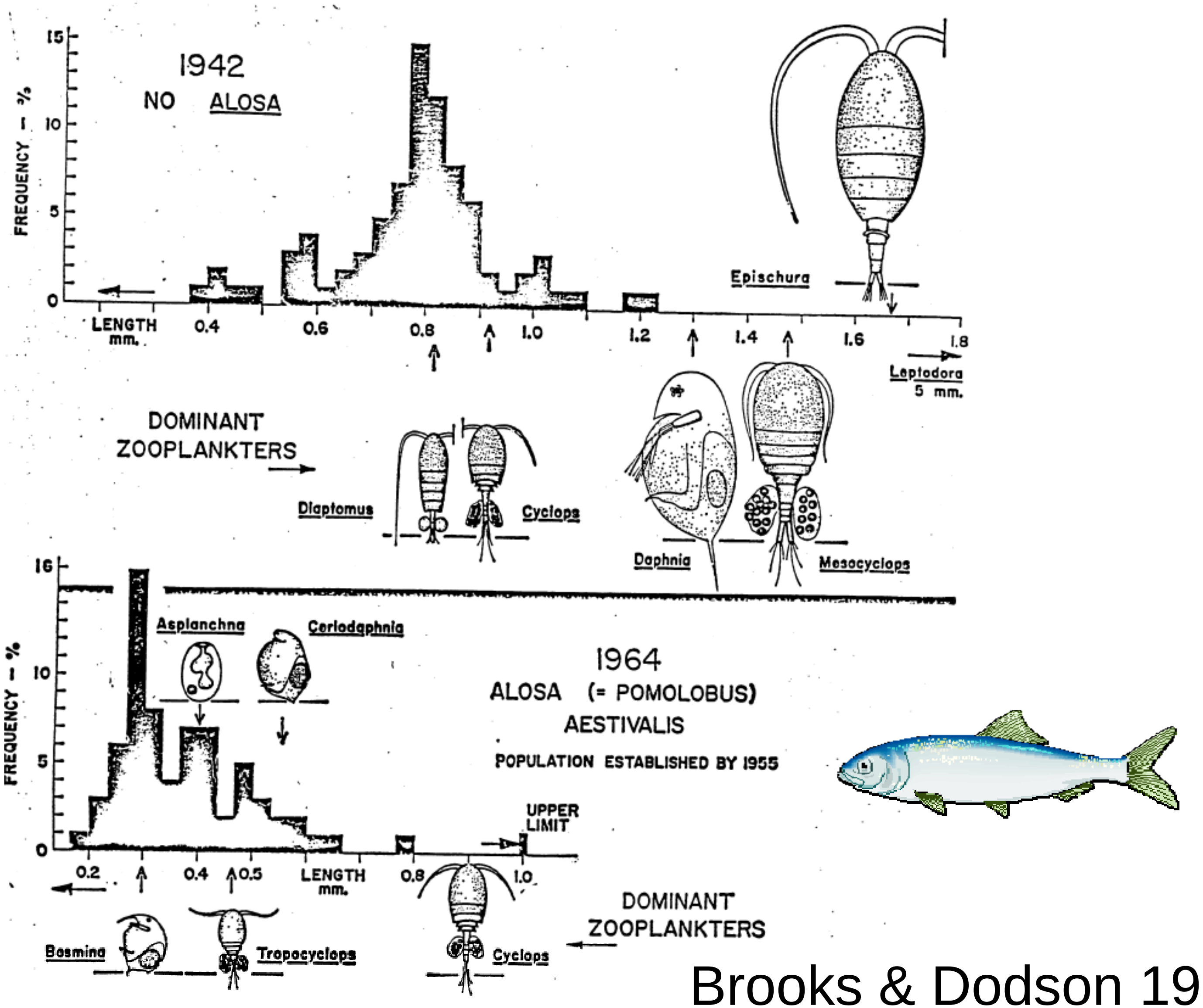




Fish-plankton interaction primer..

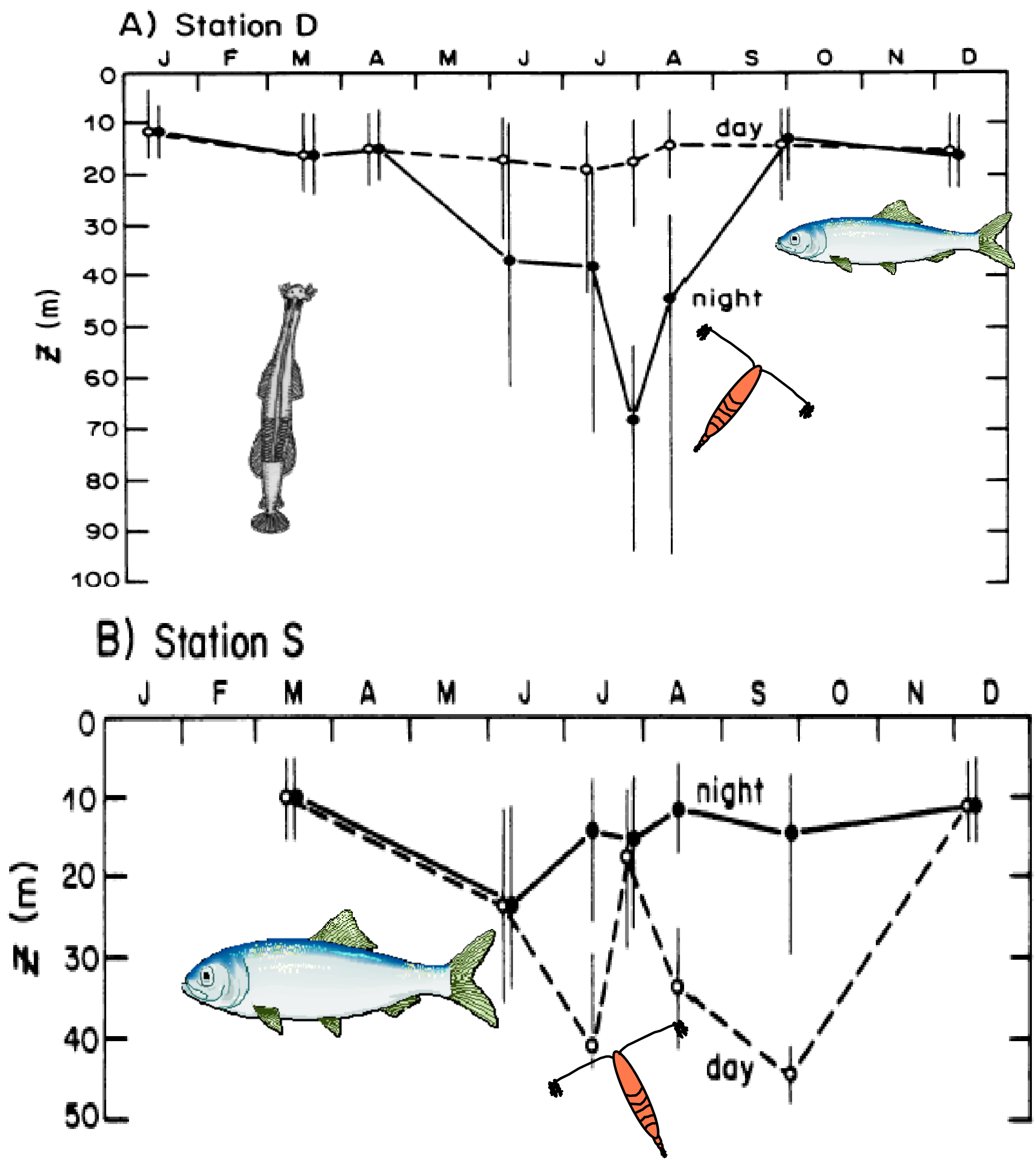


Fish can structure plankton communities



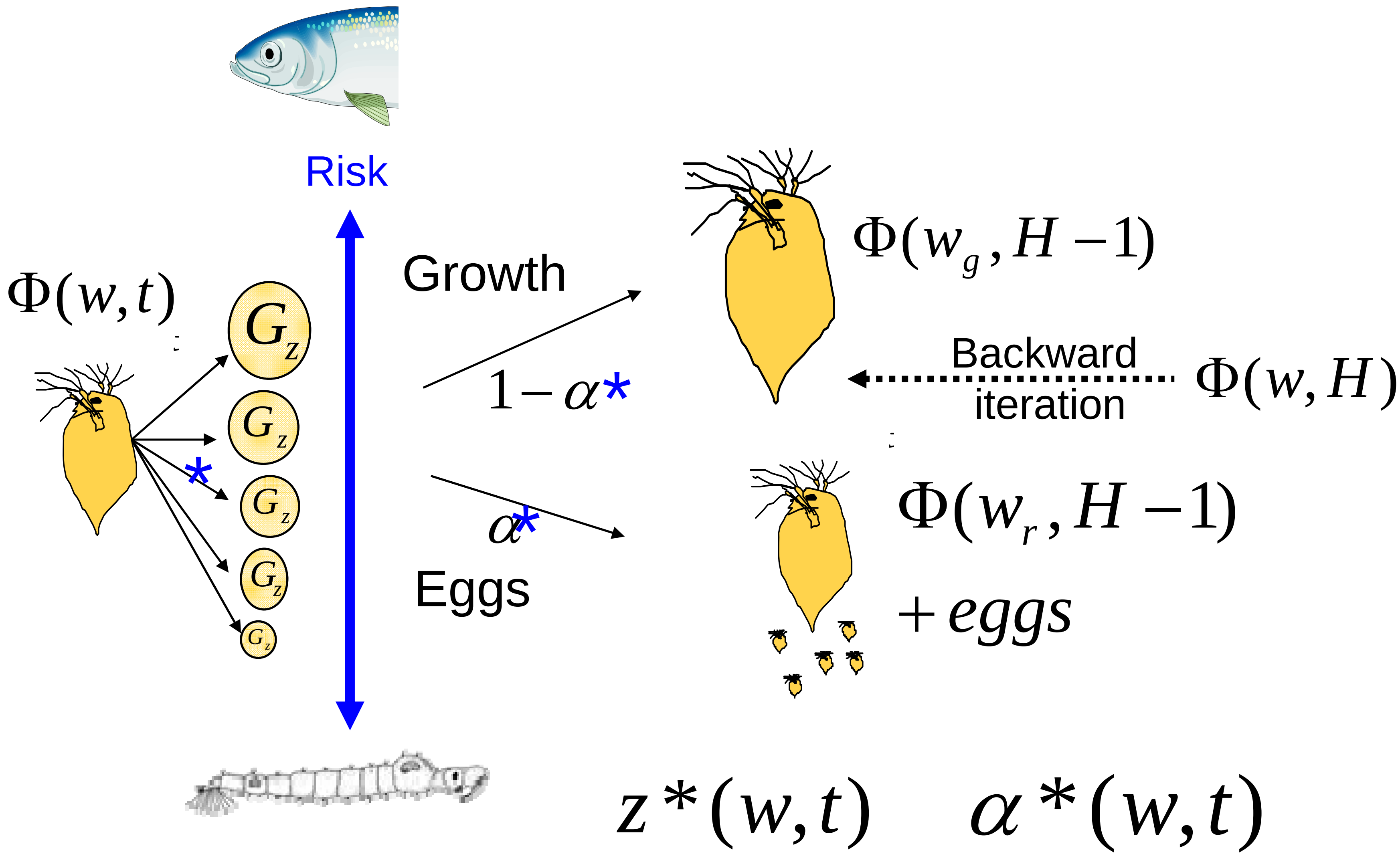
Brooks & Dodson 1965

Plastic behaviour – also in marine zooplankton



Ohman 1990

Optimal habitat selection and allocation of energy by dynamic programming..



