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Adaptive foraging behaviour and the role of the overwintering strategy

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Abstract: The overwintering strategy is a common feature among fishes from temperate to arctic regions and yet the overwintering has never been studied from the perspective of evolutionary ecology. In the present study our focus is on the overwintering of sandeel ecotypes in relation to the conflicting concerns of foraging and avoiding predation. We construct an IBM model for sandeel that combines bioenergetics, environmental forcing and behaviour. We then identify the timing of the overwintering that maximizes fitness (life time expected reproduction) for various environmental scenarios. We show for sandeel ecotypes that the optimal timing of the overwintering is affected by a combination mortality

rate in the refuge, mortality rate associated with foraging, spring bloom intensity and spring bloom duration. Natural selection should therefore favour individuals that are able to adapt overwintering to this combination of environmental variables.

Introduction

Overwintering is about reducing metabolism and predation mortality during seasons where conditions (e.g. temperature and/or food availability) are suboptimal. Overwintering is a widespread behavioural trait in fishes from temperate to arctic regions, yet insight into the evolutionary and ecological mechanism underlying the overwintering of fishes has so far remained elusive. The overwintering phenomenon has therefore also so far been largely ignored in fish stock assessments and management.

It has long been recognized that the individual organism aims at maximizing net reproductive rate through adaptation of its life history strategies. This is the very force that drives evolution and shapes life history strategies. On the macro evolutionary level natural selection has resulted in a variety of genetically fixed life history strategies among higher taxa. However within the species, and even in some cases within the individual, there is room for phenotypic variation, around some stereo type life history characteristic. It is this plasticity that allows the organism to achieve reproductive success in a heterogeneous and changing environment.

In simple cases the optimal foraging behaviour may simply be the behaviour that maximizes net energy gain. However, many organisms face high mortality rates and may

not life long enough to reproduce. Making behavioural decisions that increase the probability of surviving then becomes an element in the measure of reproductive success that is of equal importance to rate maximization. The evolutionary rationale behind this was clearly expressed in Lima (1998): “Natural selection should act to produce animals that can somehow arrive at an appropriate trade-off between the benefits of energy intake and the cost (in terms of Darwinian fitness) of an early death due to predation”. This has also been termed the energy-predation trade-off (Houston and McNamara, 1999). Identifying the ecologically and evolutionary processes of the energy-predation trade-off and understanding how this trade-off can be mediated by behaviour (risk-taking vs. risk adverse behaviour) has large implications in studies of population and ecosystem dynamics (Lima, 1998), as they for example leads to within species-variation in growth patterns additional to what is predicted based on food abundance (Mangel and Stamps 2001; Biro et al. 2006), and temporal and spatial variation in distribution of prey organism and their predators (Biro et al. 2003; Schmitz et al. 2008).

Sandeel (*Ammodytes* sp.) is ideal to study the overwintering behaviour from the perspective of the energy-predation trade-off. They are a short lived trophic key species in many temperate to arctic ecosystems. The role of sandeel in the ecosystems they inhabit and their behavioural characteristics seems to apply for the entire family (*Ammodytidae*), though some species such as Small sandeel (*Ammodytes tobianus*) and Lesser sandeel (*Ammodytes marinus*), which supports a large commercial fishery in the North Sea, have been subject to the bulk of sandeel related studies. Particularly since a collapse of the North Sea stock came close in 2002 (anon, 2007). Sandeel display a strong overwintering behaviour. Dispersal of sandeel larvae (*Ammodytes marinus*) is limited (Christensen et al. 2008) and adults are highly residential (Pedersen et al. 1999; Gauld 1990), adaptations to

local conditions are therefore likely to occur. Lesser sandeel appear to reside submerged in sandy sea beds from late summer until spring (Winslade, 1974a), with the exception of age-0 individuals which have been reported to postpone the beginning of the overwintering (Reeves, 1994). When zooplankton becomes abundant in spring sandeel emerge in vast abundances from the sea bed during day hours in order to feed (Winslade, 1974a), and at the same time they expose them self to a large variety of predatory organisms covering both birds, fishes and marine mammals (Engelhard et al. 2008; Furness 1990; Hain et al 1995; Furness 2002; Frederiksen et al. 2005). They reach sexual maturity around age-2 and subsequently spawn in December/January (Macer 1966; Bergstad et al. 2001). The eggs stick to the substrate until they hatch during February and March (Wright & Bailey 1996; Macer 1965), whereupon larvae are found in most of the water column (Conway et al. 1997). After metamorphosis they settle in sandy seabeds into the residential aggregations of adults.

