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Ideal free distribution of copepods under predation risk

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Abstract

Optimal vertical distribution of a copepod population of equal competitors under predation hazard is modelled by ideal free distribution (IFD). The foragers may be limited by both depletable (food) and non-depletable (temperature) resources. Individuals are assumed to maximize growth rate per mortality risk (g/M). Mortality risk is assumed density-dependent whenever the copepod concentration is high enough to satiate predators. The growth rate depends upon temperature or food concentration in absence of competition, and is density-dependent under competition. These relationships may yield peaked habitat profitability curves. For L depths with peaked profitability curves, the computational complexity scales to 3^L. Simplifying restrictions to allow numerical solutions when a large number of depths are available are presented and discussed. At moderate and high copepod stock size, the restrictions find the optimal distribution much faster, but at low stock sizes they may predict suboptimal distributions. The model predicts that individuals shall be more sensitive to predation risk at low and moderate competitor abundance and more sensitive to resource input rate at higher competitor abundances. Deviations from a food-based IFD are therefore most pronounced at low copepod population size. The IFDs are compared with predictions from a dynamic programming model with state- and time-resolved motivation of the copepods. © 1997 Elsevier Science B.V. All rights reserved

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1. Introduction

This paper explores the possibility of modelling the spatial distribution of copepods based on fitness-maximization under density-dependent habitat profitability. The aim of this paper is three-fold: (1) to incorporate predation risk in the habitat descriptor of the ideal free distribution (IFD) of copepods, (2) to develop methods for finding the IFD in a situation of multiple depths and complex habitat descriptors, and (3) to compare these density-dependent results with models with state- and time-resolved individual motivation based on dynamic optimization (SDP).

Optimal spatial distributions have been investigated by several modelling approaches. Individual motivation for behavior in life history theory (LHT) accounts for factors influencing fecundity and survivorship, and generates predictions of optimal trade-offs between environmental forces over a long period (McLaren, 1963; McLaren, 1974; Werner and Gilliam, 1984; Aksnes and Giske, 1990; Giske and Salvanes, 1995). Typical for LHT models is that individuals are characterized by their age and not

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individual characteristics as competitive ability or hunger.

Dynamic optimization (SDP: Houston et al., 1988; Mangel and Clark, 1988) allows descriptions of the internal state of individuals, which may lead to both variable and fluctuating motivation among individuals over short time periods. SDP has yielded considerable attention lately, and has been used to study diel (Clark and Levy, 1988; Rosland and Giske, 1994) and ontogenetic (Fiksen and Giske, 1995) vertical distribution of zooplankton and fish, large-scale horizontal distributions (Mangel, 1994; Fiksen et al., 1995) and optimal group sizes (Mangel, 1990). A disadvantage with SDP for ecological modelling is that optimal solutions in dynamic programming depend on the future of the individual and the environment. As this expectancy of the future also incorporates food availability and predation risk, trophodynamics can not be modelled by the backwards-calculating SDP. For this purpose, a forward running approach is needed.

The ideal free distribution (IFD) is a theoretical model for studying density-dependent effects on the spatial distribution of optimal individuals in a group (Fretwell and Lucas, 1970). The model has been widely used on the distribution of consumer populations (Milinski, 1979; Milinski, 1984; Harper, 1982) although Fretwell and Lucas (1970) also discussed patch profitability based on predation risk. A few investigations have added effects of density-independent factors on habitat quality, e.g. metabolic costs and environmental temperature (Grubb and Greenwald, 1982; Tyler and Gilliam, 1995). However, the density-dependency does not only relate to resources, but also to predators (and pathogens) and their efficiencies. While density-dependent effects on resources in most situations (Clark and Mangel, 1986) yield diminishing return with increased competition, this may be compensated by reduction in predation risk (Hamilton, 1971; Neill and Cullen, 1974; Milinski, 1977; Jakobsen et al., 1994). Thus, the return rate of the habitat, which in classical IFD theory (Fretwell and Lucas, 1970) is a monotonically decreasing function with competitor density, may also be constant (density-independent) or increasing. While a peaked habitat profitability curve was discussed by Fretwell and Lucas (1970) and termed the Allee curve (Allee, 1931; Allee et al., 1949), it has been given little attention in the IFD literature later. Lately, some IFD models have included both predation risk and food supply. Hugie and Dill (1994) have modelled IFD among fish predators and fish prey in a three trophic level system (with a static resource for the prey). Gilliam and Fraser (1988) constructed a 2-habitat IFD for juvenile fishes for whom generation time was a function of growth rate. The measure of fitness gain was 'minimize M/f' (where M is mortality rate and f gross foraging rate), derived from the 'minimize M/g' rule (where g is growth rate) of Werner and Gilliam (1984).

