

An effective algorithm for approximating adaptive behavior in seasonal environments



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ABSTRACT

Behavior affects most aspects of ecological processes and rates, and yet modeling frameworks which efficiently predict and incorporate behavioral responses into ecosystem models remain elusive. Behavioral algorithms based on life-time optimization, adaptive dynamics or game theory are unsuited for large global models because of their high computational demand. We compare an easily integrated, computationally efficient behavioral algorithm known as Gilliam's rule against the solution from a life-history optimization. The approximation takes into account only the current conditions to optimize behavior; the so-called "myopic approximation", "short sighted", or "static optimization". We explore the performance of the myopic approximation with diel vertical migration (DVM) as an example of a daily routine, a behavior with seasonal dependence that trades off predation risk with foraging opportunities in aquatic environments. The myopic approximation proves to be a robust replacement for the life-history optimization, deviating only up to 25% in regions of strong seasonality. The myopic approximation has additional advantages in that it can readily accommodate density dependence and inter-annual variations, aspects that can only be accessed in dynamic programming approaches with escalating computational costs. Furthermore, the explanatory power of the myopic approximation is notably higher than when behavior is not implemented, highlighting the importance for adaptive DVM behavior in ecological models where techniques such as dynamic programming are simply too computationally demanding to be implemented.

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1. Introduction

Life history strategies emerge from the integrated effects of the moment-to-moment decisions taken by an individual organism over its lifetime (Fisher, 1930; Aksnes and Giske, 1990; Houston et al., 1993). The decision schedules (McNamara and Houston, 2008; Feró et al., 2008) that best promote the reproductive success of individuals are those that are most likely to be selected for, and should be the most prevalent in natural populations (Lotka, 1925).

The reproductive success of an organism depends not only on its own decisions, but also on the decisions of other organisms – predators, prey, and competitors – as well as on environmental conditions which in turn are shaped partly by actions of those same organisms. As a result, natural selection of behavior and life history strategies is a dynamic game with density

dependence. Although powerful theoretical frameworks have been established to resolve this dynamics, for example adaptive dynamics (Metz et al., 1996) and genetic algorithms (e.g. Hamblin, 2013), these frameworks involve significant computational complexity which yield them impractical to include in large-scale ecosystem models.

There is a need to include behavior in ecosystem models, but this requires simplified models for predicting behavioral responses. A major simplification is obtained by ignoring density dependence and game theoretic aspects, in which case the problem reduces to life-history optimization: In an environment that fluctuates in a specified way, how should an individual behave so as to optimize life-time reproductive success? This question can be answered with different computational methods such as dynamic programming (Houston et al., 1999; Mangel and Clark, 1988) or genetic algorithms (Hamblin, 2013); the optimal solution should ideally be independent of the computational approach (e.g. Joh et al., 2001; Strand et al., 2002). Optimal strategies can be expected to vary strongly with ontogeny as well as between seasons, in response to cycles of food availability and predation risk (Varpe, 2012).

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Despite the simplification achieved by considering single-agent optimization, these schemes remain computationally intensive (Bellman, 1957). Thus, they are applicable in simple model set ups but not as a dynamic component of ecosystem or biogeochemical models. A case to illustrate this problem is diel vertical migration (DVM) of zooplankton (Angel and Pugh, 2000; Pearre, 2003), which has implications for the structure and function of marine ecosystems (Hays, 2003). It is also a behavior playing a role in the oceans' biogeochemistry, promoting the vertical transport of particulate matter and dissolved gases (Bianchi et al., 2013). The rationale for DVM can be found in a trade-off between feeding at the surface and avoiding the attention of visual predators (Zaret and Suffern, 1976; Lampert, 1989; Aksnes and Giske, 1993; Fortier et al., 2001; Sainmont et al., 2013). The payoff of a specific DVM behavior (when, how long and how deep to migrate) may be expected to be a function of latitude, time of year, food availability, predator abundance and the state of the zooplankton (Fiksen and Giske, 1995; Fiksen and Carlotti, 1998); the optimality of which can only be assessed when placed in the context of a full game theoretic life history strategy. Thus, to produce an exact optimality model of DVM and its impact on, for instance biogeochemical cycling on a global or ocean basin scale, is simply too intensive to be feasible.

An alternative to the full life-history optimization is to base the decision of habitat choice only on the current internal state (e.g. hunger, size, lipid reserves) and the environment (Castellani et al., 2013). Such a decision is in contrast to the life-history optimization that integrates future events into behavior. A celebrated example of such a decision rule is "Gilliam's rule" (Gilliam and Fraser, 1987) stating that an organism should maximize the ratio between growth and mortality. We refer to a decision that only considers the current state of an organism and its immediate environment, with no relation to past or future, as a "myopic" decision (Hutchinson and Gigerenzer, 2005), sometimes referred to as "static optimization" (Leonardsson, 1991). While myopic decisions are simple, intuitive and quick to formulate, they are less than ideal, and we need to know how well such decisions perform relative to alternatives in terms of fitness.

It should be noted that the cost-accuracy trade-off in optimization schemes is not just an issue in modeling, but may have a direct analogy in nature. As with the complexity of modeling full lifetime fitness, there is likely a significant overhead cost in maintaining the genetic coding for life-time optimization rules. In addition, such rules may actually be less proficient than those based on immediate conditions, particularly in a stochastic environment (Giske et al., 2003). Evolution will favor simple myopic approximations that are quite robust in yielding behaviors with high success in bringing organisms to produce many surviving offspring. Myopic approximations to behaviors, based only on immediately available informations and cues (e.g. irradiance, temperature, foraging success), have been shown to perform well in conservation ecology when the problem was small and the time horizon was short (Costello and Polasky, 2004; Wilson et al., 2006), or when the environment is relatively stable.

Our aim here is to explore when a simple decision rule provides a reasonable approximation to the optimal solutions achieved from a full life-history optimization. First, we develop a rigorous proof that Gilliam's rule is a solution to the Dynamic Programming problem when the environment is constant. We then explore the validity of Gilliam's rule when the environment is variable (i.e. seasonal). Finally we discuss whether Gilliam's rule would be an approximation also in the game problem (i.e. taking density dependence into account and in uncertain environments). This facilitates informed decisions on which algorithms to use for including adaptive DVM behavior in more complex ecosystem models.

2. Materials and methods

To simplify the DVM problem, we consider only two distinct habitats: a surface habitat where food is plentiful, but where visual predators are also efficient (the "arena"), and a deeper and darker habitat without food but with much reduced risk from visual predators (the "refuge"). Our aim is to calculate the fraction of time τ an organism should spend in the arena as a function of the body size and environmental conditions, assuming that it spends the remaining fraction $(1 - \tau)$ in the refuge. In the following we identify the τ which maximizes fitness measured as the expected future reproductive effort. This is done with a single-agent optimization approach, i.e. we ignore games and density dependence. Next, we explore a specific case of a diel-migrating zooplankton in a seasonal environment. We consider the state of an organism to be its individual weight w . This state, along with time and behavioral choice τ , determines the instantaneous income energy $g(w, t, \tau)$ and the instantaneous mortality $\mu(w, t, \tau)$. We assume that energy is allocated to growth in juveniles ($\psi(w) = 0$ whenever $w < w_a$, with w_a being the adult weight) while adults allocate all energy to reproduction ($\psi(w) = 1$ whenever $w \geq w_a$). The parameters and variables are described in Table 1.