The dynamic programming equation

Maximise fitness = find the behavioural and life history decision that maximises the sum of current and expected future reproduction:

Fitness (size, time)

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

Survival

Eggs

Future fitness (new state, time)

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

The dynamic programming equation for seasonal environments

Maximise fitness = find the behavioural and life history decision that maximises the sum of current and expected future reproduction:

Fitness (size, time)

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

Survival | Eggs | Egg fitness at t+1 | Future fitness (new state, time)

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

Computer pseudo-code

```
DEFINE TERMINAL FITNESS(STATE,H)

DO TIME = H-1, 1, -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,T+1) + REPRODUCTION]

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

      ENDDO ALLOCATION
    ENDDO HABITAT
  ENDDO STATE
ENDDO TIME
```

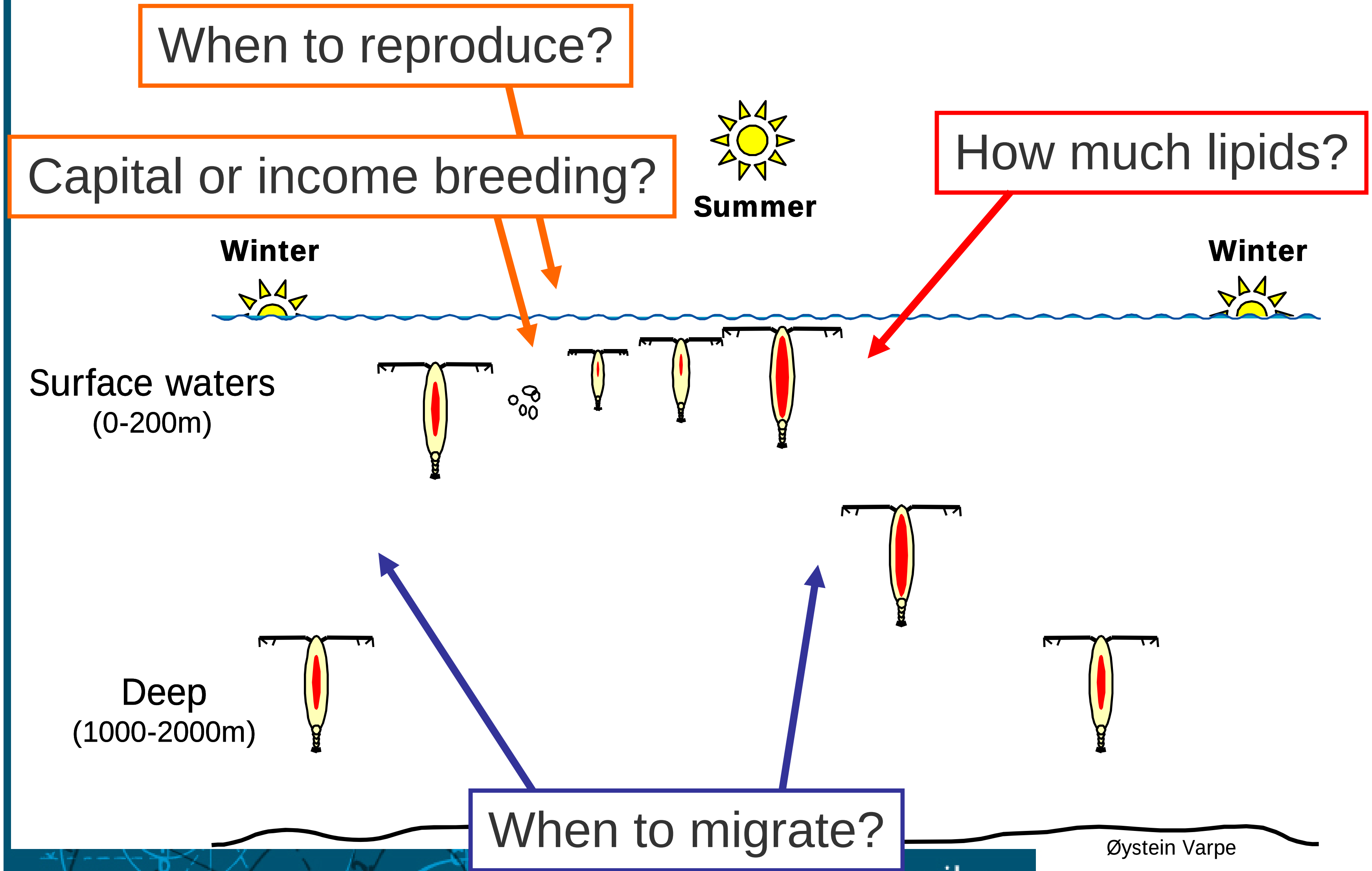
Loop over time, state, and decisions

State dynamics (physiology)
&
mechanics

Evaluate consequences of actions
in terms of fitness and store the best


Photo: Malin Daase

Seasonal migrations in *Calanus* – the annual routine



Optimal Life History by Dynamic Programming

Fitness of an optimal individual at time t

Residual RV given LH-decisions

$$V(x,y,z,t) = \max_{\alpha,\varepsilon,\sigma} \left\{ P_s(y,z,t) \cdot \left[\begin{matrix} V\left(x_{t+1}, y_{t+1}, z_{t+1}, t+1 \middle| \alpha, \varepsilon, \sigma\right) \\ + b(G, y, \varepsilon) \cdot V_{young}(1, t+1) \end{matrix} \right] \right\}$$

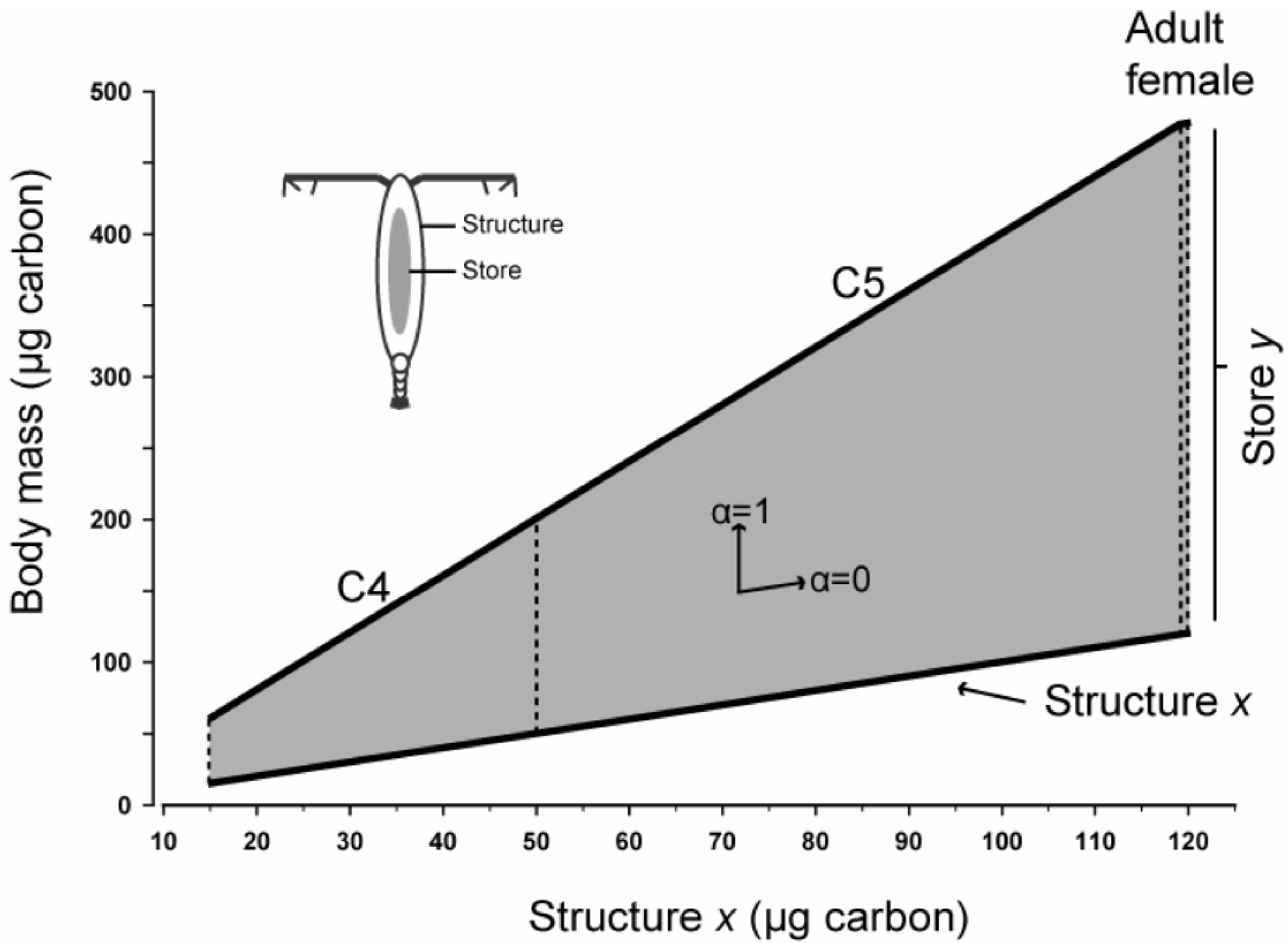
Survival probability

Fecundity

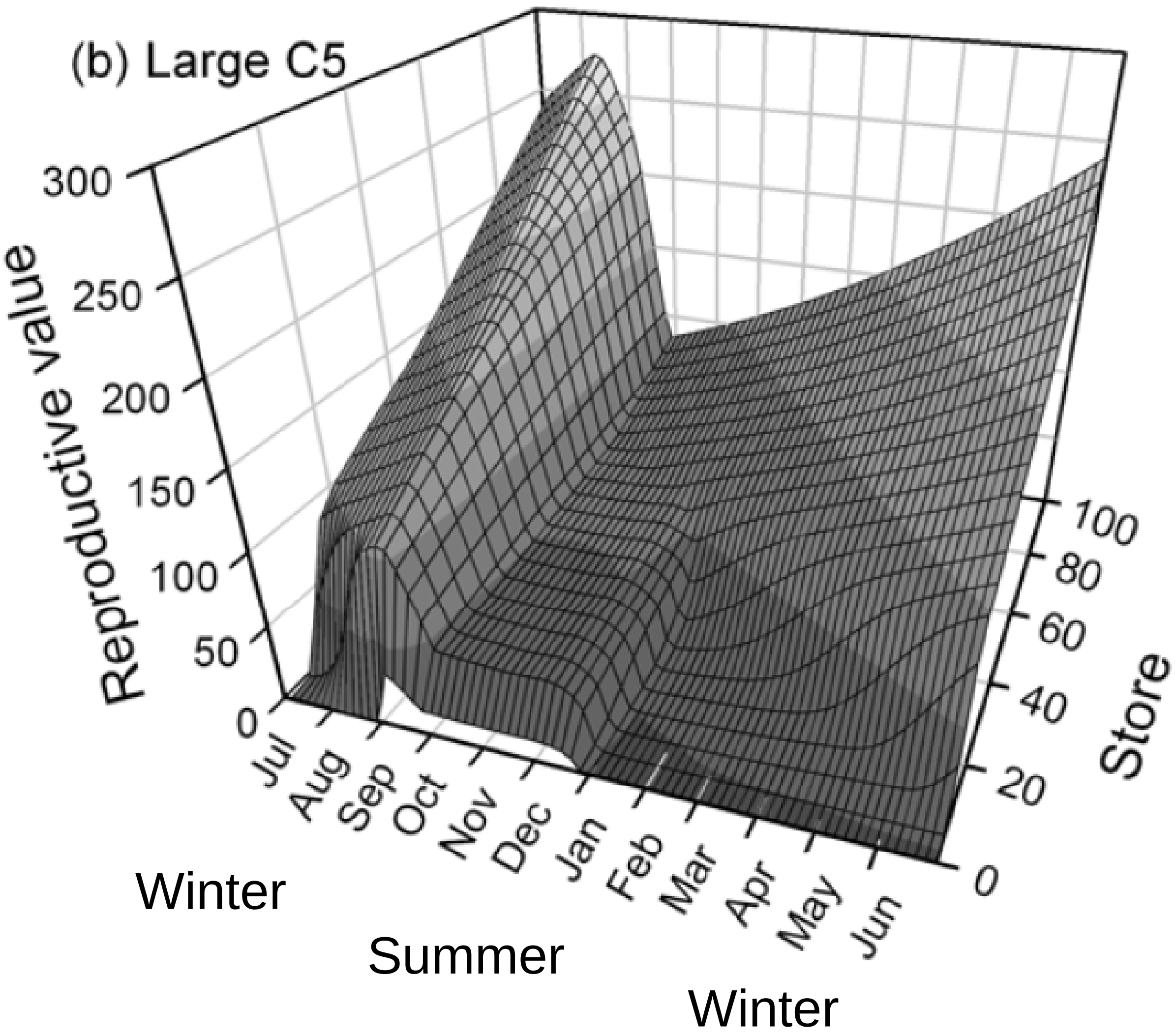
R_0 – fitness of an egg at time t+1

Varpe, Jørgensen, Tarling and Fiksen. (2007). Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos* 116:1331-1342.