In the present study we consider the overwintering behaviour in relation to the energy-predation trade-off. We expect that maximum fitness (life time reproductive index R_0) is achieved by making a compromise between energy uptake and probability of surviving. We assume that either the population or the individual carry repertoires of overwintering behaviours from which the solution to this compromise is selected based on fitness optimization principles. If the annual cycle consists of two periods, an overwintering period and a foraging window, then we can define the overwintering behaviour as being simply a pair of decisions made once a year, namely the timing and duration of the overwintering period. We construct a generic holistic individual based model (IBM) that combines physiology, bioenergetics, behaviour and environmental forcing. The model returns the fitness values resulting from the various possible combinations of timing and duration of

the foraging window. We apply the model on a specific case, sandeel in the North Sea (*A. marinus* and *A. tobianus*). A few sandeel specific parameters were available in the literature. However, standard metabolism as a function of temperature, metabolic cost of routine activity, stomach evacuation rate as a function of temperature and stomach capacity were all derived experimentally specifically for the present study, but will not be presented in this CM paper. We focus on three central questions: 1) How do predation mortality rates influence the optimal (optimal in terms of fitness) foraging window? 2) How do spring bloom properties (intensity and duration) influence the optimal foraging window? 3) How do physiological and behavioural constraints influence the optimal foraging window?

Methods and material

A conceptual overview of the model

The developed IBM model is based on a bioenergetic description of an adult individual that have reached its asymptotic size whereby all surplus energy is allocated to gonads. Energy gain is based on stomach size and evacuation rates and energy losses are determined by the assimilation efficiency, standard metabolism and activity costs related to swimming. Temperature dependencies are included in the stomach evacuation rate and the standard metabolic cost. The habitat is described as a two-box system. The individual can either be buried in the seabed (refuge), where predation mortality is low and food

supply is zero, or the individual can be in the pelagic zone (arena), where the individual can feed on the expense of a higher predation mortality. The simulation period is the entire adulthood and addresses the optimal strategy for investing foraging effort, and we determine the strategy which will give the highest outcome of the energy-predation trade-off. The model explicitly accounts for processes at four nested time scales: hourly (foraging processes, in relation to availability and stomach evacuation), daily (mortality as a result of behaviour and energy budget), seasonal (total gonad build-up in foraging period until December 31, where it reproduces and thereby sheds all stored energy in the gonads at spawning) and lifetime (the expected life time reproductive output). Water temperature, day length and food availability varies according to natural seasonal patterns in a temperate area. The model applies climatological time series and neglects inter-annual variability, since we are interested in the generic aspects of overwintering strategies. We determine the strategy which will give the highest outcome of the energy-predation trade-off. This means that in the winter period they will stay in the refuge and access the arena during the spring bloom. The timing of the shifts between the arena and refuge defines the timing of the overwintering period and foraging window. As sandeel also within the foraging window will bury in the seabed during night time and during parts of the day (Winslade, 1971) we resolve the model on a hourly time step allowing the individual in the model to only spend time in the arena during day hours starting at sunrise and only as long as the stomach is not full. The daily mortality in the feeding period will therefore depend on day length and the stomach filling/evacuation dynamics. Individuals that undertake an overwintering strategy that will not let them accumulate enough energy to cover the energy costs during the simulation year are dying from starvation. The energy uptake, energy expenditure and mortality that accumulate over the course of the adult life cycle, are by the

end of year combined into the life time reproductive output R_0 as fitness measure, corresponding to the chosen timing of the overwintering period.

Consumption

Within the foraging window consumption is described by the number of prey items consumed in caloric values and also accounting for the assimilation efficiency:

$$C(t) = N(t) \cdot \varepsilon, \quad (\text{eq. 1})$$

Where, $N(t)$ is the number of ingested food particles at day t and ε is a constant accounting for the caloric value of a prey item and the assimilation efficiency. The number of encountered (but not necessary eaten) food particles is determined by the available prey and the period at which the individual can forage.

$$N_{enc}(t) = v_{swim} f(t) \tau(t), \quad (\text{eq. 2})$$

Where, v_{swim} is the cruising velocity, $f(t)$ the feeding regime defined by the concentration of suitable food items on day t and τ is the day length. Both f and τ are forcing functions set by conditions in the local habitat. The upper limit on the number of ingested food particles is determined by available stomach volume at feeding time:

$$N_{max}(t) = V - S(t-1) + \sum_{dt=24h} E(t), \quad (\text{eq. 3})$$

Where, V is the capacity of the stomach (in numbers of prey items), $S(t-1)$ is the stomach fullness on day $t - 1$, and $E(t)$ is the evacuation rate, which is determined by the fullness of the stomach and the temperature:

$$E(t) = e^{\ln(S(t-1) + a - bT(t))}, \quad (\text{eq. 4})$$

Where $T(t)$ is a forcing function describing the water temperature, a and b are fitted coefficients. Both N_{max} and N_{enc} are upper bounds on the ingested number of food items. In our model, the actual number of ingested food items is assumed to be

$$N(t) = \min(N_{enc}(t), N_{max}(t)), \quad (\text{eq. 6})$$

which is used in eq. 1.