2.1. Dynamic programming

Dynamic programming (Bellman, 1957; Houston et al., 1999) is a mathematical and computational technique for dynamic optimization. In our context, its aim is to determine the optimal strategy τ at each point in time t and for each possible state w of the organism. To this end, the core of dynamic programming is an equation governing the future reproductive output $F(t, w)$ of an optimal individual at time t and in state w :

$$\dot{F} + \max_{0 \leq \tau \leq 1} \left[\frac{\partial F}{\partial w} (1 - \psi)g + \psi g - \mu F \right] = 0. \quad (1)$$

Here, the over-dot indicates time derivative, $\dot{F} = \partial F / \partial t$. The arguments t, w and τ are omitted from the functions F, ψ, μ and g for brevity. The term $(\partial F / \partial w)(1 - \psi)g$ represents increase in fitness due to growth and combines the growth rate $(1 - \psi)g$ with the sensitivity of fitness to animal size $\partial F / \partial w$. The term ψg represents immediate reproductive effort while the term $-\mu F$ determines expected loss of fitness due to mortality. The maximization in this equation expresses a trade-off between avoiding mortality (maximizing $-\mu F$), reproducing immediately (maximizing ψg) and investing in growth thus facilitating future reproduction (maximizing $(\partial F / \partial w)(1 - \psi)g$); this maximization determines the optimal strategy τ for each time t and state w . The equation is solved numerically by iteration backwards in time from a boundary condition stating that the future reproductive output at any age is zero in the distant future: $F(\infty, \cdot) = 0$.

2.2. Myopic approximation

The dynamic programming Eq. (1) can be simplified when the environment is constant (aseasonal): $\dot{g} = \dot{\mu} = 0$. It follows that the fitness function (F) will not depend explicitly on time, $\dot{F} = 0$, and Eq. (1) simplifies to:

$$\max_{0 \leq \tau \leq 1} \left[\frac{\partial F}{\partial w} (1 - \psi)g(\tau) + \psi g(\tau) - \mu(\tau)F \right] = 0 \quad (2)$$

Here we exclude the w arguments for brevity, but include the τ argument to clarify which terms depend on instantaneous behavioral choice. Since the mortality is always positive, $\mu(\tau) > 0$ [nothing

Table 1List of symbols and parameters. The units used are liter (L), microgram carbon (μgC), meter (m), individuals (ind), second (s) and days (d).

	Descriptions	Values	Units
Symbols			
F	Future reproductive output		Biomass
R_0	Lifetime expected reproduction output		Number of eggs
R	Encountered food		$\mu\text{gC d}^{-1}$
w	Weight		μgC
P	Probability to be alive		
t	Time		d
ξ	Standard metabolism		$\mu\text{gC d}^{-1}$
g	Available energy		$\mu\text{gC d}^{-1}$
g_s	Available energy at the surface		$\mu\text{gC d}^{-1}$
μ	Mortality rate		d^{-1}
μ_p	Total predation mortality rate		d^{-1}
μ_s	Predation mortality rate in the surface habitat		d^{-1}
μ_d	Predation mortality rate in the deep habitat		d^{-1}
v	Ratio surface/deep predation mortality	μ_d/μ_s	
N_f	Density of fish		Fish m^{-3}
C_{max}	Maximum consumption rate		$\mu\text{gC d}^{-1}$
f	Feeding level	[0, 1]	
f_c	Critical feeding level	[0, 1]	
f_{max}	Maximum feeding level possible	[0, 1]	
τ_{day}	Fraction of daylight per day	[0, 1]	
τ_s	Fraction of time at the surface	[0, 1]	
L_c	Individual length		μm
ϕ	Latitude		$^\circ$
D_d	Depth of the deep habitat (individual size dependent)		m
V_s	Clearance rate		L d^{-1}
Parameters			
w_e	Egg weight	1	μgC
w_a	Adult weight	1000	μgC
γ	Factor of reduction in critical feeding level and predation mortality during diapause	10	
D_s	Depth of the surface habitat	30	m
v	Swimming speed coefficient	7200	
α	Assimilation efficiency	0.6	
ψ	Fraction of available energy allocated to reproduction	0, 1	

lives forever], and the maximum equals 0, we can divide with μ and single out those terms that depend on τ to obtain

$$\left[\frac{\partial F}{\partial w} (1 - \psi) + \psi \right] \cdot \max_{\tau} \left[\frac{g(\tau)}{\mu(\tau)} \right] = F \quad (3)$$

since $\left[\frac{\partial F}{\partial w} (1 - \psi) + \psi \right] \geq 0$.

From Eq. (3) it follows that the optimal fraction of time in the arena is given by Gilliam's rule (Gilliam and Fraser, 1987):

$$\tau^*(w) = \arg \max_{0 \leq \tau \leq 1} \left[\frac{g(w, \tau)}{\mu(w, \tau)} \right]. \quad (4)$$

Note that the optimal fraction of time τ^* is independent of the reproductive effort ψ , so that e.g. both juveniles and adults should follow Gilliam's rule. Even though juveniles and adults differ in their energy allocation strategy (juveniles grow; adults reproduce), the myopic rule applies equally well for both life stages because it concerns the energy gain, not the allocation (growth or reproduction).

Gilliam's rule (4) may be adopted also in situations where there is no life history argument supporting the optimization, for example in situations where the environment changes. In that case, we refer to the rule (4) as the myopic strategy. Myopic means short-sighted and reflects that maximizing the ratio g/μ does not take future changes in conditions into account. In this case, we use the symbol $F^*(w, t)$ to denote the resulting fitness of an animal which follows the myopic strategy. This raises the question: how near is $F^*(w, t)$ to $F(w, t)$, or what is the loss of fitness by using the myopic strategy? To examine this, we turn to a specific example of DVM in a seasonally varying environment.

2.3. DVM in a seasonal environment

We consider a zooplankton (copepod) that has to make a decision on how to divide the hours of daylight between feeding at the surface and seeking refuge in a deep, safe habitat. Encountered food $R(t, w)$ (cf. Appendix A) at the surface varies over the year. Mortality risk from visual predators μ_p is influenced by light intensity which vary over the year and over the daily cycle depending on latitude. We assume the surface habitat to be as safe during night-time as the deep habitat is at full daylight. It follows then that the individuals should move to the surface to feed at least during the night. The question which remains is how long a time the individuals should reside at the surface during daytime (Fig. 1).