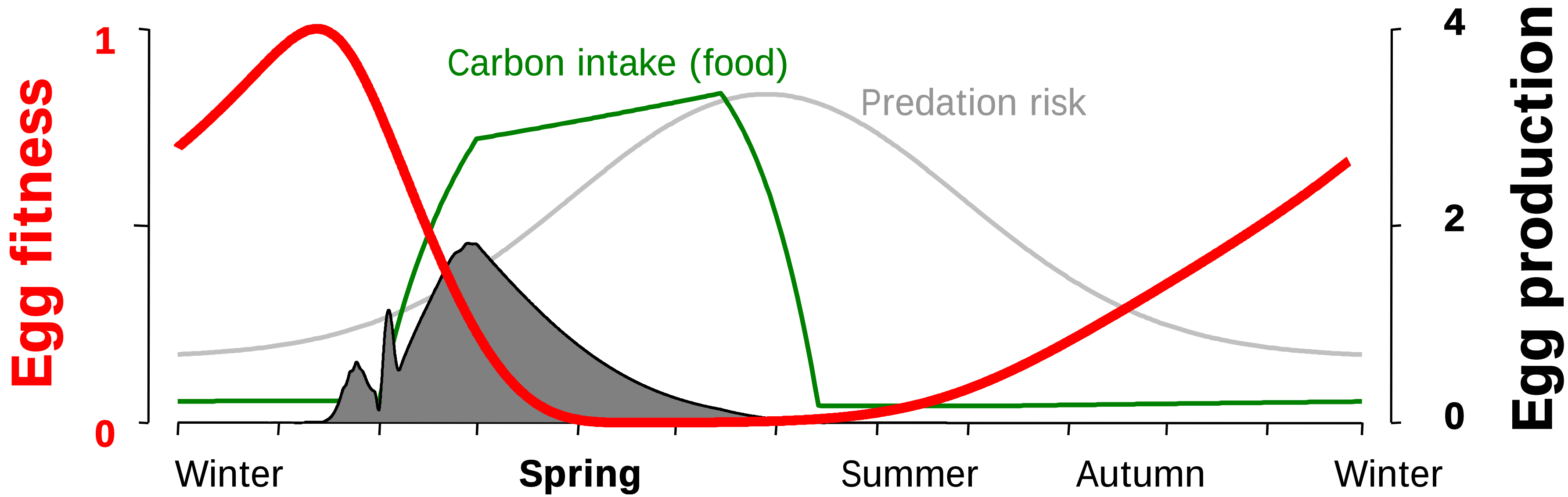
Energy allocation and state space



Fitness as a function of state and time

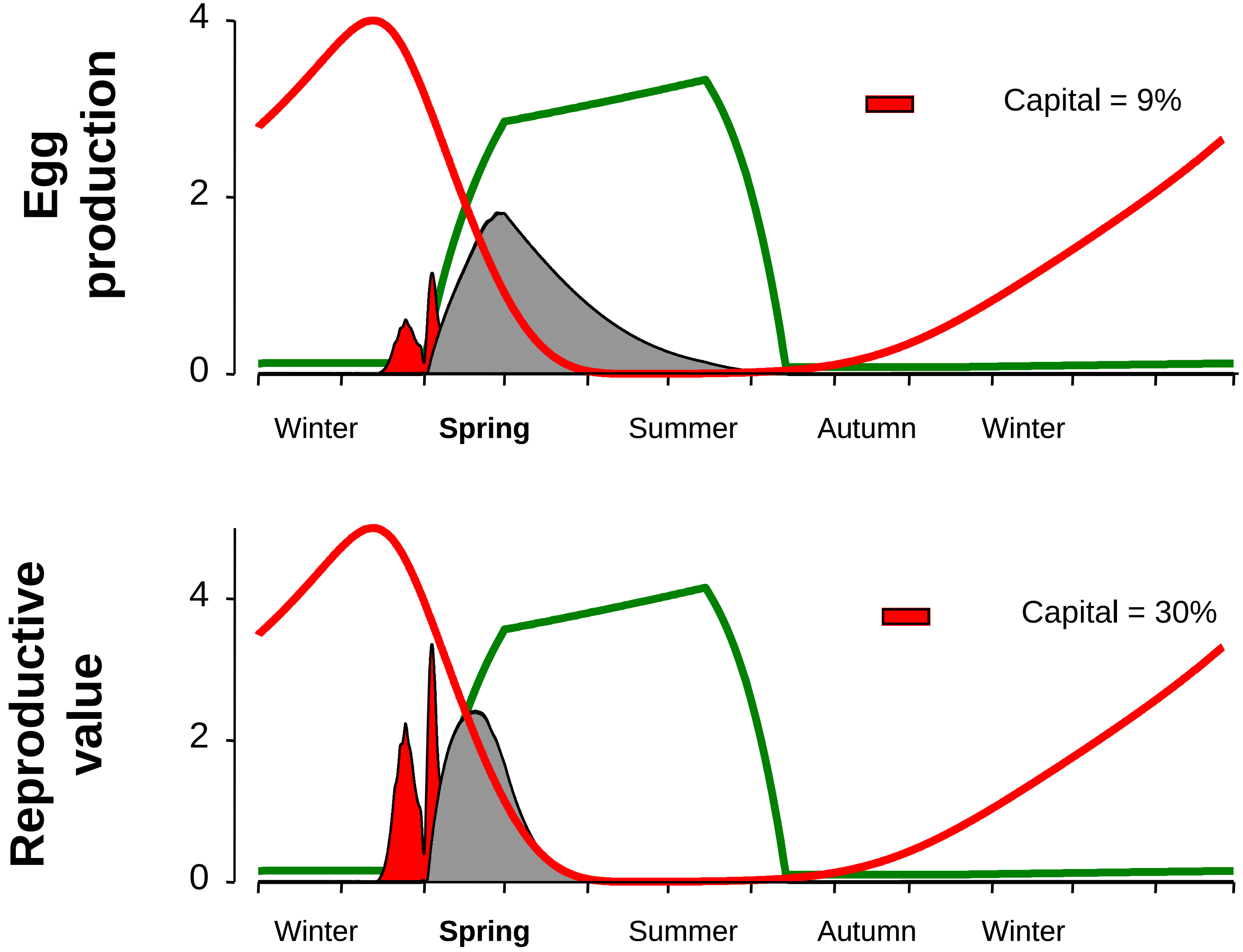


Egg fitness and population egg production



Varpe, Jørgensen, Tarling and Fiksen. (2007). Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos* 116:1331-1342.

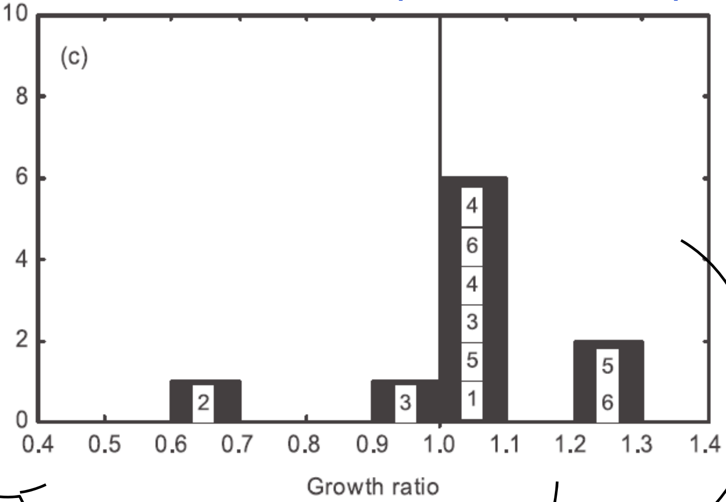
Capital and income breeding

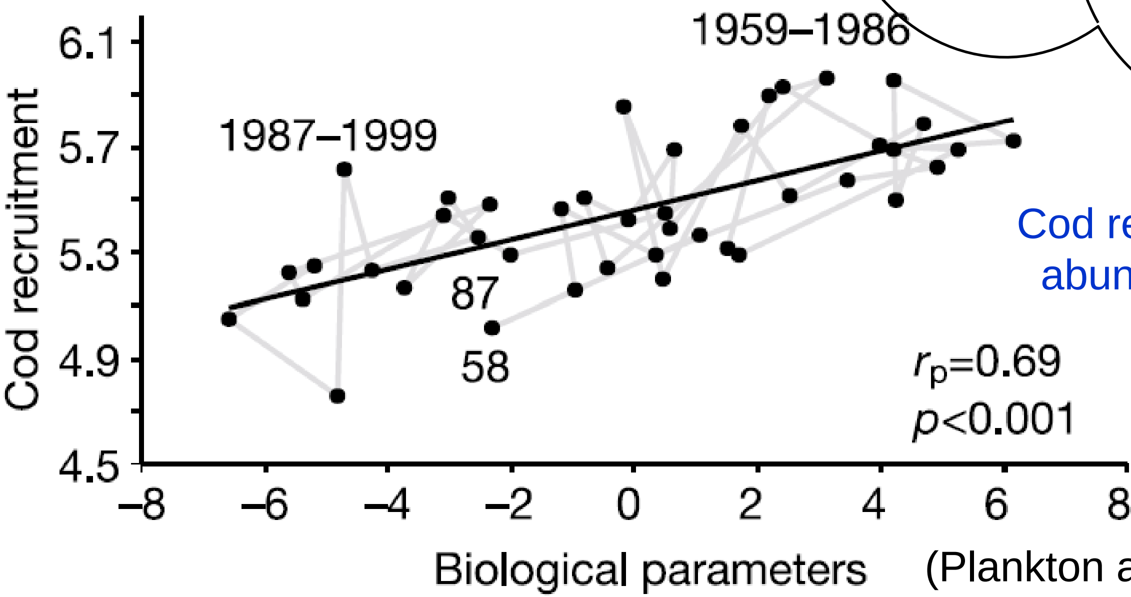


Ø Varpe, C Jørgensen, G. A. Tarling and Ø. Fiksen. (2009). The adaptive value of capital breeding in seasonal environments. *Oikos 118: 363-370.*

Larval behaviour and an apparent contradiction

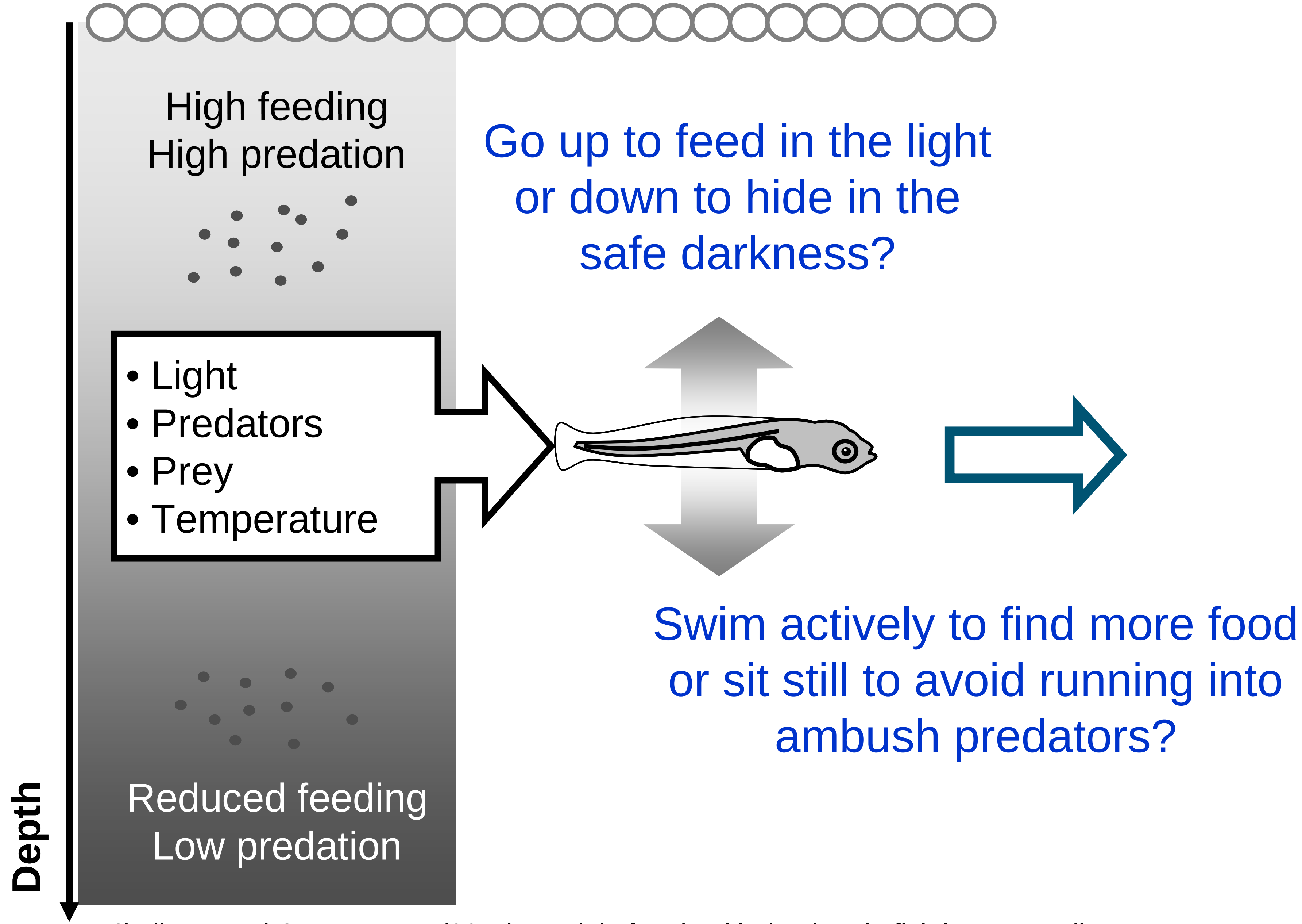
Larval cod tend to grow at maximum rates in the field (Folkvord 2005)