Behavior

The adult sandeel can be in two states during the season: feeding ($\sigma=1$) or hibernating ($\sigma=0$). Our model determines $\sigma(t)$ for the climatological season corresponding to optimal lifetime reproductive output. The model accounts for the assumption that the sandeel does not spend unnecessary time in the feeding arena (with higher mortality), but goes to the refugium (the sediment) when its stomach is full. The time in hours spend in the feeding arena is

$$H(t) = \tau(t) \frac{N(t)}{N_{enc}(t)}, \quad (\text{eq. 7})$$

Energetic cost

The daily metabolic cost is a function of the combined costs to standard metabolism and activity costs:

$$R(t) = \begin{cases} R_S(t) \cdot 24k + k(R_A \cdot H(t)) & \text{for } \sigma(t) = 1 \\ R_S(t) \cdot 24k & \text{for } \sigma(t) = 0, \end{cases} \quad (\text{eq. 5})$$

where R_S and R_A are hourly standard metabolism and the extra metabolism associated with routine swimming activity. The conversion factor k converts oxygen consumption to kcal/h. R_A is constant, whereas R_S depends on temperature and was derived from the following equation:

$$R_S(t) = cT(t) - d, \quad (\text{eq. 6})$$

where c and d are fitted coefficients.

Mortality

The daily mortality is described by the time spent in the refuge and the arena in periods where the individual feeds in the arena:

$$Z_d(t) = \begin{cases} \sum_t H(t) \cdot Z_A + (24 - H(t)) Z_R & \text{for } \sigma(t) = 1 \\ \sum_t (24 - H(t)) Z_R & \text{for } \sigma(t) = 0 \end{cases}, \quad (\text{eq. 7})$$

where Z_A and Z_R is mortality per hour in the arena and refuge respectively. From the daily mortality, the survival chance for one feeding season is given by

$$P[\sigma] = e^{-\sum_{t=1}^{365} Z_d(t)}, \quad (\text{eq. 8})$$

which is a function of the feeding strategy $\sigma(t)$.

End point fitness measure

In order to calculate an end point fitness measure associated with a given timing of the overwintering $\sigma(t)$, the equations for consumption (eq. 1), energetic cost (eq. 5) and mortality (eq. 7+8) was summed up over a the entire year, corresponding to a feeding strategy $\sigma(t)$. Thereby it is possible to evaluate the life time reproductive index R_0 as a function of σ

$$R_0[\sigma] = \omega \frac{P}{1-P} \sum_{t=1}^{365} (C(t) - R(t)), \quad (\text{eq. 9})$$

which is proportional to the expected number of offspring during the life time. ω is the survival chance up to first season, where gonads are developed, which is a constant independent of adult feeding strategy σ . C-R summed up over a the entire year is

accumulated annual surplus energy gain (G). Because we have neglected inter-annual variability in the physical conditions, the reproductive output can explicitly be summed over the entire life span. We assume that population density affects the individual either by increased larval/juvenile mortality (ω) or by reducing $C-R$ (competition). This corresponds to population density effects of type 1 and/or type 3 in the classification of Mylius and Diekman (Mylius and Diekman, 1995), and thereby optimization of R_0 rigorously finds the $\sigma(t)$ that corresponds to the evolutionary stable strategy for $\sigma(t)$ (Mylius and Diekman, 1995). This is a considerable simplification compared to explicitly including population density effects in the model. In our work we therefore simply optimize R_0 with respect $\sigma(t)$ to predict the optimal overwintering strategy.

Forcing functions

The default temperature forcing function (T) applied to the model is a cosine function ($T(t) = T_{min} + (0.5(T_{max} - T_{min})(1 - \cos(2\pi(t - t_{min}))))$) with minimum temperature of 5 °C (T_{min}) on January 31st (t_{min}) and a maximum temperature of 20 °C (T_{max}) on July 31st. Day lengths (τ) correspond to the annual cycle on Dogger bank, North Sea. Feeding regime or prey availability (f) is described by a Gaussian distribution, where the mean defines the timing of the spring bloom peak and the standard deviation defines the width of the spring bloom. The spring bloom intensity (prey abundance) is determined by multiplying the Gaussian distribution with a factor.