The state of an individual during its life is characterized by its weight w . Size is used to scale rates of search efficiency, maximum consumption rate (C_{max}) and standard metabolism (ξ). Predation is from a herring-like predator (Huse and Fiksen, 2010), an abundant and important visual predator of zooplankton. Fish visual prey detection range and predation efficiency is affected by ambient light radiance, prey size and contrast (Aksnes and Utne, 1997). Thus, predation at the surface increases with prey body size as prey are more easily detected by the visual predator. In the deep habitat, predation rate decreases with size because individuals can swim to deeper and darker habitats as their ability to swim increases with size. The specific parameterization of food availability, day length, physiological rates and predation mortality rely on previously published models described in Appendices A–C. Finally during the winter, zooplankton migrate to the deep habitat to over-winter safely and come out of dormancy when the next spring bloom starts.

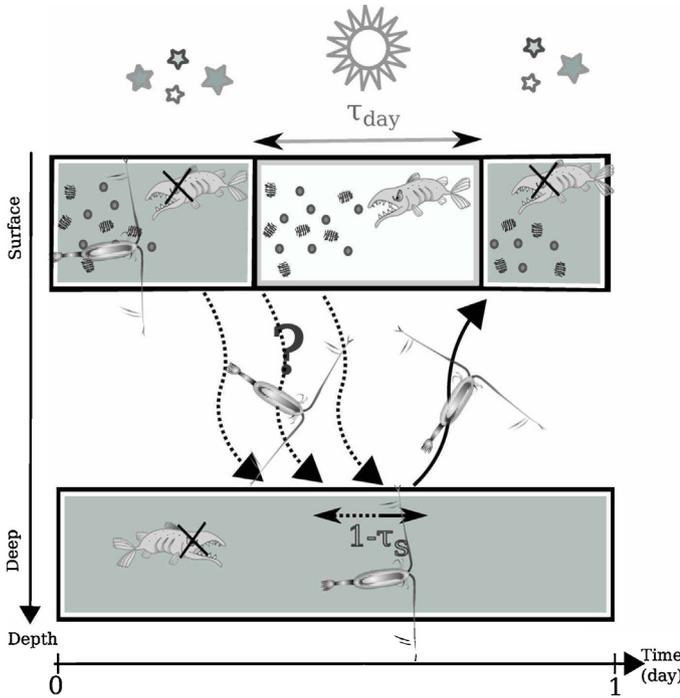


Fig. 1. Schematic representation of the DVM issue. Zooplankton come to the surface at dusk to enjoy the food availability while the visual predation efficiency is reduced. At dawn zooplankton has the choice between finding refuge at depth or staying at the surface to feed. The fraction of time zooplankton stay in the deep is $1 - \tau_s$.

2.3.1. Growth and mortality

The assumptions about environment and individual physiology together with the behavioral decision determine available energy and mortality at the surface (g_s and μ_s) and the deep (μ_d).

Available energy is determined by consumption, assimilation efficiency and standard metabolism. We introduce the feeding level ($0 \leq f(t, w) \leq 1$) to indicate the proportion of food ingested compared to the maximum consumption ($C_{\max}(w)$, cf. Appendix C). It is described by a functional response type II with the available food reduced by the fraction of the time spent at the surface τ_s :

$$f = \frac{\tau_s R}{\tau_s R + C_{\max}} \quad (5)$$

Similarly, we introduce f_c the critical feeding level ($0 \leq f_c(w) \leq 1$) as the minimum ingested food required to cover metabolic costs ($\xi(w)$, cf. Appendix C):

$$f_c = \frac{\xi}{\alpha C_{\max}} \quad (6)$$

where α is the assimilation efficiency. Available energy at the surface is thus defined as:

$$g_s = \alpha C_{\max}(f(\tau_s = 1) - f_c). \quad (7)$$

Predation mortality in the two habitats depend on environmental conditions (latitude and time of the year) and body size. We assume that the surface habitat is located close to the phytoplankton layer at a depth of $D_s = 30$ m while the refuge depth is function of the zooplankton swimming capacity. Assuming zooplankton can swim the equivalent of one body length per second (Kiørboe et al., 2010) over 2 h, the depth of the refuge is:

$$D_d = D_s + \nu L_c(w) \quad (8)$$

where the length L_c of the individual is converted from its weight (see Appendix D, Eq. (D.5), Rey-Rassat et al., 2002), and ν is the

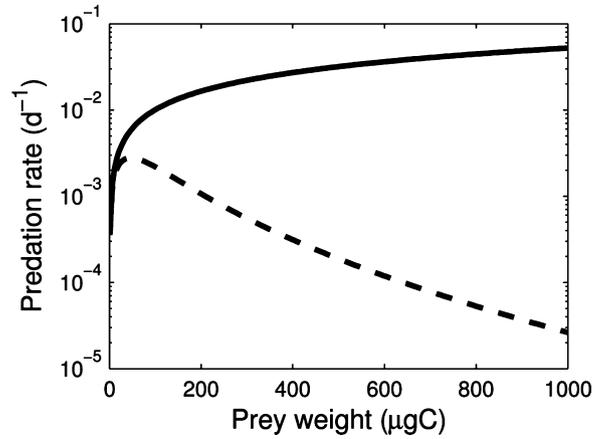


Fig. 2. Predation rate as a function of the prey weight, at 140 Julian day and a latitude of 70° N at the surface habitat (solid), and the refuge (dashed). The depth of the surface habitat does not change with individual weight, therefore the predation rate increase with the surface area of the prey. In contrast, larger individual can swim deeper, and therefore the refuge become safer with the increase of individual size.

swimming speed coefficient ($\nu = 7200$). The depth determines predation mortality in the surface and the deep habitats (Fig. 2).

The average growth and mortality during a day will be determined by the fraction of time spent in the two habitats and the fraction of time with daylight τ_{day} . The individual will feed during the night $1 - \tau_{\text{day}}$ and during the fraction of the daylight when it is at the surface $\tau_s - (1 - \tau_{\text{day}})$, while standard metabolism uses energy irrespective of the habitat. Likewise, it will experience surface predation rates (μ_s) while located at the surface habitat during daylight hour $\tau_s - (1 - \tau_{\text{day}})$ and reduced predation rate due to darkness (μ_d) during the night $1 - \tau_{\text{day}}$ and in the deep habitat $1 - \tau_s$. The total predation mortality rate is therefore:

$$\mu_p = \mu_s(\tau_s - 1 + \tau_{\text{day}}) + \mu_d(2 - \tau_{\text{day}} - \tau_s) \quad (9)$$

and the total available energy and mortality rate μ are thus:

$$g = \alpha C_{\max}(f - f_c) \quad (10)$$

$$\mu = \mu_0 + \mu_p \quad (11)$$

where μ_0 is a size and time-independent non-predation background mortality. Note that growth and mortality are both function of size although no specific distinctions are made between juveniles and adults. Finally, we assume that individuals will enter diapause to overwinter when the maximum possible growth is negative, i.e. when $f(\tau_s = 1) - f_c < 0$. During diapause individuals migrate to the very deep habitat and reduce standard metabolism by a factor γ . Down there, they are even safer from predation than in the deep habitat (we assume that the predation rate is also reduced by γ , such as $\mu_p = \mu_d/\gamma$).