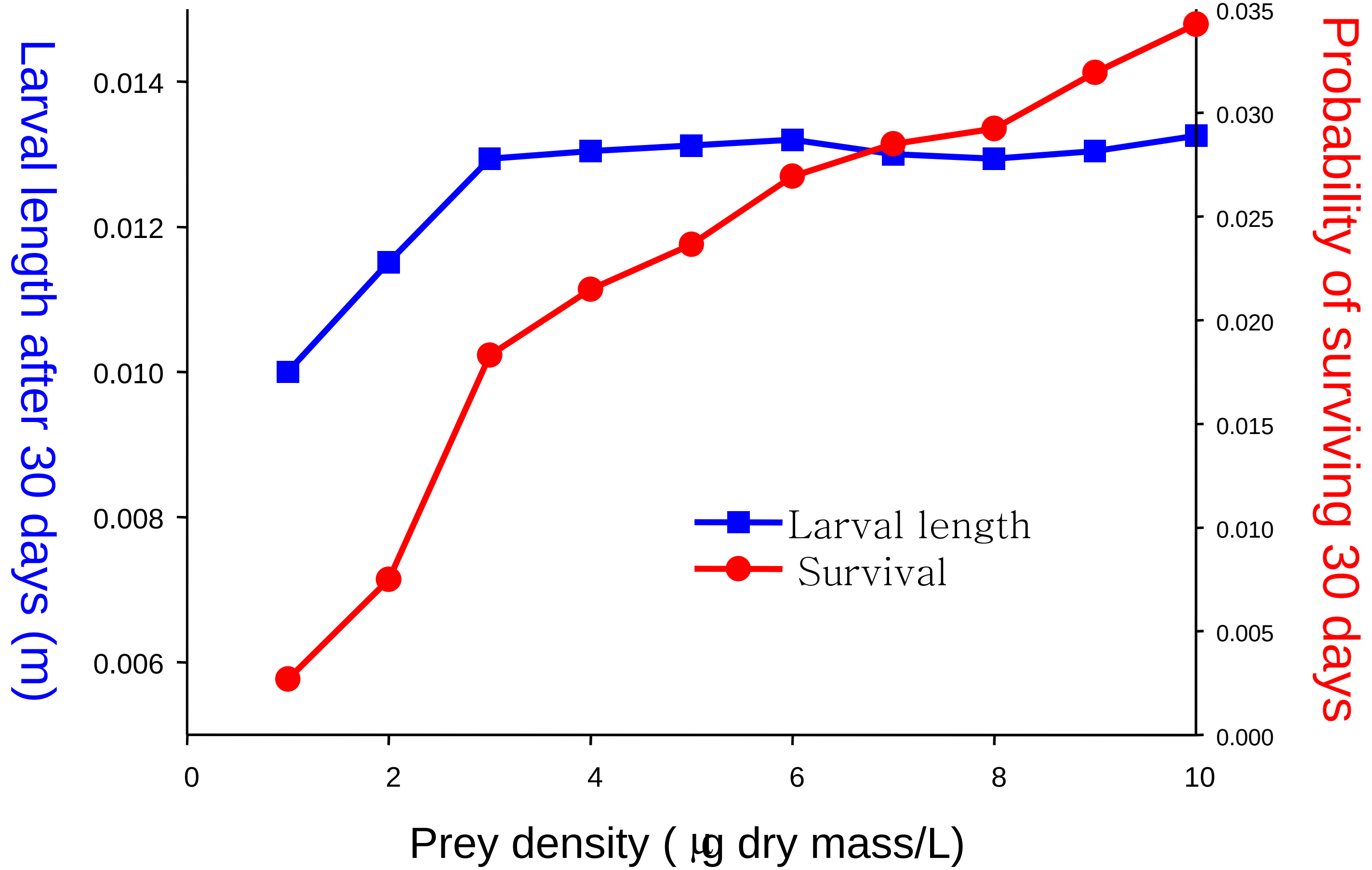
(Plankton abundance)

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

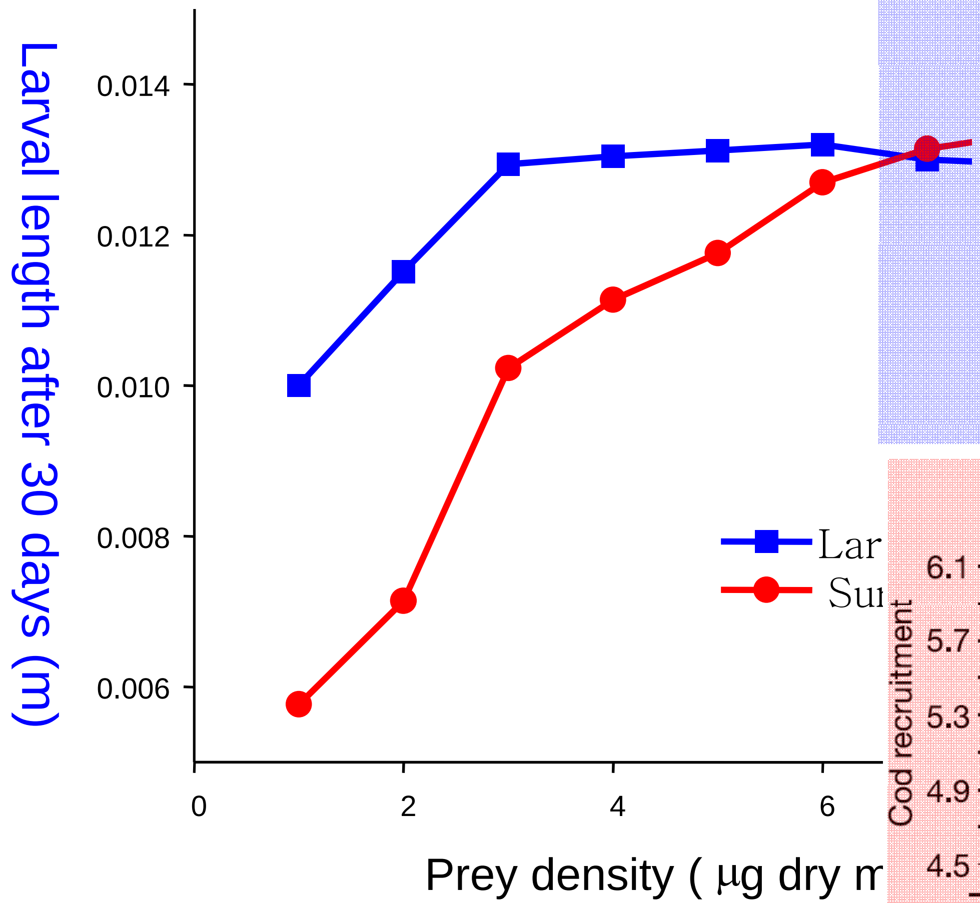


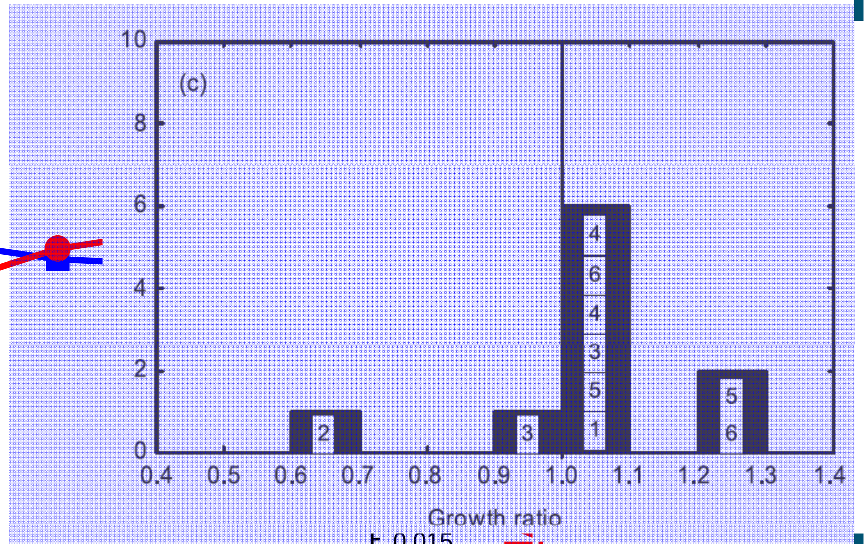
Ø Fiksen and C Jørgensen (2011). Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. *MEPS*. 432:207-219.