Results

The parts of the study that includes the experimental work based on which the model was parameterized is not included in this CM paper.

Overwinter starvation is in general not an issue. In all environmental scenarios explored did the optimal solution result in energy accumulation sufficient to avoid overwinter starvation. Even when the fish foraged for only 7 weeks and never used more than 1/3 of its stomach capacity within a day (peak of Gaussian spring bloom) was half of the energy accumulated during foraging available for production while the other half was sufficient to pay the metabolic cost of overwintering.

Elevated mortality in the foraging arena leads to risk adverse behaviour. The optimal foraging window is more or less symmetrically distributed around the Gaussian shaped spring bloom and considerably narrower than the spring bloom. The general trend of the overwintering strategy is that the width of the optimal foraging window under a given feeding regime depends on mortality rates. An Increase in mortality rates in the arena (Z_A) results in a decrease in the width of the optimal foraging window. In contrast an increase in refuge mortality rates (Z_R) results in an increase in the width of the optimal foraging window. The reduction in fitness (R_0) and annual survival chance (P) following elevated arena mortality rates is highest in the lower range of arena mortality rates and level out toward the upper range of arena mortality rates (Fig. 2).

Spring blooms of high intensity leads to risk adverse behaviour. Spring bloom intensity was varied either by varying the multiplying factor or by changing the standard deviation defining the Gaussian shaped spring bloom. The latter also affected the duration of the spring bloom, in such a way that the longer the spring bloom last the smaller are the intensity and vice versa. Spring bloom intensity in the present model is expressed as realized feeding rate during times of foraging, whereas a more relevant measure is realized daily surplus energy uptake ($C-R$). At low spring bloom intensity the distribution of daily realized surplus energy uptake resembles the Gaussian shaped distribution of feeding rates, and feeding rate can be said to be the limiting factor. However, at high spring bloom intensities, distribution of realized daily surplus energy uptake becomes flat on top, as the stomach capacity (V) and evacuation rate (E) becomes a limiting factors. Increasing spring bloom intensity and/or decreasing spring bloom width resulted in a reduction of the width of the optimal foraging window (Fig. 3 and 4a). However, there is a maximum level of spring bloom intensity above which the optimal foraging window remains at a constant width despite further increase in spring bloom intensity. This maximum level is determined by the shift from prey concentration limited surplus energy uptake to stomach capacity/evacuation rate limited surplus energy uptake (Fig. 4a & b). Increased spring bloom intensity results in increased annual accumulated energy available for reproduction (G), increased fitness and increased annual survival chance. However, when realized surplus energy uptake becomes limited by stomach capacity, annual accumulated energy available for reproduction levels out (Fig. 4c). In the lower range of spring bloom intensities the increase in annual survival chance is due to the reduction in the width of the foraging window. Whereas in the upper range of spring bloom intensities increase in

annual survival chance is caused by the high prey abundance leading to a reduction in the number of hours spent in the arena per day.

Counter acting behavioural and physiological forces prevent the optimal foraging window from being located asymmetrically relative to the spring bloom peak.

A closer look at the flat top of the distribution of daily realized surplus energy uptake reveals asymmetry (Fig 4b), with relatively higher surplus energy uptake to the right. This asymmetry is caused by a combination of longer days and warmer water as summer is progressing. Warmer water increases stomach evacuation rates and assimilation efficiency (A), which in combination with increased day length elevates daily consumption (Fig 5b). Warmer water also increases the standard metabolic cost. However, the benefits of increased consumption outweigh the increased standard metabolic cost. Thus, looking at daily surplus energy uptake in isolation, one would expect the optimal foraging window to be asymmetrically positioned relative to the spring bloom with the centre of the foraging window located to the right (towards summer) of the spring bloom, which it is not (Fig 5a). However, the fish also spent more hours foraging in the arena as days become longer, which in turn increases the accumulated daily mortality and therefore drags the optimal foraging window to the left (Fig 5a).

Natural selection should favour individuals with an adaptive overwintering strategy.

For example, for a spring bloom with a standard deviation of 25 days a 14 days mismatch between the centre of the foraging window and the spring bloom peak (in either directions) results in ~20 % loss in fitness, and a 25 days mismatch results in ~50 % reduction in fitness (Fig 6a). However, the wider and more intense the spring bloom is, the weaker

becomes the natural selection pressure for adaptive overwintering strategies (Fig 6a). Contraction or expansion of the optimal foraging window also results in notable fitness reduction. Contraction of the foraging window eventually leads to negative fitness which means that the metabolic cost of overwintering exceeds surplus energy accumulated during the foraging period (Fig 6b).