2.3.2. Simulation

The simulations with the two methods starts at the beginning of the year, with a single individual starting with an initial body mass $w_0 = 100 \mu\text{gC}$. We follow the development of the individual weight, survival probability and reproductive output through a 10-year simulation, long enough to avoid terminal effects on behavior with the individuals following the dynamic programming decision rule (Mangel and Clark, 1988). In the case of the dynamic programming method, the optimal time individual should spend at the surface has to be solved numerically, following Eqs. (E.4) and (E.8)

developed in Appendix E. The myopic approximation, however, admits an analytical solution to Eq. (4):

$$\tau_s^* = \frac{1}{(1-f_c)} \left(f_c + \sqrt{f_c + f_{\max}(1-f_c) \left(\frac{\nu}{1-\nu} - 1 + \tau_{\text{day}} \right)} \right) \quad (12)$$

with $\tau_s \in [1 - \tau_{\text{day}}, 1]$ during the spring bloom and 0 in diapause, where $f_{\max} = R/C_{\max}$ is the maximum feeding level possible. The comparability between the two methods numerical implementation is verified in a constant (aseasonal) environment, where the two methods should (and do) predict the same behavior (see Fig. 7, Appendix F).

The expected lifetime reproductive output R_0 is used to compare the two methods. Based on evolutionary reasoning this should be maximized, and this is what the optimization does. The question is how close the proximate myopic approach can come to this baseline. For dynamic programming $R_0 = F(0, w_0)/w_e$ while for the myopic decision $R_0 = F^*(0, w_0)/w_e$ is calculated as:

$$R_0 = \frac{1}{w_e} \int_0^\infty P(t) \psi(w(t)) g(w(t)) dt. \quad (13)$$

where the probability to be alive is found by solving $\dot{P} = -\mu(t)P$. There is no density dependence in the model.

3. Results

We compute the life-time reproductive value for three individuals: one following the optimal dynamic programming method (individual DP), one following the myopic approximation method (individual MA), and a third that does not migrate daily (null strategy; individual H_0). The null strategy serves as a baseline when DVM is not taken into account in the model. We first compare the three individuals in detail in a 2-year simulation, where we set latitude to 70° N (i.e. above the Arctic circle), and to 15 days feeding season duration (Fig. 3). Note how poorly the null strategy individual is doing compared to the other two individuals (panel e), mainly because its survival decreases much faster than the other two individuals (panel c).

Both migration strategies (DP and MA) predict that individuals should come to the surface most of the day at the beginning of the bloom (panel a) in order to maximize their consumption (panel b), and growth (panel d), at the expense of their survival (panel c). The myopic method predicts that individuals should stay all day long, while dynamic programming predicts a short migration to the deep. When the available food increases and consumption approaches its maximum, both individuals reduce the time spent at the surface to night-time duration (gray background, panel a), thereby reducing their feeding below their maximum potential (the lines are lower than the maximum consumption in dark gray, panel b). Individuals following the three alternative strategies mature at about the same age (panel d). The individuals obeying H_0 remains at the surface and get the maximum feeding level but survival is much reduced compared to the migrating individuals.

When the night gets too short to maintain a sufficient feeding level, the migrating individuals commence feeding during part of the daytime. During midnight sun, the adaptive strategy is to spend more time at the surface (panel a). In this situation, individuals with the optimal strategy DP spend a bit more time at the surface than individual MA (panel e). When food becomes scarce, individual DP prescribes a safer strategy than individual MA which maximizes growth by spending all day feeding at the surface. As a consequence, individual MA ends up with a lower survival probability but have a longer reproductive period than individual DP and which partly make up for the lower survival.

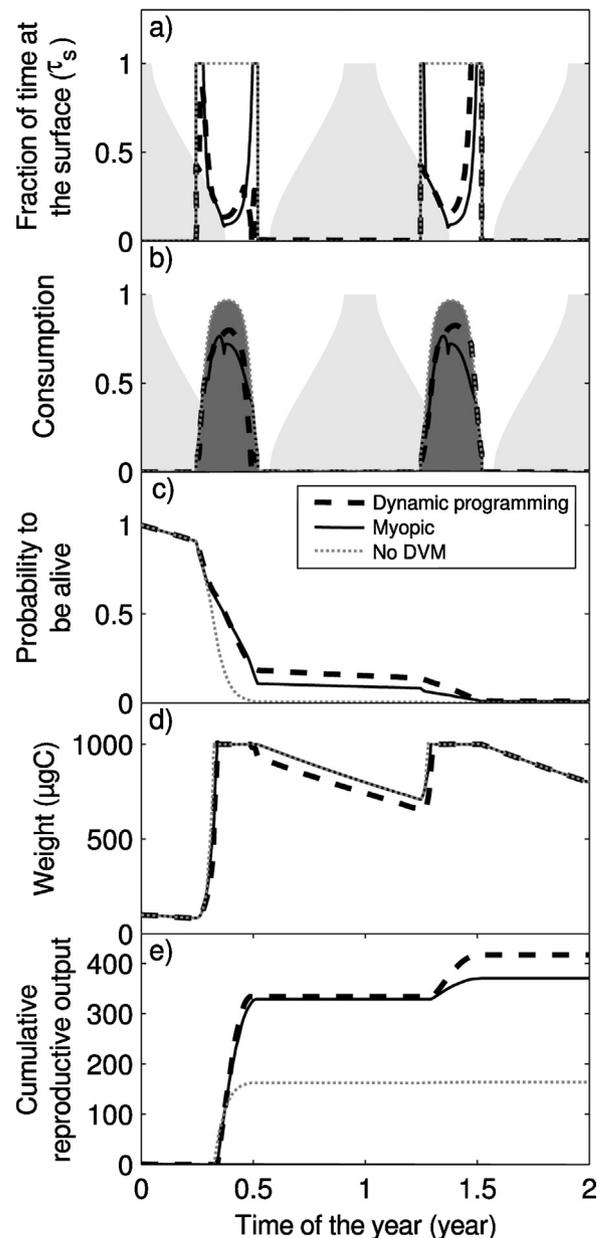


Fig. 3. Comparison between individuals following dynamic programming (thick dashed line), the myopic approximation (thin black line) and a non-migrating behavior (grey line). The fraction of time the individual spend at the surface with night length represented by the grey patch (a and b) and the maximum feeding level in dark gray background (b). For clarity, we run the model for only 2 years in this case. Weight at the start of the year is $100 \mu\text{gC}$, the fish density is $10^{-6} \text{ fish m}^{-3}$ and the latitude 70° N.

During winter, all individuals overwinter and slowly lose weight due to metabolic maintenance. When the bloom starts the following year, individual MA maximizes its growth to regain adult size as fast as possible, while individual DP plays a safer strategy by returning to the surface to feed only at night. Both migration strategies (DP and MA) predict that individuals should come to the surface to feed only during the night when food is plentiful, but increase their daytime feeding when the night gets too short. However, individual MA plays it slightly safer than individual DP. Unlike MA, DP optimizes with the benefit of knowing the future and disregard predation risk to maximize its remaining opportunity for reproduction at the end of the season.