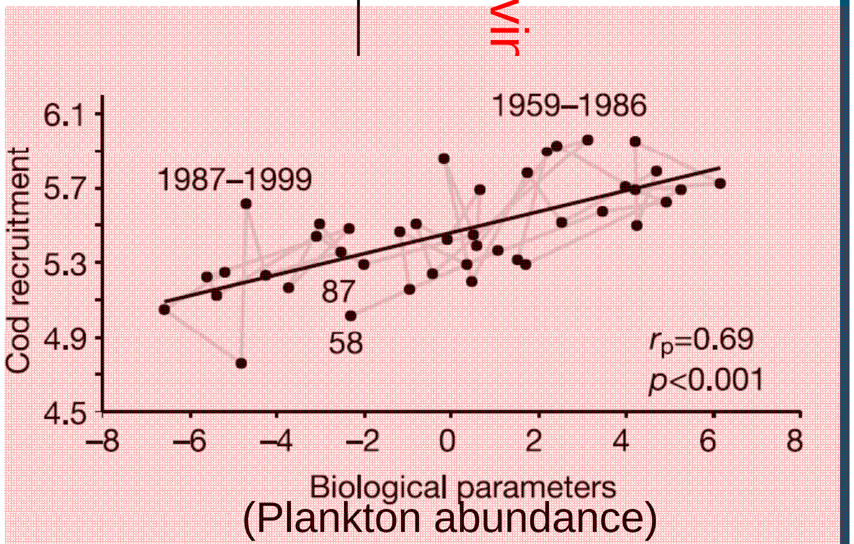
Prey density and recruitment success

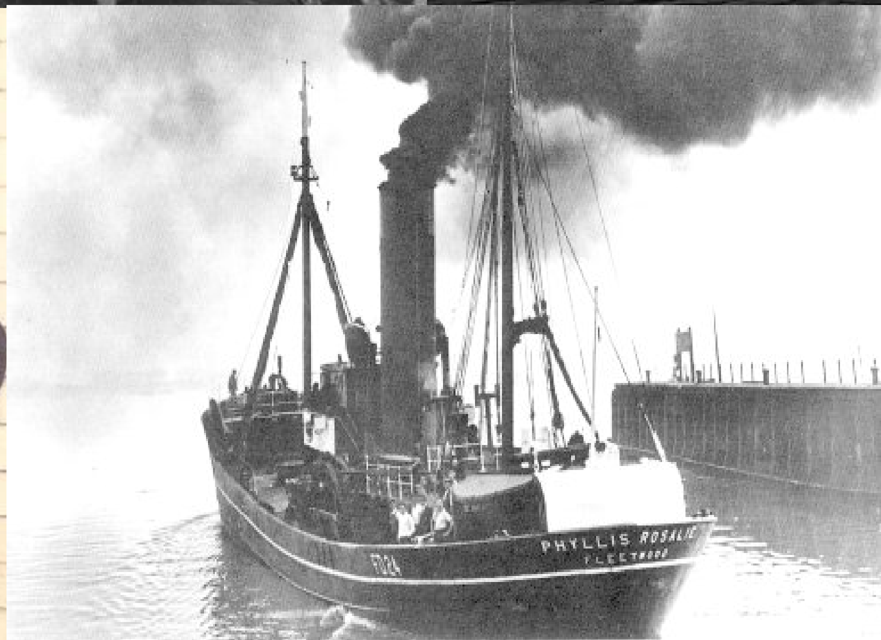


Prey density and recruitment success

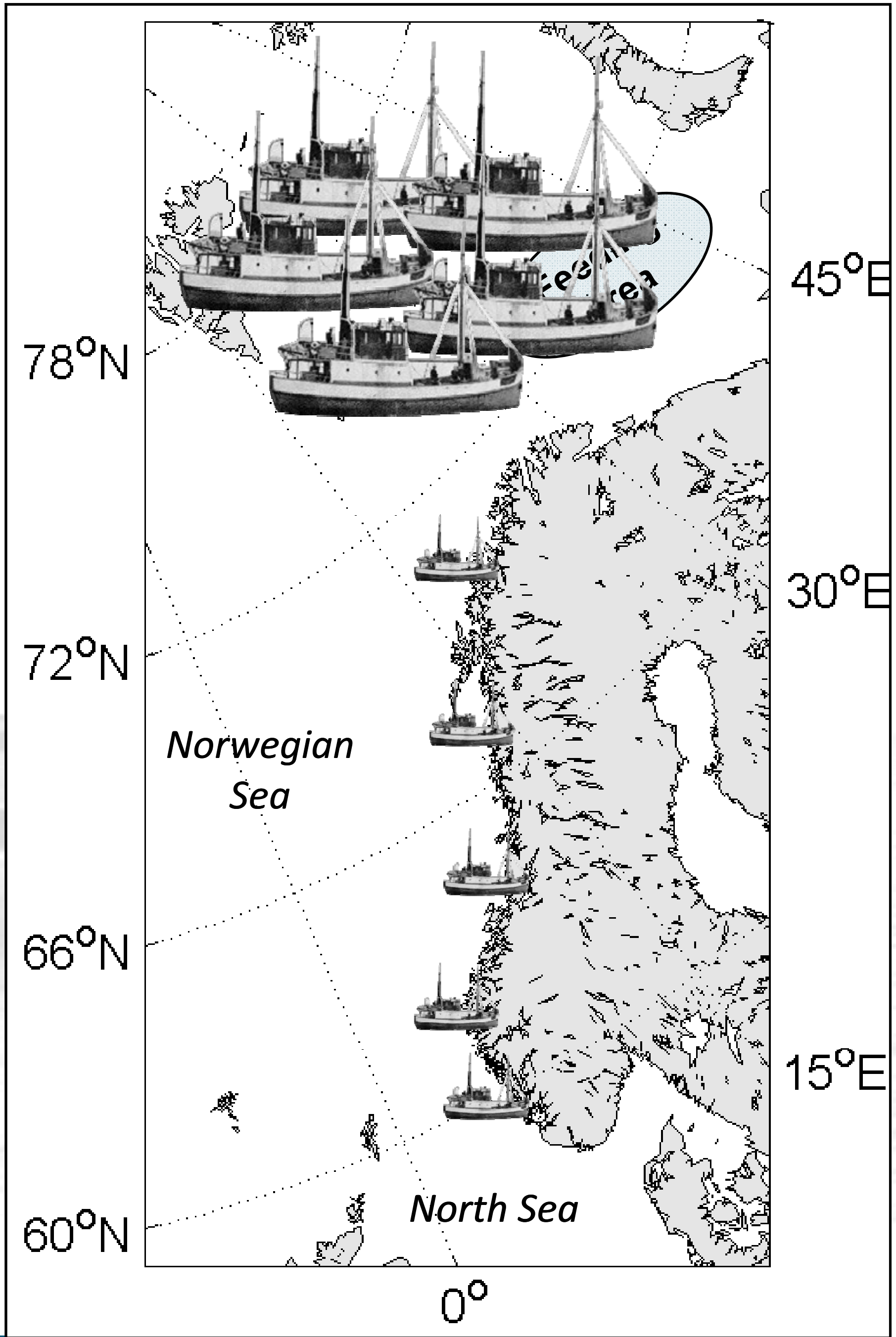




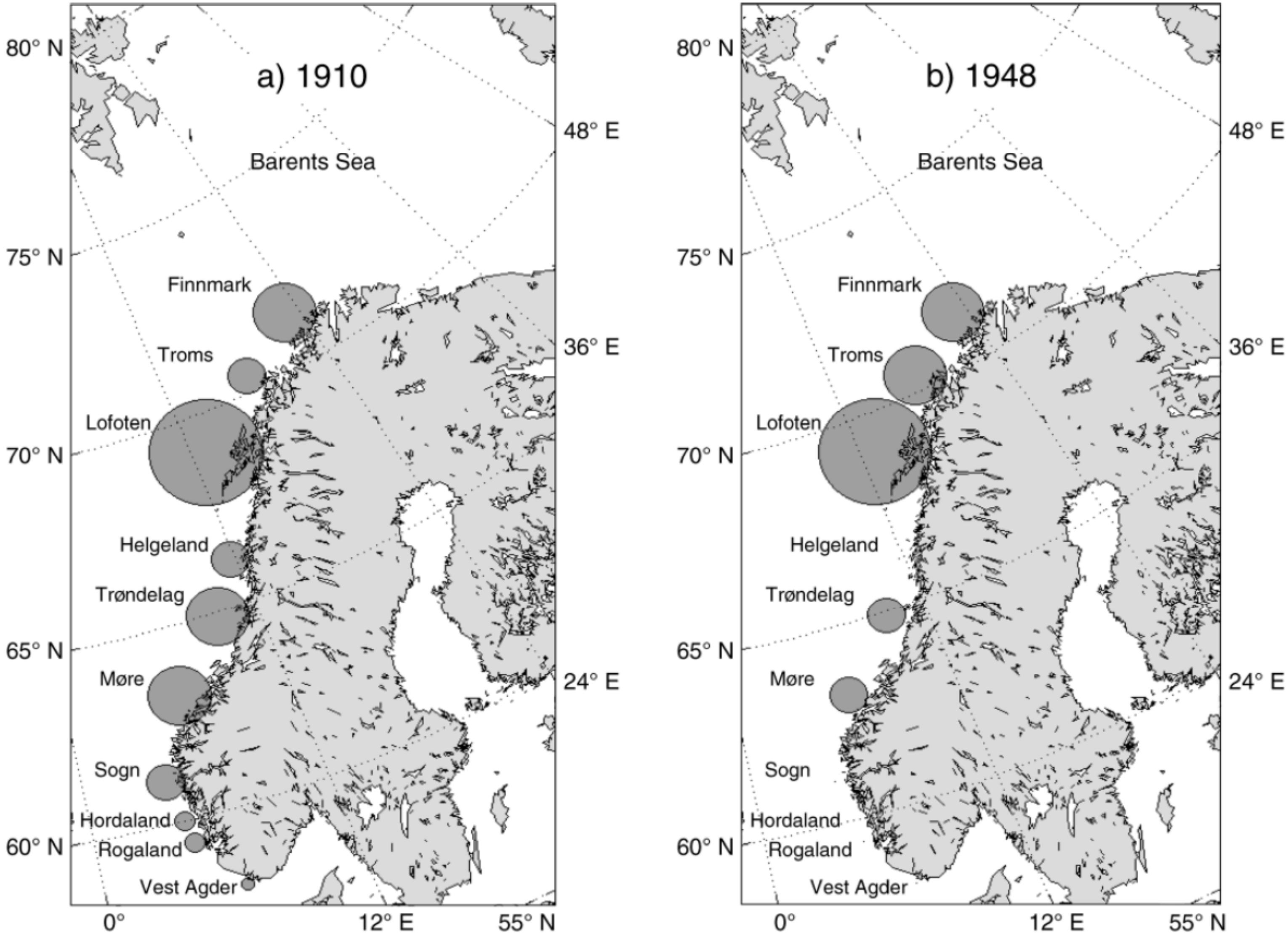



PHYLLIS ROSALIE
FLEETWOOD

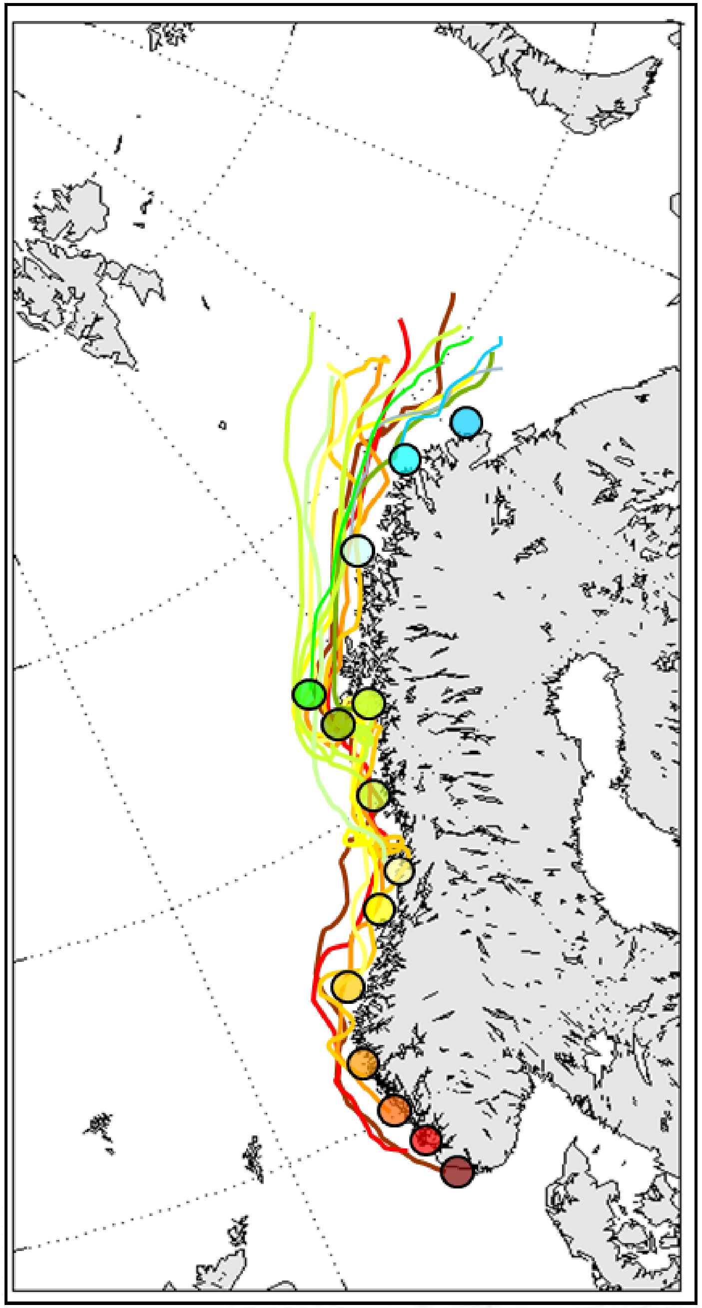
- **Before the 1920s, fishing was conducted at the spawning grounds**
- **In the early 1920s, trawl-fishing started in the Barents Sea**
- **Fishing intensity in the Barents Sea increased rapidly within a few years**