Discussion

The present study is the first to consider the energy-predation trade-off in relation to the overwintering behaviour of fishes. We provide a generic model framework that combines physiological mechanisms and natural selection considerations and applies it on sandeel ecotypes. We found for sandeel ecotypes that the standard metabolic cost related to the overwintering period constitute only a fraction of annual accumulated energy even when spring bloom related food abundances is low. The optimal width and timing of the overwintering period is instead driven by a combination of mortality rate in the refuge, mortality rate associated with foraging, spring bloom intensity and spring bloom duration. Natural selection should therefore favour individuals that are able to adapt the overwintering behaviour to this combination of environmental variables.

It is generally accepted that the predation risk experienced by a prey organism is proportional to the foraging activity level of the prey organism. The rationale behind this is that predators are attracted by movement and predator-prey encounter rate is increased.

Furthermore, some fish, for example sandeel, withdraw to a safe where predators have limited access during non-feeding periods. Therefore intuitively the optimal solution to energy-predation trade-off in situations where mortality rates related to being active goes up would be to reduce foraging activity, as long as a critical minimum energy uptake is not compromised. Our model support this intuitively driven conclusion as it predict that when mortality rates associated with foraging increase the foraging window contract. A number of previous studies also confirm this behavioural pattern (e.g. Lima and Dill 1989 (review); Biro et al. 2003; Biro et al. 2006). However, previous studies of behavioural decisions made under the risk of predation have focused on daily activity levels and/or the choice between productive high-risk habitats and less productive low-risk habitats. In contrast the present study focus on activity on an annual time scale with a strong seasonal environmental cycle, leaving the daily activity level to be regulated by day length and stomach filling/evacuation dynamics. It is therefore noteworthy to see that the optimal solutions to the energy-predation trade-off follows the same overall patterns or “rules” regardless of the time-scale studied.

Fish studies on how feeding condition affects the willingness to take risk are rare, and the outcome of such a study may very well depend on the specific study design. An increase in food abundance would in general increase the energetic reward of engaging in additional feeding activity. On the other hand an increase in food abundance would also allow the fish to maintain surplus energy uptake similar to that at lower food abundance while at the same time reducing activity levels and thereby mortality. Our predictions suggest that the overwintering behaviour follows the latter rationale. However, we also show that when food abundance exceeds a certain level, physiological constraints, such as the stomach filling/evacuation dynamics, prevent the fish from taking energetically

advantage of the increased food abundance. Instead the fish may benefit from the high food abundance if daily accumulated mortality is related to feeding rate. Furthermore, we found that the assumptions underlying the mortality associated with foraging is essential for the timing of the foraging window. If mortality is proportional to the number of hours spent foraging the fish should focus foraging when prey abundance is at its maximum, rather than after the peak where daily surplus energy uptake is maximized due to longer days and higher water temperatures. However, in the literature we find reporting of diurnal variation in predatory activity with a primary peak during sunrise and in some case a secondary peak at sunset. This type of predator-prey interaction has also been reported for sandeel (Hobson 1986), and suggest that daily mortality is independent of the number of hours spent foraging.

Previous studies of the behavioural mediated energy-predation trade-off have focused on daily activity levels and/or the choice between productive high-risk habitats and less productive low-risk habitats. In contrast the present study focus on activity on an annual time scale with a strong seasonal environmental cycle, leaving the daily activity level to be regulated by day length and stomach filling/evacuation dynamics. It is therefore noteworthy to see that the optimal solutions to the energy-predation trade-off follows the same overall patterns or “rules” regardless of the time-scale studied.

Large temporal and spatial variability and catchability of sandeels constitute a major problem for fishery biologist dealing with sandeel stocks. In example the use of catch per unit effort measures as index of fish abundances are associated with large uncertainties and has therefore so far been of little use in stock assessments and monitoring. The present study provides a new insight into how adaptive behaviour may explain parts of the

observed temporal and spatial variability. Of course more field studies is needed to confirm how capable the sandeel is of adapting its overwintering behaviour according to environmental variation. One important question to answer is whether the adaptive potential applies on the individual level, on an inter-annual time-scale, or merely are adaptations occurring on the population level resulting in spatial variability in the timing of the foraging window reflecting long-term averages of local environmental conditions. If we accept that adaptations could occur on the individual level, we need to confront the question of how the individual perceive mortality rates and feeding conditions.

Compensatory increased feeding activity is some of the primary mechanisms underlying climate-induced mortality in fish populations (Biro et al. 2007). Quoting Biro et al (2007) “The effect of climate change on plant and animal populations is widespread and documented for many species in many areas of the world. However projections of climate impacts will require a mechanistic understanding of ecological and behavioural responses to climate change and climate variation”. We propose that the type of model presented here can play a role in this type of projections.