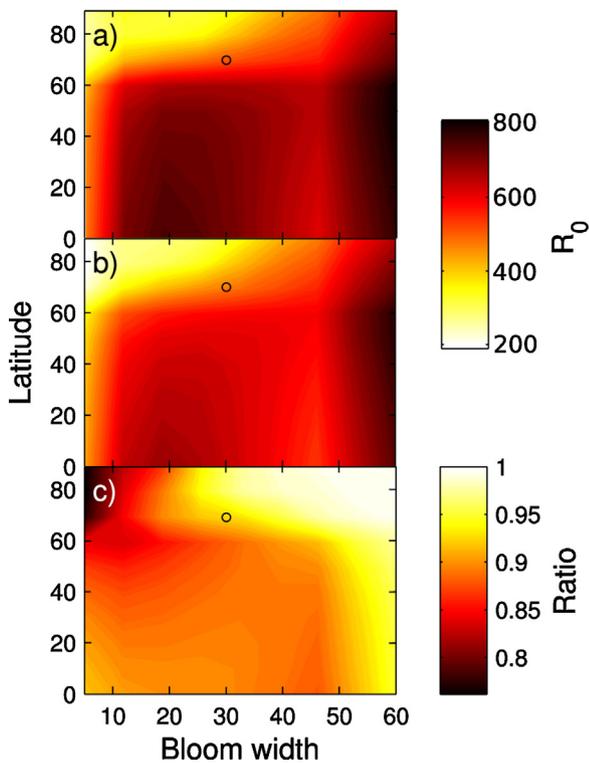


Fig. 4. Influence of latitude and duration of the feeding season on the fitness of individuals following the dynamic programming (a) and the myopic approximation (b), along with the ratio myopic over the dynamic programming fitness (c). Running time 10 years, fish density 10^{-6} fish m^{-3} . The open dots indicate the parameters used to compute Fig. 5.

3.1. Latitude and feeding season duration

In a cyclic (seasonal) environment, one can expect differences to arise between the dynamic programming and the myopic approximation methods, as individuals following the dynamic programming method optimize their decisions considering their full life time. Mainly, they have knowledge of the duration of the feeding season and their future survival expectancy, and adapt their behavior to this. When looking at the fitness distribution over the latitudinal gradient in seasonal day-length (from the equator to the pole), we see a general decrease in fitness, as individuals have to take more risk to feed when the fraction of daylight hours increases during the summer (i.e. latitude, Fig. 4).

The relationship is slightly more complex when looking at the feeding season duration. In a short bloom, any extra days of feeding increase fitness. However, as we keep the net annual production constant in the system (describing a constant turn over of nutrients, cf. Appendix A), food concentration drops and the peak level decreases as the bloom become longer. When the bloom length becomes long enough, individuals become food limited and they have to spend more time at the surface. Furthermore, when the bloom lasts over the summer, the fraction of daylight hours per day decreases at the end of the bloom, and individual can forage longer at low predation risk. Thus an alternation of increasing and decreasing fitness is observed when looking at the feeding season duration gradient, evident for both myopic and dynamic programming decision rules (Fig. 4a and b).

When comparing the two strategy outputs, the larger differences are found in the short feeding season and at high latitude (Fig. 4c). However, the decrease value of the ratio in high latitude could be an artifact due to low fitness values, enhancing any existing differences.

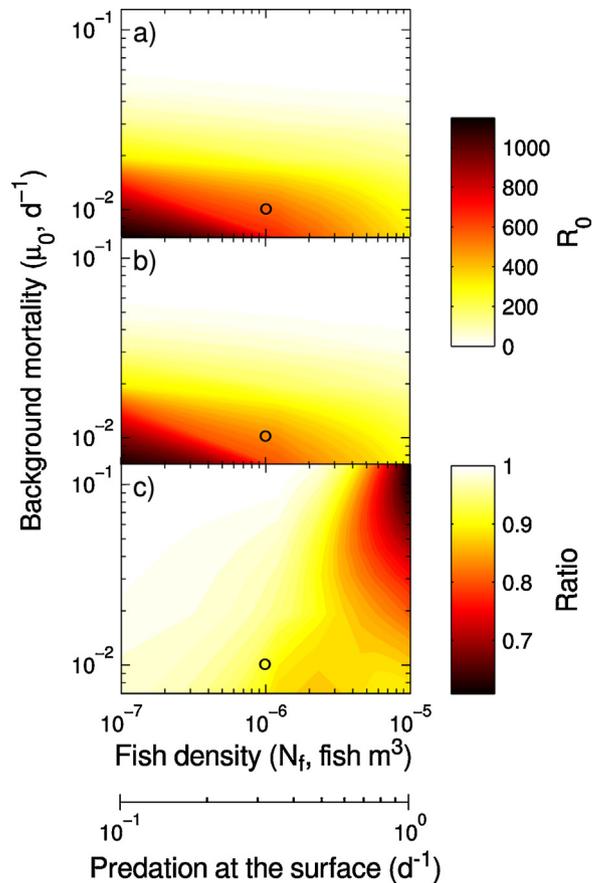


Fig. 5. Influence of the size independent background mortality (μ_0), and fish density (N_f) on the fitness of individuals following the dynamic programming (a) and the myopic approximation (b), along with the ratio myopic over the dynamic programming fitness (c). The fish density affects the individuals as a function of their size, but also as a function of the environment (latitude, time of the year). We used a latitude of 70° N and a bloom width of 30 days for the calculation. The second x-axis indicates the corresponding predation rate at the surface for an adult individual, during the summer (at 140 Julian day). The open dots indicate the parameters used to compute Fig. 4.

Overall, the difference between MA and DP individual fitness is at most 25%, and is only evident in strongly seasonal situations (high latitude with short feeding season).

3.2. Mortality

When increasing background mortality and fish density, individual fitness decreases as expected (Fig. 5a and b). The highest differences is found when the predation mortality is high, as the myopic method often prescribe more risk than the dynamic programming method at the beginning of the bloom, with consequences for life-time fitness. When the fish density is lower than 10^{-6} fish m^{-3} , the myopic approximation explains more than 90% of the optimum fitness. When both the background mortality and the fish density are high, the myopic approximation loses its power, and drops to around 60% of fitness. This is in any case much higher than the non-migrant strategy which for many cases only scores a small fraction of the possible fitness (Fig. 6).