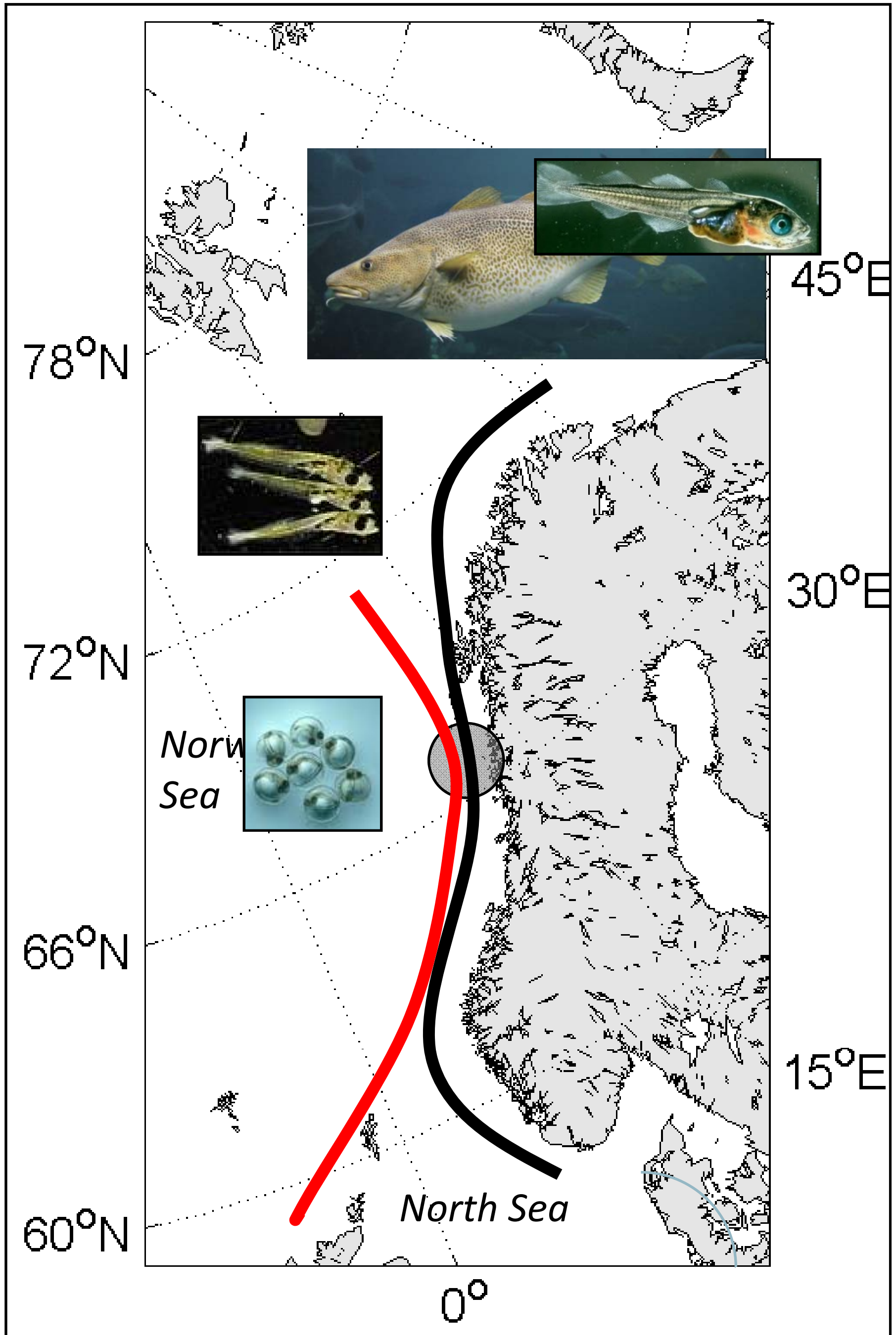


Historic spawning distributions

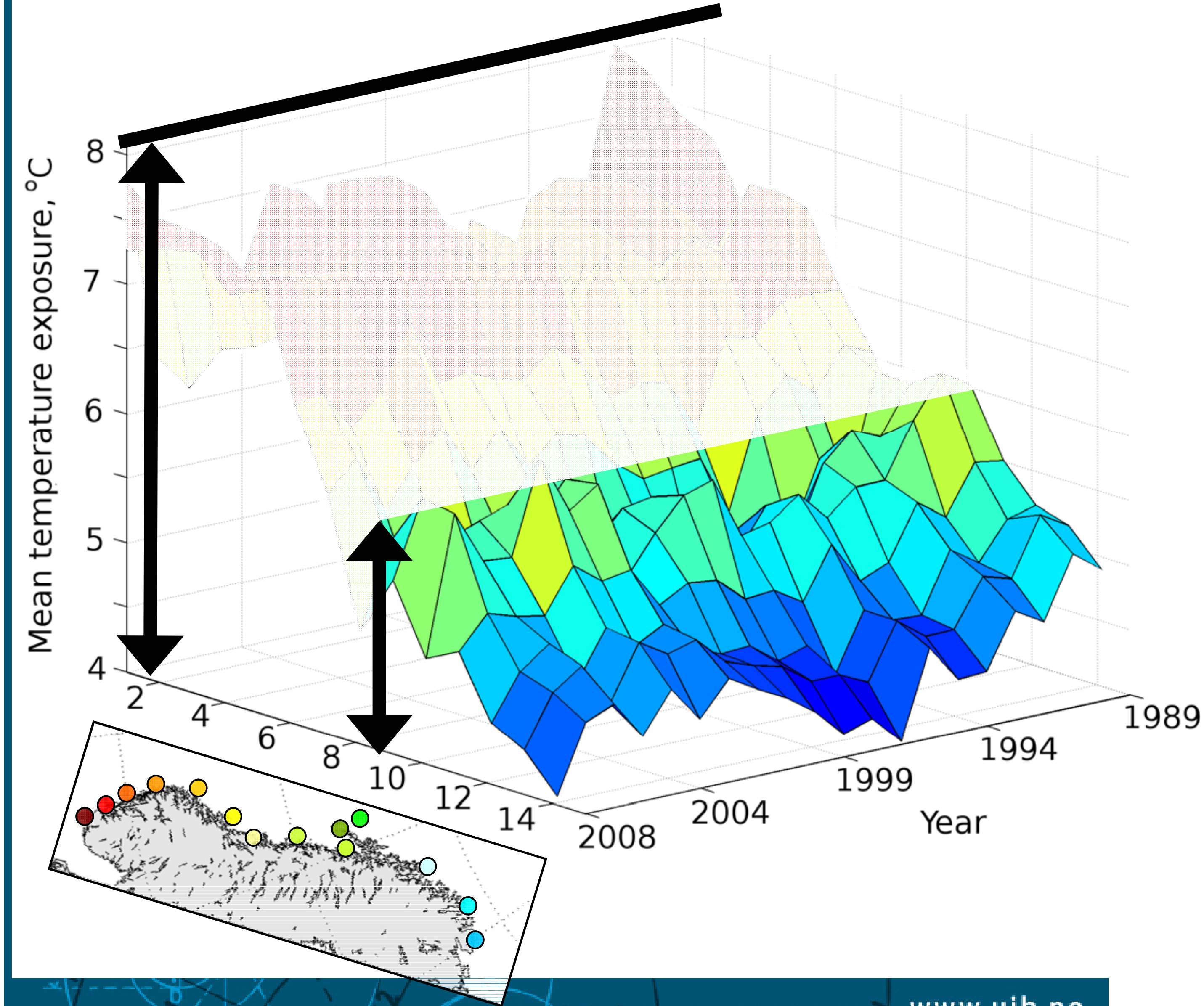


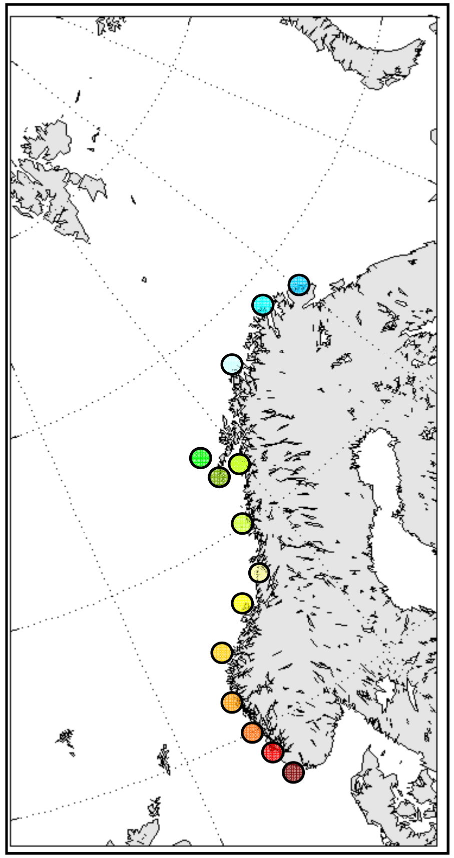
Jørgensen C, Dunlop ES, Opdal AF, Fiksen Ø. 2008. *Ecology* **89**:3436-3448.

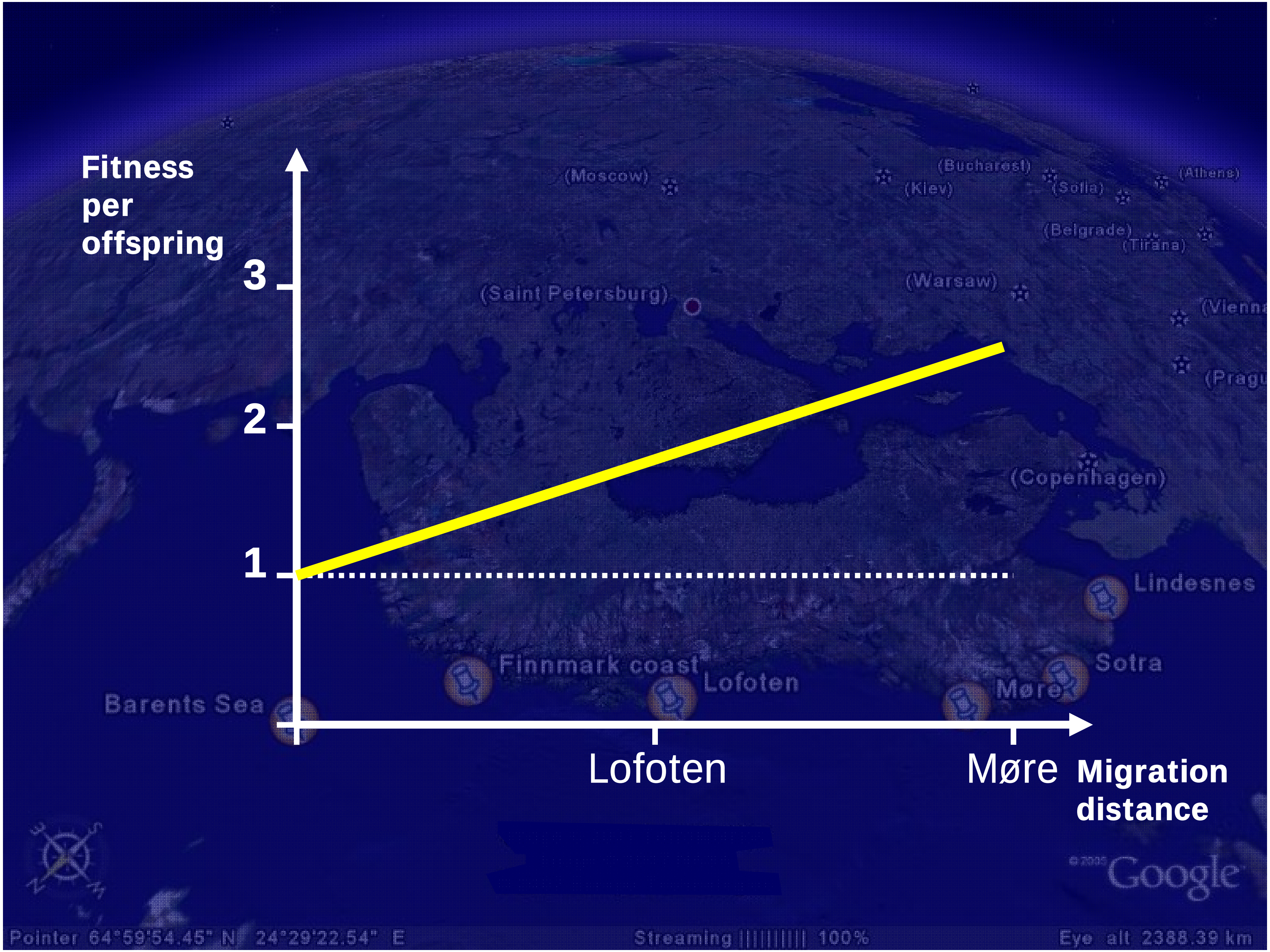



45°E
30°E
15°E
78°N
72°N
66°N
60°N
Norw
Sea
North Sea
0°

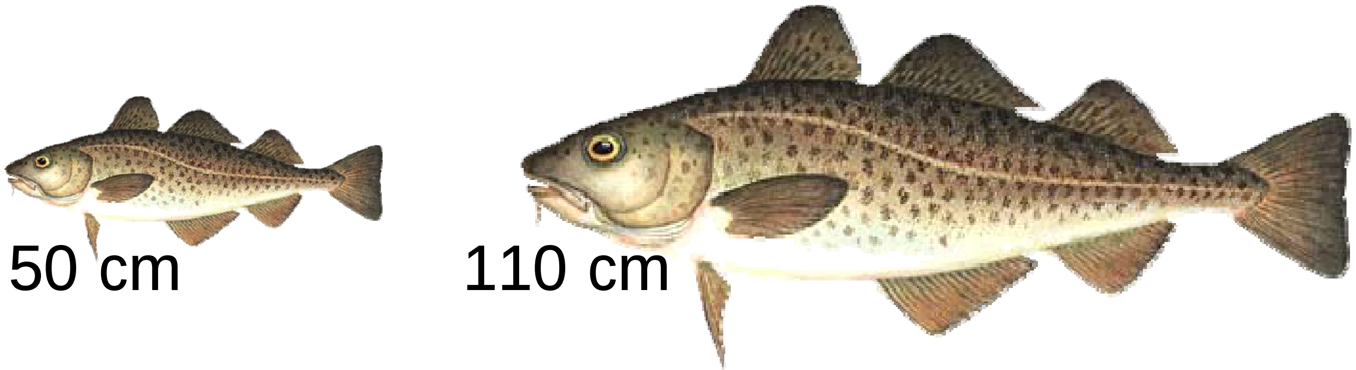
Larval temperature exposure





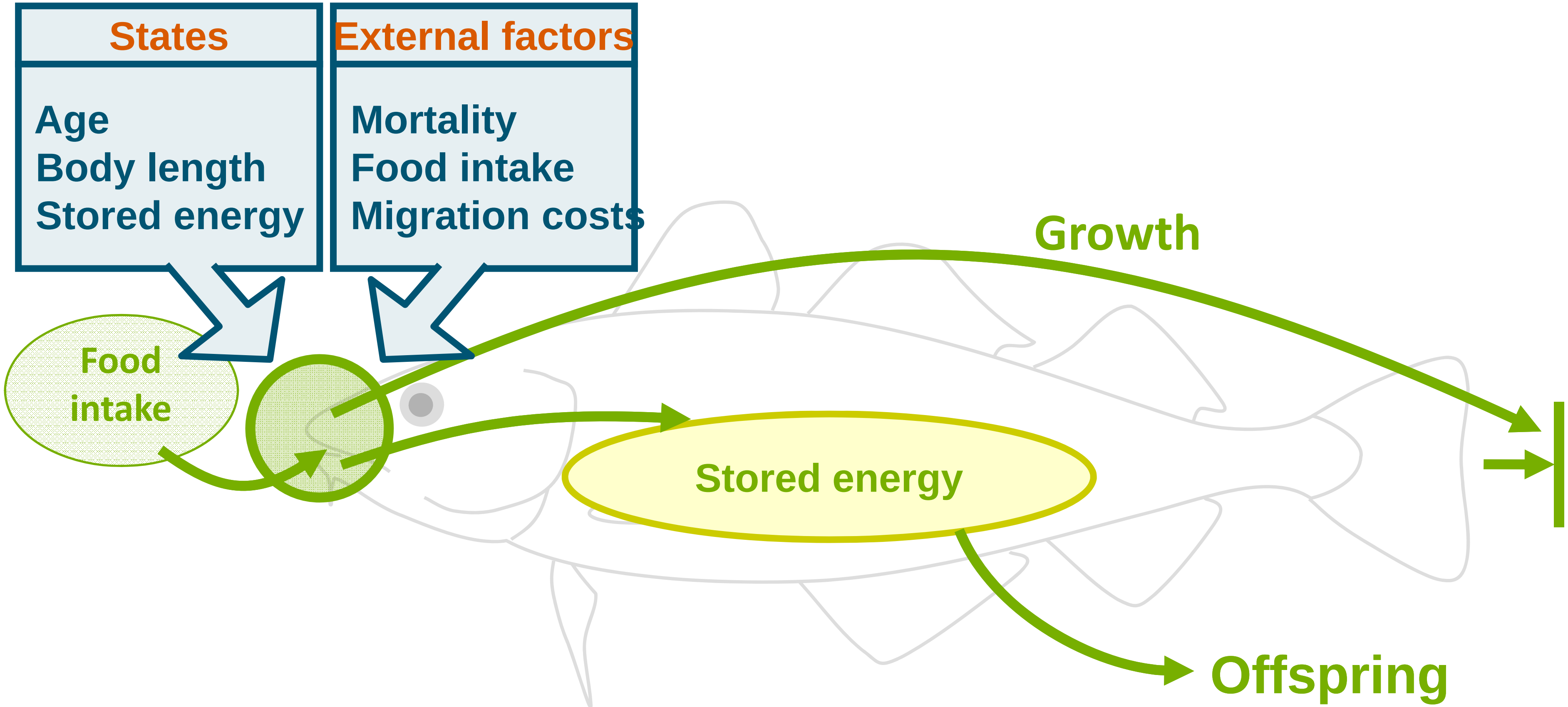

Fitness per offspring
3
2
1
Lofoten
Møre
Migration distance
(Moscow)
(Bucharest)
(Kiev)
(Sofia)
(Athens)
(Belgrade)
(Tirana)
(Saint Petersburg)
(Warsaw)
(Copenhagen)
Lindesnes
Sotra
Finnmark coast
Lofoten
Møre
Barents Sea
Google
Pointer 64°59'54.45" N 24°29'22.54" E
Streaming 100%
Eye alt 2388.39 km