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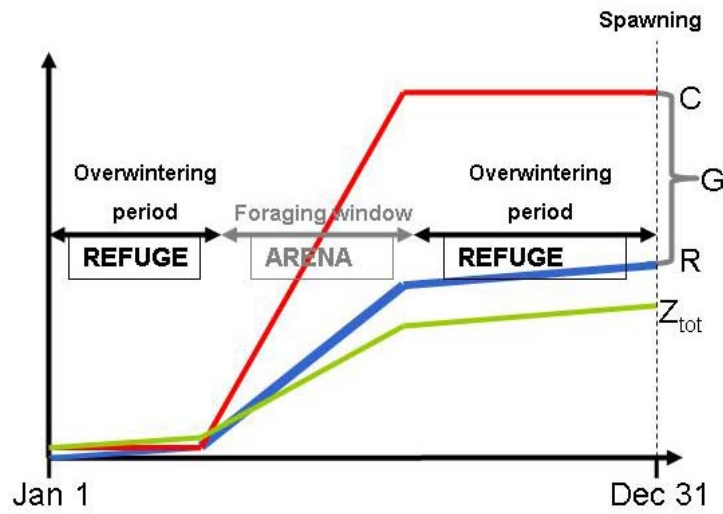


Figure 1. A schematic illustration of the model.

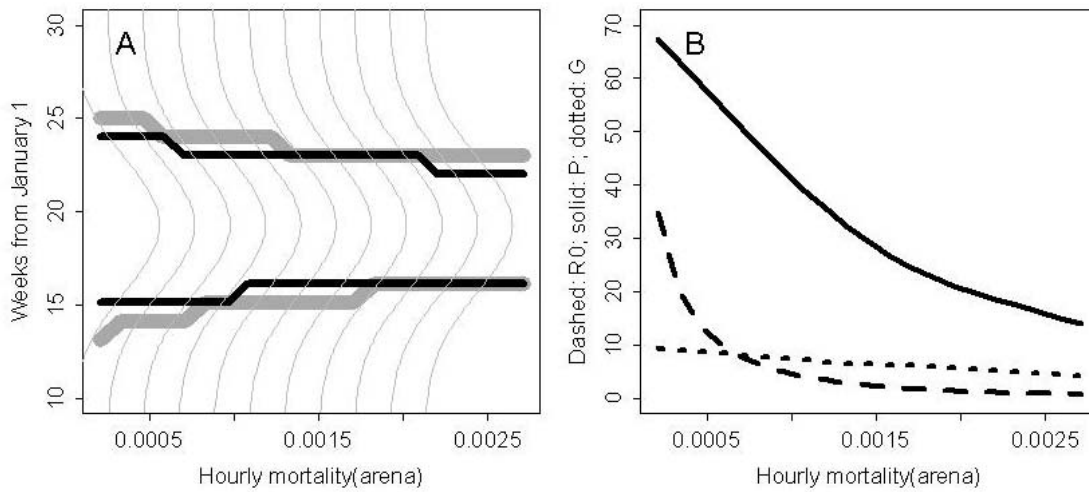


Figure 2. The optimal foraging window in relation to mortality rates. A: The onset and offset of the optimal foraging window as a function of Z_A , for $Z_R/Z_A = 0.01$ (grey) and $Z_R/Z_A = 0.1$ (black). For illustration purposes the spring bloom has been superimposed as thin grey lines. B: Fitness (R_0), annual survival chance (P), and energy available for reproduction (G) as a function of Z_A , with $Z_R/Z_A = 1\%$.

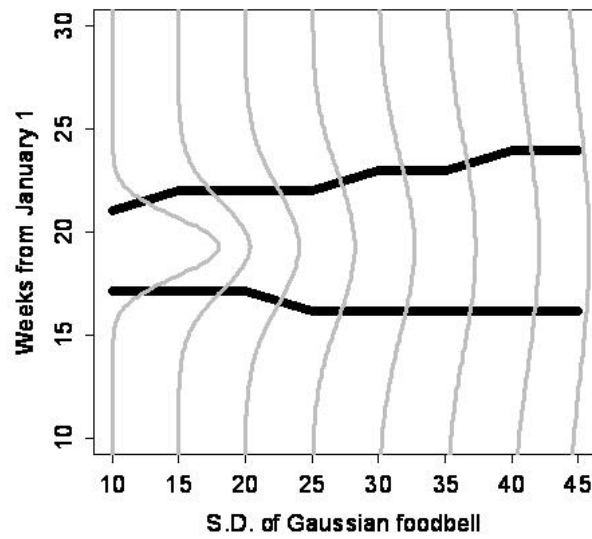


Figure 3. The optimal foraging window in relation to the width of the spring bloom. The onset and offset of the optimal foraging window as a function of the standard deviation of the Gaussian shaped spring bloom. For illustration purposes the shapes of the spring blooms has been superimposed as thin grey lines