4. Discussion

We have provided a proof that Gilliam’s rule is indeed a solution to the full dynamic programming problem in the case where the environment was constant (i.e. aseasonal). In the DVM example,

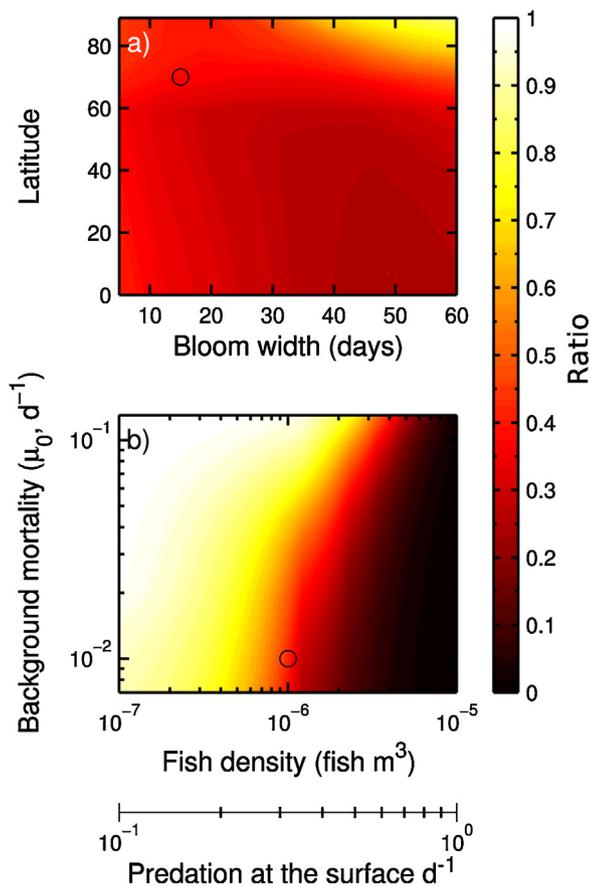


Fig. 6. Ratio between the non-migrating behavior and the life time optimization calculated with dynamic programming, for a variation in latitude and bloom duration (a), and over variation of background mortality and density of fish (b). The second x-axis on panel b indicates the corresponding predation rate at the surface for an adult individual, during the summer (at 140 Julian day). The circles show the parameters used to compute the other panel: a background mortality of 0.01 d^{-1} , and a fish density of $10^{-6} \text{ fish m}^{-3}$ for panel a, and a latitude of 70° with a 30 days of bloom width for panel b.

the myopic approximation method seemed to perform well under most of the parameter space studied, with only 10% differences in predicted life-time reproductive output relative to the life-time optimization. To put this in context, a relative fitness of 0.9 means that the population of DP individuals will be double of the MA's after 6.6 generations. This difference is minimal compared to the internal ecosystem and environmental variability. The simplicity and the low computer power needed by the myopic approximation suggests this to be an efficient alternative to life-time optimization methods such as dynamic programming or genetic algorithms. This makes the myopic approximation well suited to be used for describing spatial behavior of higher trophic levels in large circulation models or end-to-end models.

The myopic strategy was inferior to dynamic programming in high latitude regions with short blooms and under high predation pressures, with up to 25% differences between the two strategies. In the presence of a short bloom, the myopic method fails to predict the imperative to feed before the winter settles in, while dynamic programming provides the perfect knowledge of the imminent end of the bloom and copepods are then prudent enough to feed and hence taking higher risks. The co-occurrence of the bloom with mid-night sun at high latitude enhances this phenomena, since the temporal bolt-hole with a safe feeding period is removed.

This parameter space corresponds to the polar region, where the high seasonality and high production produce a short intense bloom that is sufficient to sustain a large concentration of fish (e.g. Dommasnes et al., 2004), sea birds (e.g. Harding et al., 2009), jellyfish and ctenophores (e.g. Purcell et al., 2010) and, even marine mammals (e.g. Laws, 1977; Laidre et al., 2007). Zooplankton in this area often display multi-year cycles (Conover, 1988) and therefore mortality rate could have a larger effect on the individual than growth (e.g. Aksnes and Giske, 1990). Furthermore, in a short feeding season environment, spawning time could have a larger impact on the individual reproduction success than the number of eggs produced (Varpe et al., 2007; Sainmont et al., 2014a). In such systems, the myopic approximation should be used with care or rules other than Gilliam's rule should be considered.

In every point of the parameter space explored, the myopic method prevailed over a non-migrating strategy (Fig. 6 and Kristiansen et al., 2009). Indeed, even in the region where myopic method was found significantly inferior to dynamic programming (high latitude environments), the non-migration behavior scored only around 40% of the optimal reproduction output against 75% with the myopic methods under moderate predation rates. Thus, including DVM is a requirement to capture growth, survival and reproduction of zooplankton in a model. Hence, modelers are faced with a choice as to how to include behavior in their large ecosystem models. Behavior can, for instance, be hard coded, although the fidelity of the resulting model hinges on how well the assumed patterns capture the actual behavioral rationale. For example, a DVM behavior which prescribes staying at the surface only during night time (e.g. Andersen and Nival, 1991) would result in individuals that starve unrealistically in presence of food availability at high latitude during mid-night sun. Alternatively, a hard coded 50% time foraging would induce a reduction of feeding opportunity in early spring. In these circumstances, implementing a myopic strategy such as the one presented in this study is an attractive alternative which yields realistic and near-optimal behavior without increasing computational demands.

The importance of DVM was illustrated by a specific model of a zooplankton in a seasonal environment. The specific results are influenced by the assumptions of the model. Regarding mortality, we overestimate the predation rate at the surface as the light level used in the daily calculation was at noon, which represent the maximum light intensity of the day. In reality the light level is varying over the day, and the inclination of the sun matters for the light penetration depth. However, as the fish eyes efficiency satiate at quite low light levels, this assumption would influence the fish efficiency only at sunrise and sunset. The timing and depth of the phytoplankton bloom was also assumed to be fixed, while it is a function of the thermocline depth, wind pattern, turbidity and of the light attenuation coefficient at the given place and time (Aksnes and Giske, 1993; Sverdrup, 1953; Sakshaug et al., 1991; Aksnes and Utne, 1997; Huisman et al., 1999). The 30 m depth, was then used as a reference to compute the depth of the refuge habitat and thus entered in the calculation of the surface and deep predation mortality rate. In the model, we do not consider temperature, even though temperature is expected to differ between the surface and the deep habitat. This difference could influence the metabolic cost and therefore the growth the individual amongst the habitats. However, the rules dictating behavior are based on the values of growth and mortality, therefore the comparisons between the two methods are independent of what governs these variables. We assumed that the zooplankton had no food available in the deep, while they can partially feed on marine snow or detritus as an alternative to the rich phytoplankton bloom (e.g. Hansen et al., 1996). Finally, we assume that there is no influence of the bloom on light attenuation. Thus, while details of the model depend on a variety of specific assumptions, we nevertheless expect that the general results regarding

the importance of resolving DVM (e.g. [Pearre, 2003](#) and present study) and the relative merit of the myopic approximation remain robust.

Our model allows the choice between two alternative habitats. However, the equations can easily be extended to n habitats, or even a continuous water column. A specific representation of depth position could be of particular interest for density-dependence and add some prudence to the organisms (e.g. “state and prediction-based theory” e.g. [Railsback and Harvey, 2013](#)), as the choice of a particular habitat could also be driven by food competition or seeking protection through numbers from predators.