Migration costs versus body size



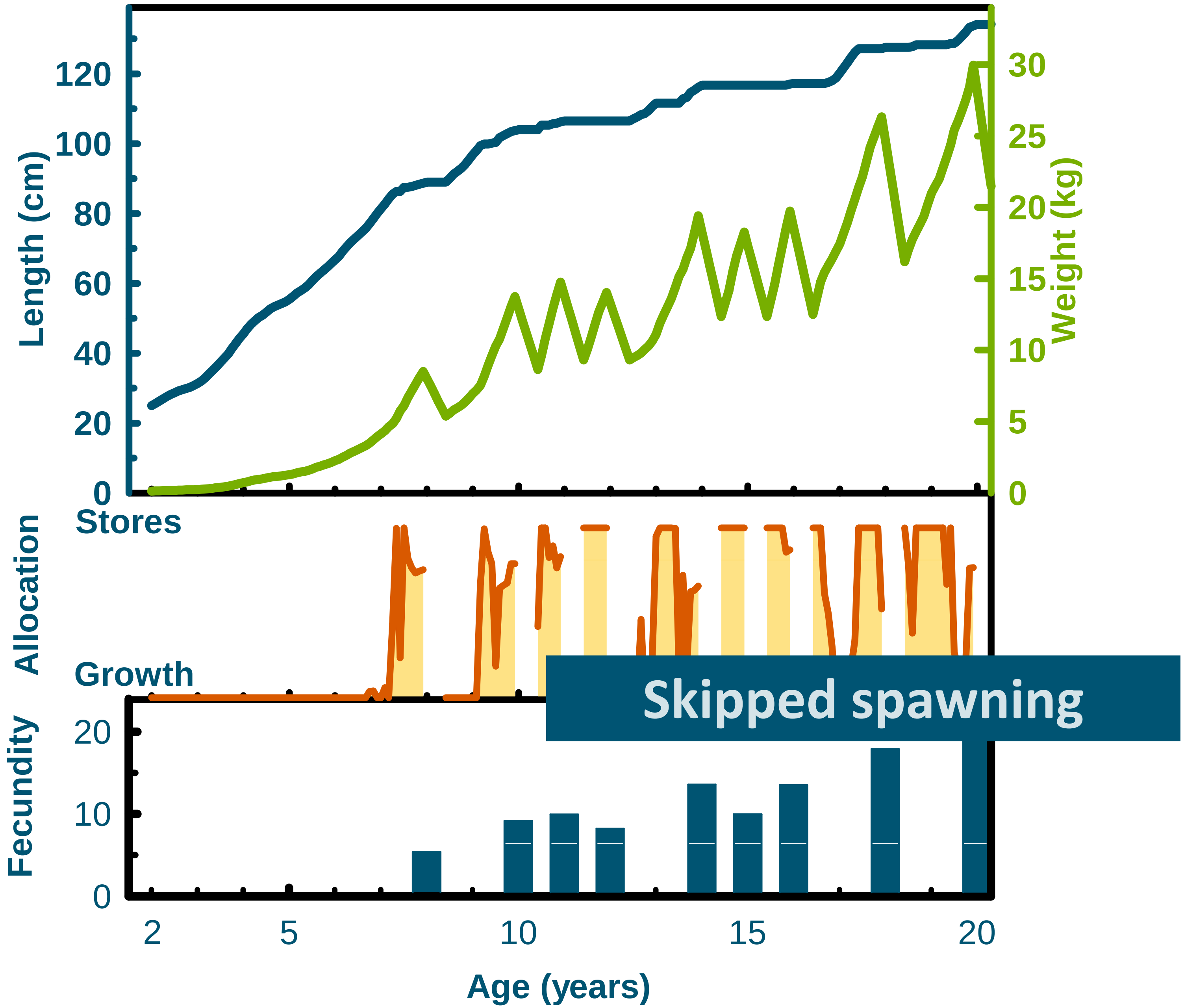
Jørgensen C, Dunlop ES, Opdal AF, Fiksen Ø. 2008. The evolution of spawning migrations: the role of individual state, population structure, and fishing-induced changes. *Ecology* **89**:3436-3448.

Energy allocation in cod



$$V(A,L,E,F) = \max_{\alpha}\left[B(E) + S \sum_{F'} P(F' \mid F) \cdot V(A+1, L', E', F') \right]$$

Jørgensen C, Fiksen Ø. **2006**. *Can J Fish Aquat Sci.* **63**:186-199



Jørgensen C and Fiksen Ø. 2006. *Can J Fish Aquat Sci.* **63**:186-199

Frequent skipped spawning in the world's largest cod population

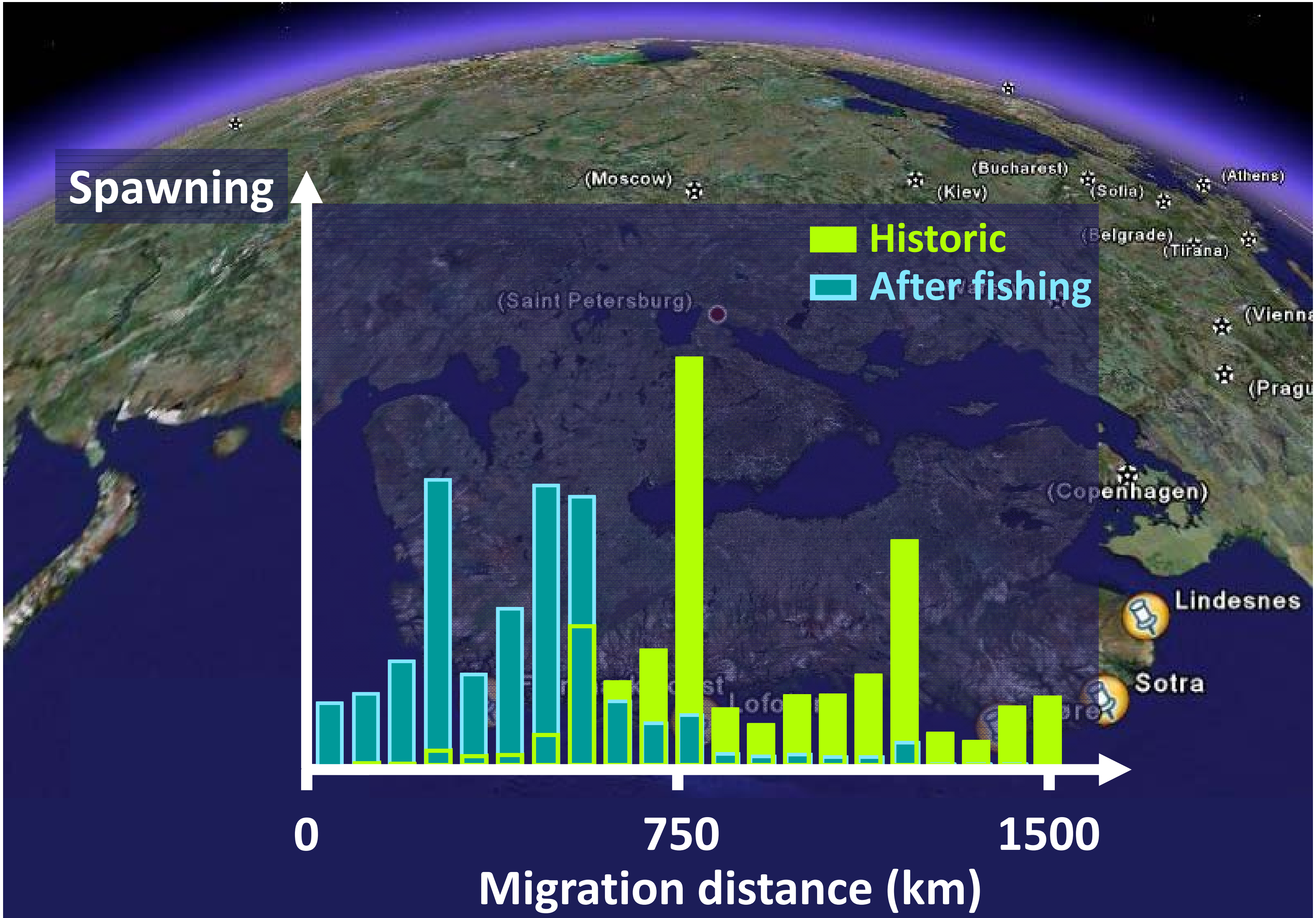
Jon Egil Skjæraasen[a,b,1], Richard D. M. Nash[b], Knut Korsbrekke[b], Merete Fonn[b], Trygve Nilsen[c], James Kennedy[d], Kjell H. Nedreaas[b], Anders Thorsen[b], Peter R. Witthames[e], Audrey J. Geffen[a], Hans Høie[a], and Olav Sigurd Kjesbu[b]

Departments of [a]Biology and [c]Mathematics, University of Bergen, N-5020 Bergen, Norway; [b]Institute of Marine Research, N-5817 Bergen, Norway; [d]Møreforskning Ålesund, N-5021 Ålesund, Norway; and [e]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, Suffolk NR33 0HT, England

Edited by Ray Hilborn, University of Washington, Seattle, WA, and accepted by the Editorial Board April 16, 2012 (received for review January 5, 2012)

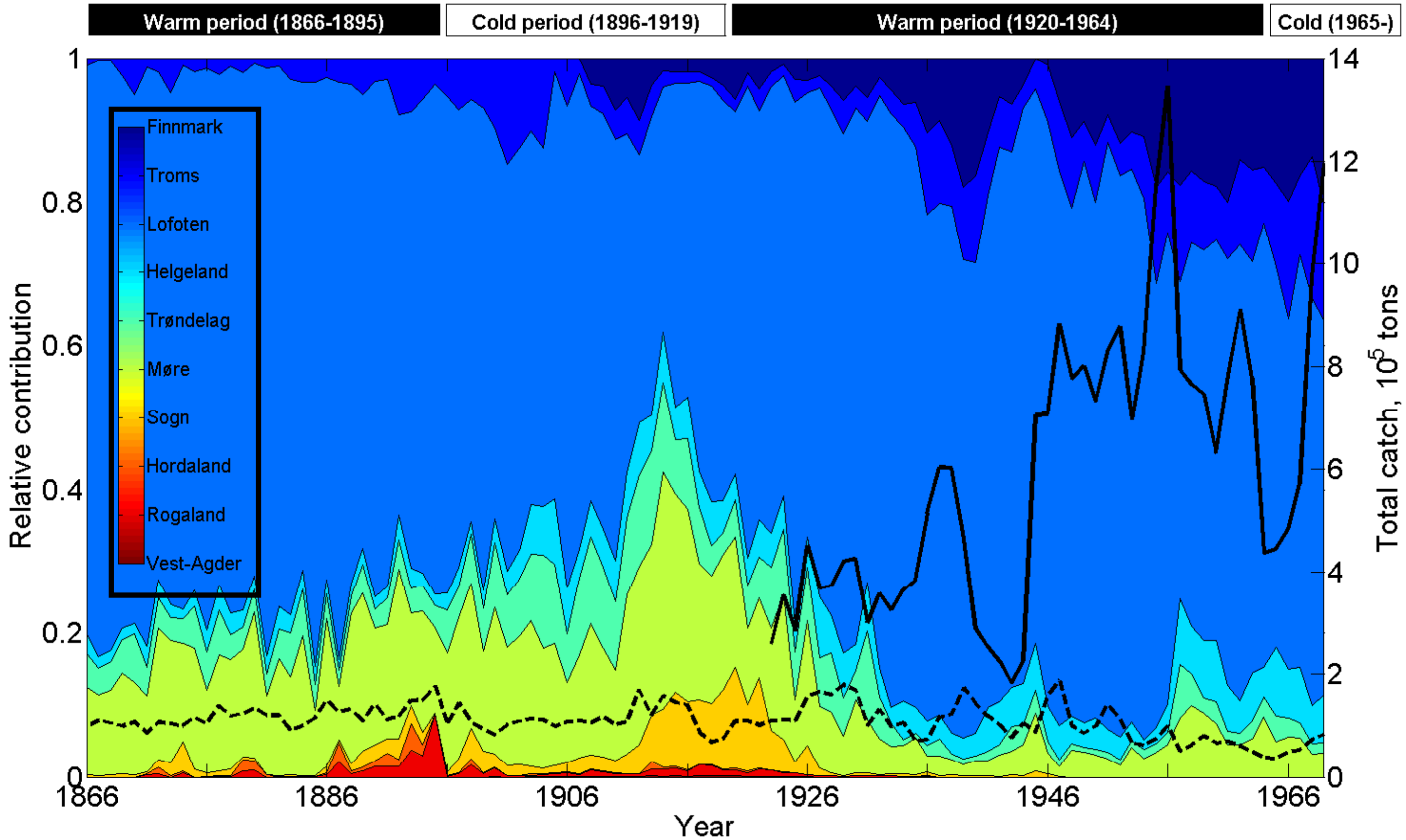
Life-history theory suggests that animals may skip reproductive events after initial maturation to maximize lifetime fitness. In

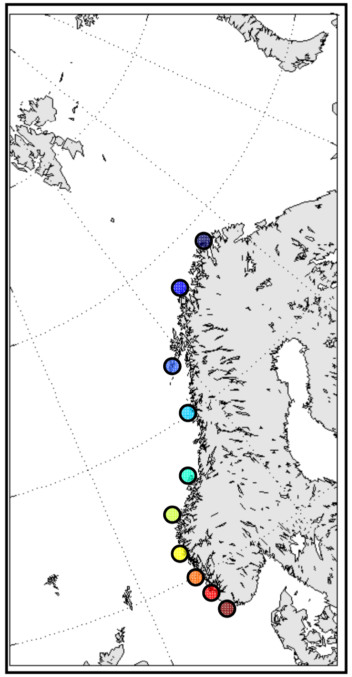
oocytes are hydrated and the eggs spawned (11). After spawning, the gonad shrinks rapidly in size, visually appearing immature,



Jørgensen C, Dunlop ES, Opdal AF, Fiksen Ø. 2008. *Ecology* **89**:3436-3448.