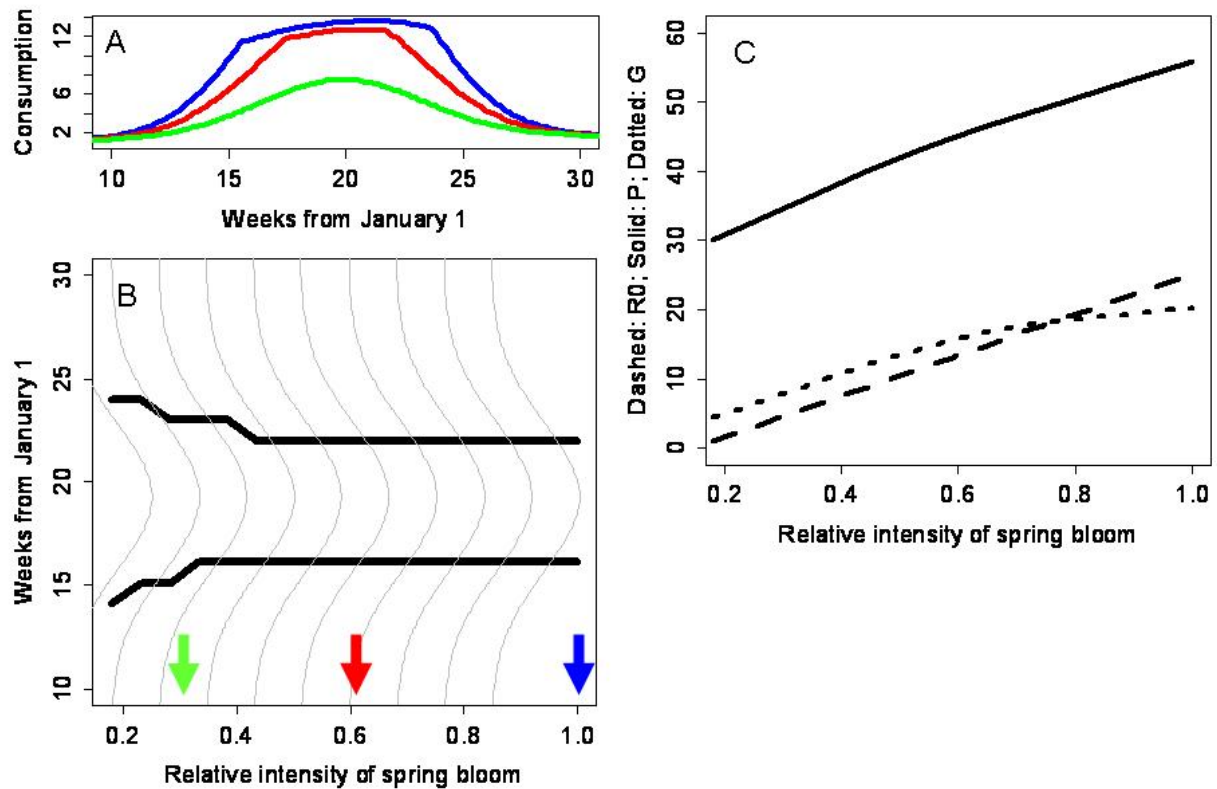


Figure 4. The optimal foraging window in relation to the intensity of the spring bloom. A: Realized consumption (given in hundreds of copepods per day) for 3 different spring bloom intensities. B: The onset and offset of the optimal foraging window as a function of relative intensity of the spring bloom. Coloured arrows match the distributions of realized consumption given in A. For illustration purposes the spring bloom has been superimposed as thin grey lines C: Fitness (R_0), annual survival chance (P), and energy available for reproduction (G) as a function of spring bloom intensity.