In our calculation of the expected reproduction output fitness measure, we assume that all the eggs have the same fitness value, independent of the time of year they are born. However, modeling studies have shown that eggs spawned prior to and at the beginning of the season have a much higher fitness compared to the offspring born at the end of the feeding season ([Varpe et al., 2007](#)). Similarly, capital breeding has been shown to be a successful strategy, especially in short feeding seasons ([Sainmont et al., 2014a](#)), thus leading individuals to store reserves to be able to spawn before the feeding season. Such capital breeding individuals that have not yet reproduced are highly vulnerable to visual predators, due to their large size and conspicuous storage reserves ([Hays et al., 2001](#); [Sainmont et al., 2014b](#)). Such individuals should give higher priority to survival than to feeding opportunities, compared to the prediction from Gilliam’s rule. We could thus expect these individuals to favor deep distribution over any kind of migration. The change of priority over the life time can emerge in dynamic programming optimization but are lacking in the myopic approximation.

The main drawback of optimization procedures is the computational complexity, which necessitates simplifying assumptions. Dynamic games between animals can be resolved with dynamic programming, but at high computational cost ([Houston et al., 1999](#)). Density dependence can not be easily implemented in dynamic programming, since density dependence is typically formulated forwards in time, while dynamic programming works backwards. Density dependence could be accommodated by techniques such as ideal free distribution (e.g. [Giske et al., 1997](#)) but this also requires significant computational efforts. In contrast, the myopic approach would integrate density in the current environmental conditions at low computational cost. We therefore expect that the myopic approximation utility improves in these cases over the dynamic programming method, even though the power of the myopic approach in such circumstances remain to be shown.

Another simplification concerns the information available to the animal and environmental stochasticity. Rapid fluctuations in the environment, such as in food availability, can easily be modeled with white noise and implemented in dynamic programming. However, when including more persistent random fluctuations in the environment, such as inter-annual variation in the timing of the bloom, optimal behavior includes predicting future environmental conditions. Although there exist theoretical approaches to this problem (the information state machinery, e.g. [Mangel and Clark, 1988](#)) computations are infeasible except in extremely simplified situations. Furthermore, the optimization problem is more than just a concern for modelers. The emergent behavior genetically encoded for and presumably triggered by environmental conditions and internal state is that which should be optimized in terms of reproductive success. There is almost certainly a trade-off involved in executing a perfectly optimal life history strategy, and the costs of maintaining elaborate sensory ability, the apparatus to react to environmental cues, and the genetic coding required to pass this ability to future generations. All organisms are limited in how well they can predict future environmental conditions (food

availability, temperature, predation risk) in different habitats and the question arises as to how much organisms should invest in ideal optimization schemes in the face of this uncertainty ([Fawcett et al., 2014](#)). Simpler, less elaborate rules could have an evolutionary advantage.

4.1. Conclusion

We have shown that resolving behavior is crucial for the lifetime reproductive output of higher trophic levels. We have shown that under certain conditions, the myopic strategy, Gilliam’s rule, is optimal in constant environments, both for juveniles and adults. Under varying conditions, the myopic approximation is a reasonable alternative to more precise life time optimization methods as dynamic programming, when the environmental conditions are not too harsh, i.e. not in high latitudes, for short feeding seasons or under high predation mortality. For the modeler, the myopic strategy can be used in regional or global bio-geochemical models where the focus is not on optimal behavior nor individual state, when computational time is an issue, or when inter-annual environmental variability or density dependence makes a complete optimization intractable. For the organism, simple strategies such as the myopic approximation may be selected for as a robust and low cost response to the unpredictability of future conditions.

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Appendix A. Food availability

The phytoplankton bloom is modeled as a Gaussian function centered around the time T_p , with a width σ and amplitude $a = 80,000 \mu\text{g C d}^{-1}$. The food concentration is multiplied by the clearance rate of an individual to arrive at the encountered food (function of the time of the year t , and the individual weight w):

$$R(t, w) = V_s \frac{a}{\sigma \sqrt{\pi}} \exp\left(\frac{-(t - T_p)^2}{2\sigma^2}\right) \cdot \mu\text{g C} \cdot \text{L}^{-1} \quad (\text{A.1})$$

where V_s is the clearance rate (weight dependent, cf. [Appendix C](#)). In moderate and high latitude, the phytoplankton bloom duration is of the order of weeks, leaving zooplankton without food the rest of the year.

Appendix B. Daylight cycle

We use the model by [Forsythe et al. \(1995\)](#). If t is the time of the year (in day), and ϕ the latitude, then τ_{day} is the daylength.

$$\begin{cases} P = \arcsin(\beta_1 \cos(\beta_2 + 2 \arctan(\beta_3 \tan(\delta(t - \theta)))) \\ \tau_{\text{day}}(t_y, L) = 1 - \frac{1}{\pi} \arccos\left(\beta_4 + \sin\left(\frac{\pi(\phi/\varphi) \sin(P)}{\cos(\pi(\phi/\varphi) \cos(P))}\right)\right) \end{cases} \quad (\text{B.1})$$

with ϕ the latitude, $\beta_1 = 0.39795$, $\beta_2 = 0.2163108$, $\beta_3 = 0.9671396$, $\beta_4 = 0.0145$, $\delta = 0.00860 \text{ d}^{-1}$, $\theta = 186 \text{ d}$ and $\varphi = 180^\circ$.

Appendix C. Individual conditions

The standard metabolism cost (ξ), the maximum consumption (C_{\max}) and the search volume (V_s) are all a function of the individual weight (Levinsen et al., 2000; Saiz and Calbet, 2007).

$$\xi = k_{\xi} w^{3/4} \quad \mu\text{g C d}^{-1} \quad (\text{C.1})$$

$$V_s = k_v w^{0.7} \quad \text{L d}^{-1} \quad (\text{C.2})$$

$$C_{\max} = k_c w^{0.7} \quad \mu\text{g C d}^{-1} \quad (\text{C.3})$$

with $k_{\xi} = 0.07 \mu\text{g C}^{1/4} \text{d}^{-1}$, $k_v = 15.8 \times 10^{-3} \mu\text{g C}^{-0.7} \text{L d}^{-1}$, and $k_c = 1.68 \mu\text{g C}^{0.3} \text{d}^{-1}$.

Appendix D. Visual predation

Fish predation efficiency is affected by the light condition (brightness, clarity of the water), by its visual detection range and by prey size. We use the predation model developed by Huse and Fiksen (2010), assuming a herring type of predator. Herring are abundant in the North Atlantic and are an important visual predator of zooplankton. Predation rate function of the prey weight (w), Main text Fig. 2). Predation rate follows the Holling type II functional response:

$$\mu_f(t, D, \phi, w) = \varrho \frac{C_f N_f}{1 + C_f h N_f} \quad \text{d}^{-1} \quad (\text{D.1})$$

with ϱ the conversion factor from second to day ($\varrho = 86400 \text{d s}^{-1}$). The predation at the surface habitat is hence $\mu_s(t, \phi) = \mu_f(t, D_s, \phi)$, and in the deep habitat $\mu_d(t, \phi) = \mu_f(t, D_d, \phi)$.

$$C_f = \pi R_f^2 v_f \quad \text{m}^{-3} \text{s}^{-1} \quad (\text{D.2})$$

and R_f , the visual detection range, can be approximated by:

$$R_f \approx \sqrt{C_{cf} A_c(w) E \frac{I(t, D, \phi)}{k_e + I(t, D, \phi)}} \quad \text{m} \quad (\text{D.3})$$

when $R_f < 0.05$.