Relative distribution on spawning grounds





‘NORGES FISKERIER’ (1866-1974)

OPDAL AF (***2010***) Fisheries change spawning ground distribution of northeast Arctic cod. **Biol Lett**

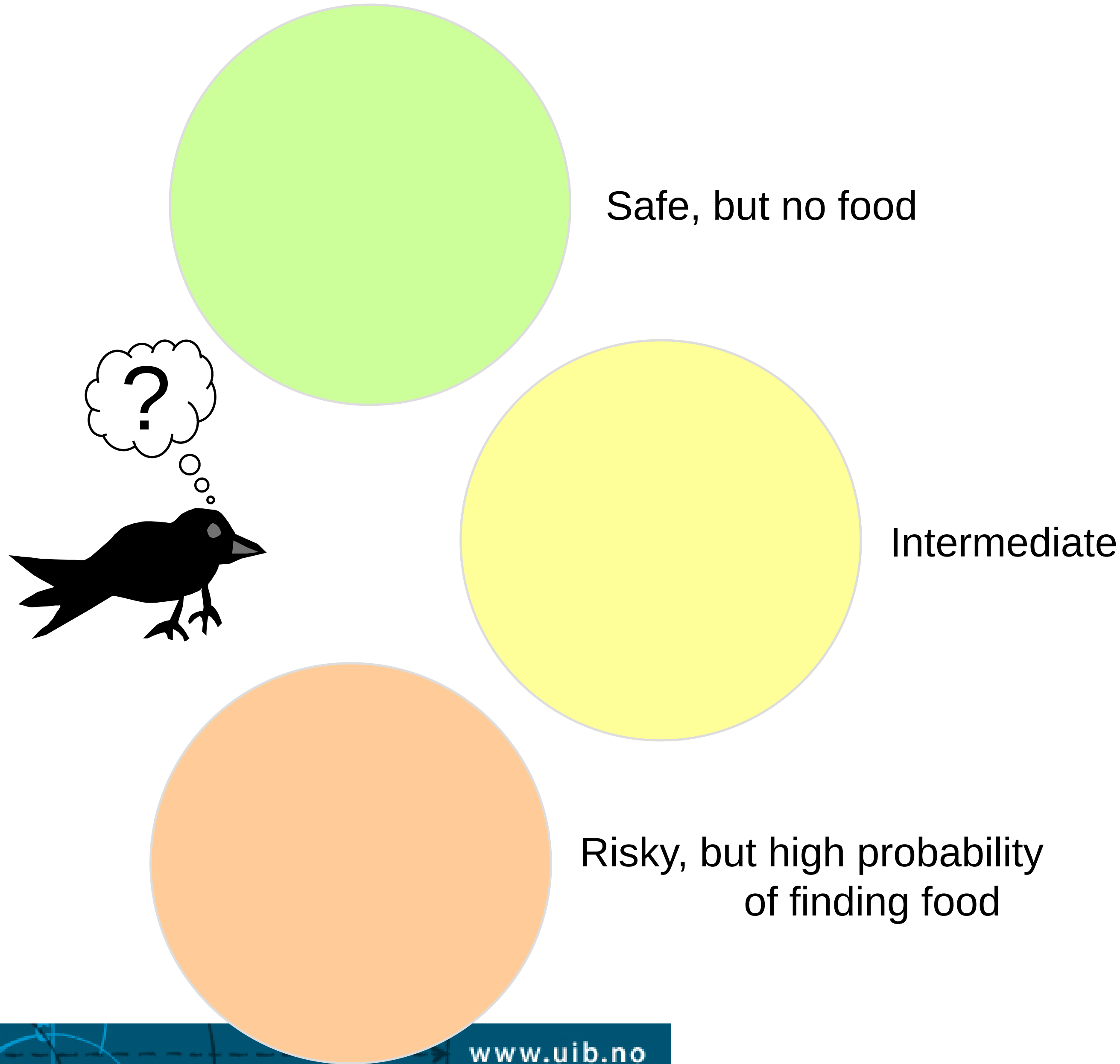
Summary

- Dynamic programming is excellent in clarifying the role of state in behavioural ecology and life history theory
- It is integrating proximate constraints, physiology, ecological mechanics and physics with evolutionary theory
- It often surprises you

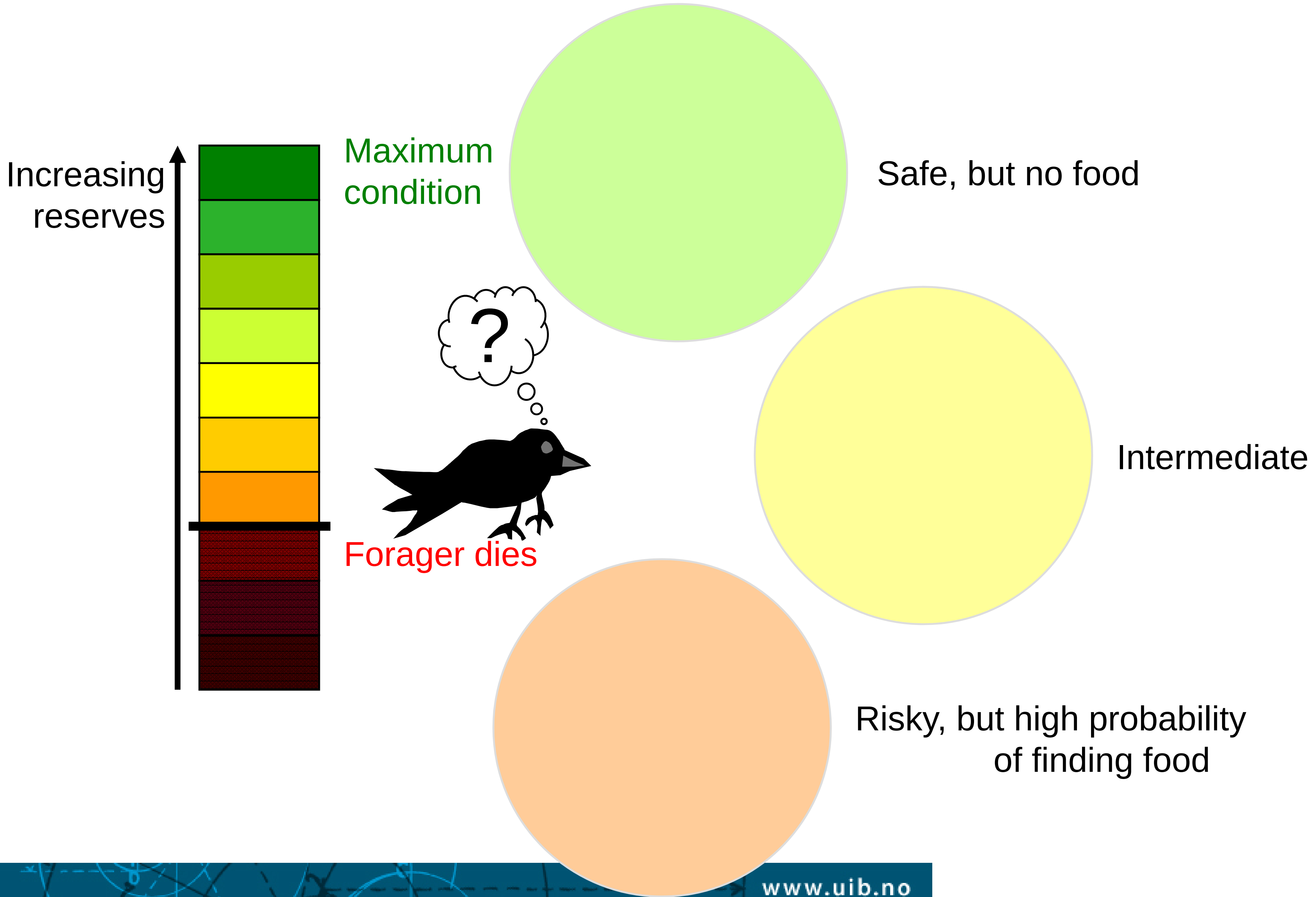
- It is not suitable for density- or frequency-dependent traits

www.bio.uib.no/modelling

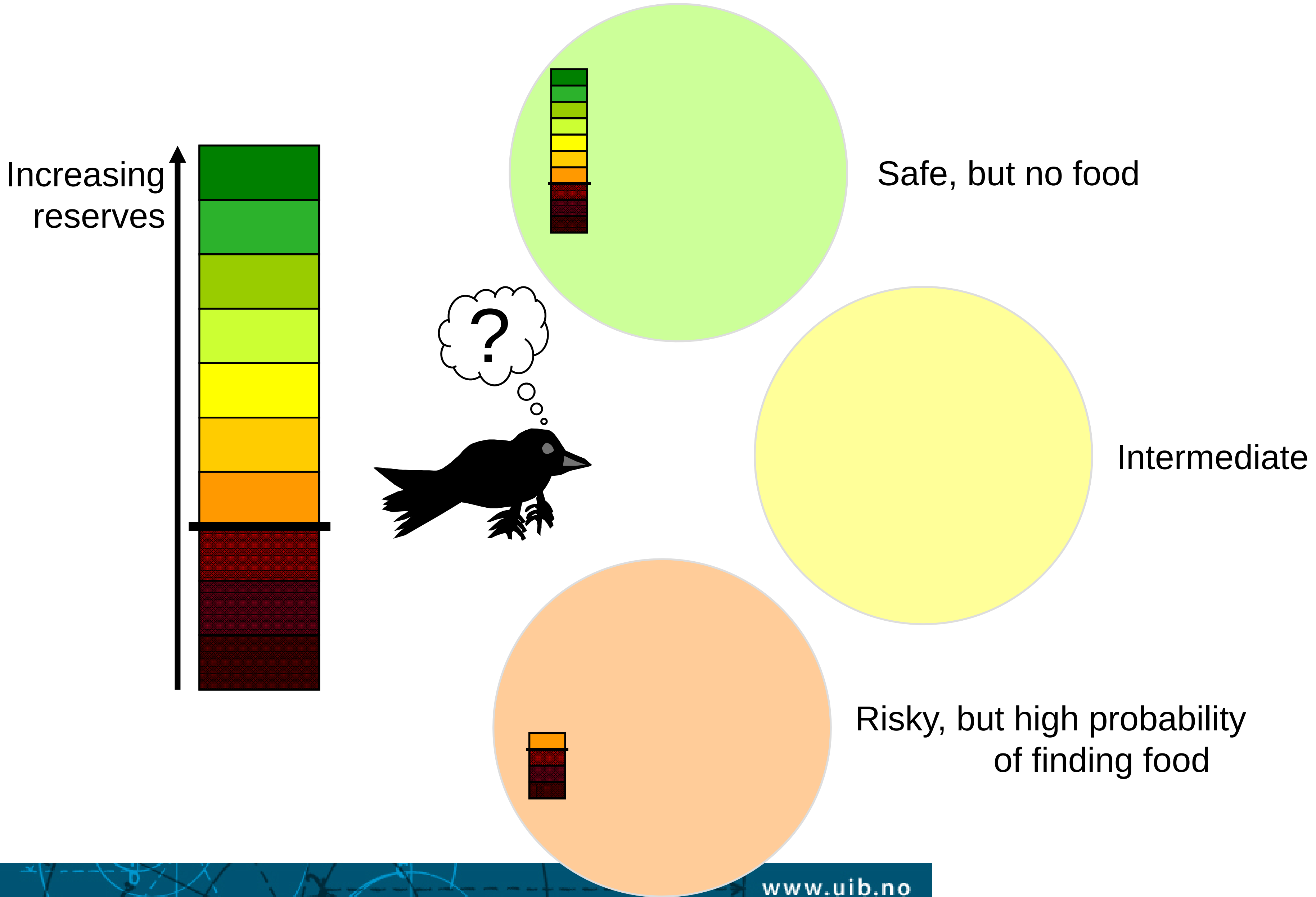
Optimal patch choice and 'ecology of fear'



Individual state: energy reserves



Individual state influences patch choice



The model

$X(t)$	State at time t. Constraint: $X(t)<C$
$F(x,t,T)$	Fitness defined as: survival from t until T of an ind in state $X(t)=x$.
α_i	Cost of staying in patch i
λ_i	Probability of finding food in patch i
Y_i	Value of food in patch i if found
x_c	Critical state value – forager dies
β_i	Predation probability in patch i

State change:

$$X(t+1) = \begin{cases} X(t) - \alpha_i + Y_i & \text{with probability } \lambda_i \\ X(t) - \alpha_i & \text{with probability } (1-\lambda_i) \end{cases} \qquad x = \begin{cases} x' \\ x'' \end{cases}$$

Survival   Food is found   No food

$$F(x,t,T) = \max_i \; (1-\beta_i) \cdot \left[\lambda_i \cdot F(x',t+1,T) + (1-\lambda_i) \cdot F(x'',t+1,T) \right]$$

A model: parameters

	Safe, but no food **Patch 1**	Inter-mediate **Patch 2**	Risky, with food **Patch 3**
Cost of choosing patch *i*, α_i	1	1	1
Predation probability, β_i	0.000	0.004	0.020
Probability of finding food, λ_i	0.0	0.4	0.6
State increment if food is found, Y_i	0	3	5
Expected return, $\lambda_i \cdot Y_i$	0.0	1.2	3.0

$$F(x, t, T) = \max_i \; (1-\beta_i) \cdot \left[\lambda_i \cdot F(x', t+1, T) + (1-\lambda_i) \cdot F(x'', t+1, T) \right]$$