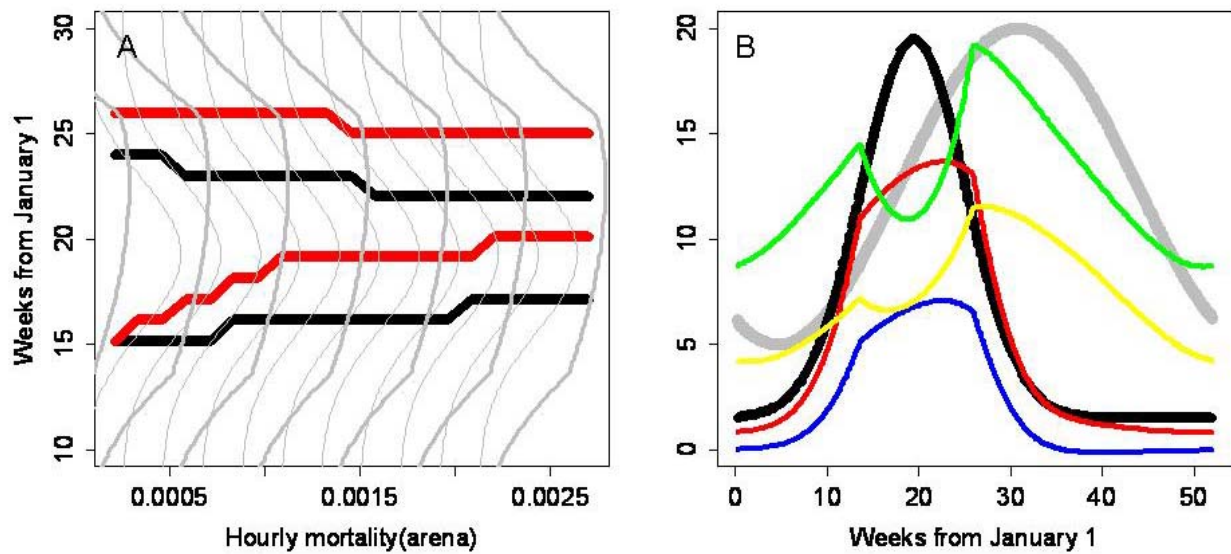


Figure 6. Behavioural and physiological control of the optimal foraging window. A: The onset and offset of the optimal foraging window as a function of Z_A for a given high intensity spring bloom for a default behavioural scenario (black) and a scenario in which daily mortality is independent of the number of hours spent foraging in the arena (red). For illustration purposes the spring bloom (thin grey lines) and relative distribution of potential surplus daily energy uptake (thick grey lines) has been superimposed. B: Various model outputs from the default model setup. Spring bloom (black), water temperature (grey), potential daily consumption (hundreds of copepods) (red), potential daily surplus energy uptake (in kcal/10) (blue), hours spent in the arena (green), and daily metabolic cost of foraging (in kcal/100) (yellow).

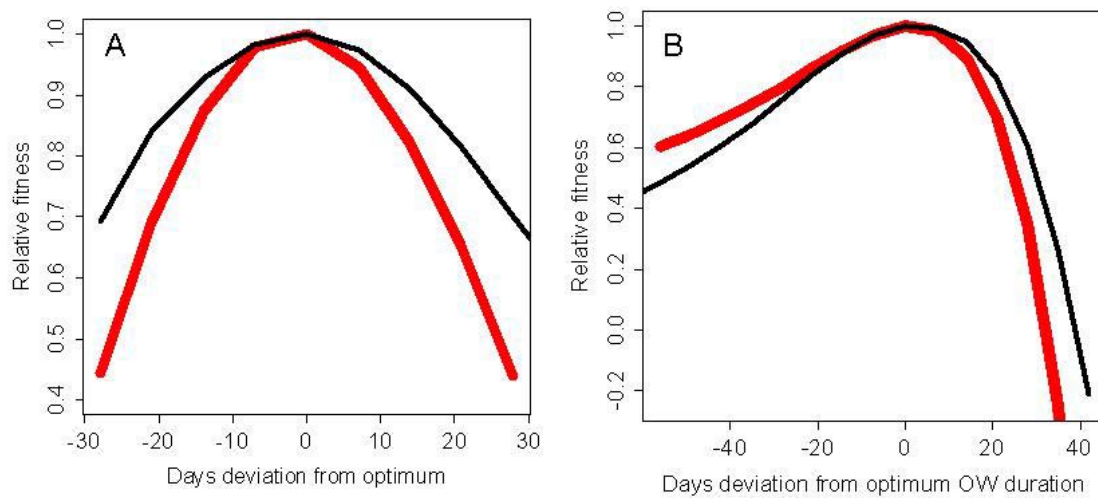


Figure 7. Fitness reduction as a function of mismatch between the foraging window and the spring bloom. A: Relative fitness as a function of a translocation of the optimal foraging window. B: Relative fitness as a function of an expansion/contraction of the optimal foraging window. The exercise was made for two hypothetical scenarios. Low intensity spring bloom of relatively short duration (red) and a high intensity spring bloom of relatively long duration (black).