The predation rate μ_f is expressed in d^{-1} , with C_f the clearance rate of the fish, N_f the density of fish (fish m^{-3}), h the handling time (1 s), v_f the fish swimming velocity (2 body length per second – m s^{-1}), C_{cf} the contrast (0.3, Utne-Palm, 2005), k_e is equal to $5 \mu\text{mol photon s}^{-1} \text{m}^{-2}$ (Aksnes and Utne, 1997). $I(t, D, \phi)$ is the irradiance at a given time of the year, latitude and depth (Eq. (D.4)), and function of I_0 the irradiance at the surface at the given time and latitude (Brock, 1981), the diffuse attenuation coefficient $k = 0.1 \text{m}^{-1}$ (Huse and Fiksen, 2010), and depth D .

$$I(t, D, \phi) = I_0(t, \phi) \exp(-kD) \quad \mu\text{mol photons}^{-1} \text{m}^{-2} \quad (\text{D.4})$$

The image area of the copepods A_c is a function of the individual weight, assuming a conversion from weight to length (Eq. (D.5), Rey-Rassat et al., 2002) and that copepods width is 3 times smaller than its length, and correcting the rectangular shape with a factor of 0.75 (Eq. (D.6), Fiksen and Folkvord, 1999).

$$L_c(w) = 3.95 w^{0.36} \quad \mu\text{m} \quad (\text{D.5})$$

$$A_c(w) = 0.75 \frac{L_c^2}{3} \quad \mu\text{m}^2 \quad (\text{D.6})$$

Appendix E. Dynamic programming numerics

Dynamic programming finds the optimal individual behavior as a function of individual's weight and time of the year. The optimal time individuals should spend at the surface is calculated backward starting from the end of the year with a null fitness for individuals smaller than the maturity size, and a fitness proportional to their

weight when bigger. Time and individual weight are discretized, and we ensure that the optimization is made within a discrete weight cell ($g \partial t < \partial w$). At each time step, the optimal fraction of time individual should spend at the surface is calculated for all the individual weight classes. At the end, we obtain a matrix of the best individual behavior as a function of their weight and the time of the year, which correspond to the best patch individuals should choose to balance mortality and growth in order to optimize their expected lifetime reproduction output within the set time horizon.

Before maturation ($w < w_a$), F being the fitness measure, g the growth rate (Main text Eq. (7)), and μ the predation mortality rate (Main text Eq. (11)), for each time step, we find τ_s the optimal fraction of time individual should spend at the surface to maximize the fitness equation (e.g. Mangel and Clark, 1988):

$$\frac{\partial F}{\partial t} + \max_{\tau_s} \left[\frac{\partial F}{\partial w} g - \mu F \right] = 0 \quad (\text{E.1})$$

by dividing by F , and by passing in the log scale we have:

$$\frac{\partial \log F}{\partial t} + \max_{\tau_s} \left[\frac{\partial \log F}{\partial w} g - \mu \right] = 0 \quad (\text{E.2})$$

At any state w_i , the present time is calculated relying on the forward time information:

$$\log F(t, w_i) = \log F(t+1, w_i) + \max_{\tau_s} \left[\frac{\partial \log F}{\partial w} g - \mu \right] \partial t \quad (\text{E.3})$$

with $\frac{\partial \log F}{\partial w} = \frac{\log F(w_{i+1}, t+1) - \log F(w_i, t+1)}{w_{i+1} - w_i}$.

The optimal τ_s^* , solution to Eq. (E.2) is:

$$\tau_s^* = C_{\max} \left(-\frac{1}{V_s R} + \sqrt{\frac{(\partial \log F / \partial w) \alpha}{\mu_s (1 - v) V_s R}} \right) \quad (\text{E.4})$$

Spawning ($w > w_a$). Once individuals reach maturity, they stop growing, and allocate the energy surplus to reproduction. The fitness function can then be written as:

$$\frac{\partial F}{\partial t} + \max_{\tau_s} [g - \mu F] = 0 \quad (\text{E.5})$$

Here g is no longer the growth rate but the energy accumulation allocated to reproduction (Eq. (7) still apply). Dividing by F , we have:

$$\frac{\partial \log F}{\partial t} + \max_{\tau_s} \left[\frac{g}{F} - \mu \right] = 0 \quad (\text{E.6})$$

The fitness at present time is thus calculated for each individual weight w_i as a function of the state at the forward time:

$$\log F(t, w_i) = \log F(t+1, w_i) + \max_{\tau_s} \left[\frac{g}{F(t+1, w_i)} - \mu \right] \partial t \quad (\text{E.7})$$

The optimal τ_s^* is therefore found by:

$$\tau_s^* = C_{\max} \left(-\frac{1}{V_s R} + \sqrt{\frac{\alpha}{\mu_s (1 - v) V_s R F}} \right) \quad (\text{E.8})$$

Appendix F. Constant environment

A simple verification of the myopic method can be done in constant (fixed) environment. Indeed, in a fixed environment (i.e. where the light regime and food abundance is constant), the myopic method should predict the same strategy (i.e. the same fraction of time at the surface τ_s) such as dynamic programming. We test the

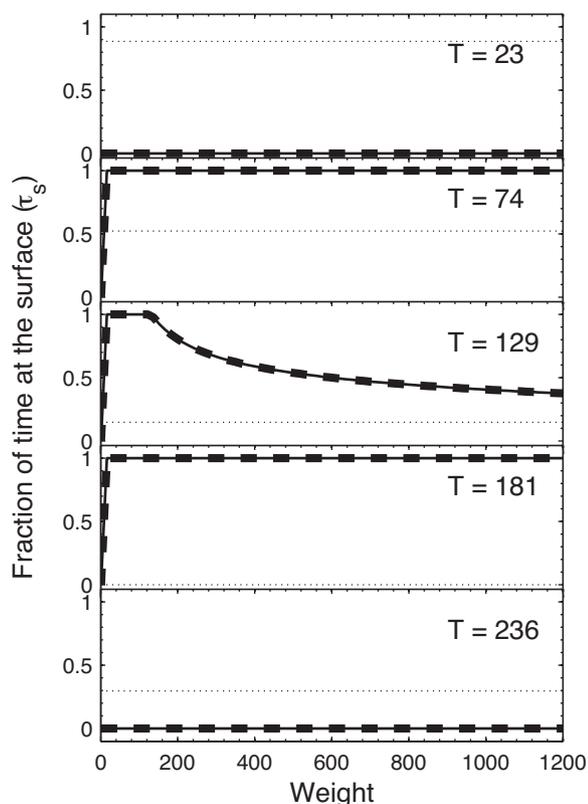


Fig. 7. Fraction of time individual should spend at the surface simulated with dynamic programming (bold dashed line), and with the myopic methods (thin line) represented at given time of the year for the range of individual weight. The thin dotted lines represent the fraction of night-time per day.

similitude of the two optimization methods for different time of the year over a range of state (i.e. individual weight, Fig. 7).

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