By including both feeding and predator avoidance in the habitat descriptor, the fitness curves may become peaked. As there are two competitor densities which yield the same profitability at each depth, one with increasing and one with decreasing profitability with increased competition, there are numerical problems associated with finding the ideal free distribution. We develop three methods for finding the optimal distribution of a large population of equal individuals among a large number of distinct patches (here: depths). In our first approach we seek the globally optimal distribution of a copepod population in a water column with 15 available depths. As this is numerically intractable for all but the simplest situations, two simplifying restrictions on gradual changes in copepod concentrations with depth allow two much faster solutions, and larger scales to be studied. Density independent effects are dominated by temperature, which strongly affects the growth of individual copepods. Density-dependent factors include both a resource gradient and a predation risk gradient mediated by light intensity. The model applies to the spring growth phase where individual fitness may be modelled by the impact of depth selection on the expected reproductive rate.

The limitation of IFD is that it can not resolve the fluctuating motivation of individuals according to time and state. Combined effects of density and internal state may be studied by SDP as a dynamic behavioral game (Mangel and Clark, 1988), but this has computational limitations for all but the simplest ecological scenarios. McNamara and Houston (1990) have constructed an SDP based IFD model that incorporates both state-dependency and mortality risk for animals maximizing survival probability under the combined threat of starvation and predation.

However, their model considers only two habitats (a safe and poor and a rich and dangerous), as model complexity (description of individual state) goes at the expense of spatial resolution in the computations. Which of the shortcomings of SDP or IFD are more important, will depend on the situation under study. It may therefore be profitable to develop alternative models of similar situations as each model may only account for some aspects of the total environment.

2. Models

The daytime and nighttime vertical distribution of copepods in a stratified water column of 30 m is modelled. Vertical distribution of food and temperature are taken from the SDP model of copepod vertical distribution by Fiksen and Giske (1995), with a mixed surface layer and a deep chlorophyll maximum (Fig. 1). Chlorophyll and water molecules create absorption and scatter of the downwelling light, which is modelled as by Riley (1956) and Fiksen and Giske (1995). Mortality risk for a single copepod in absence of conspecifics is the same as the daytime risk profile used by Fiksen and Giske (1995). The difference between day and night does only relate to light intensity and thereby efficiencies of visual predators.

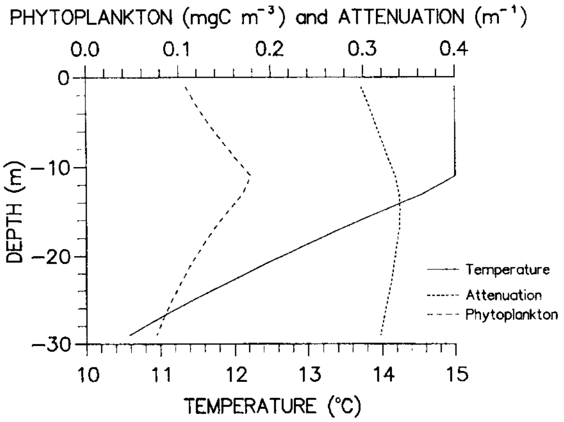


Fig. 1. Vertical profiles of food concentration (phytoplankton), temperature and attenuation of light are identical to Fiksen and Giske (1995). The profile describes a mixed surface layer overlying stratified waters. The phytoplankton maximum is found deep in the mixed layer.

2.1. *The copepod*

2.1.1. *Feeding and growth*

2.1.1.1. Density-independent feeding. Growth of copepods is restricted by food concentration only at low or intermediate feeding rates (Mullin et al., 1975). Both metabolic rates and feeding rates are temperature-dependent processes. Weight-specific ingestion follows

$$f_1 = \begin{cases} f_{\max} & F \geq F_{\lim} \\ FCW^{-1} & F < F_{\lim} \end{cases}, \tag{1}$$

where f_1 is the copepod feeding rate in absence of competition, $f_{\max}$ is the temperature-limited feeding rate under superfluous food concentrations, F is the food concentration, $F_{\lim}$ is the maximum food concentration that will limit feeding rate, W is the copepod individual weight and C the temperature-dependent clearance rate (Huntley and Boyd, 1984; Fiksen and Giske, 1995). (Symbols are explained in Table 1.)

2.1.1.2. Density-dependent feeding. We may assume that there is no interference between the copepods if each copepod has the volume needed for continuous feeding without resource depletion, i.e. if the copepod community filtering rate at a depth is lower than or equal to phytoplankton growth rate. When phytoplankton growth balances copepod clearance, we have

$$0 = \mathrm{d}F^*/\mathrm{d}t = \gamma F^* - N^* CF^*, \tag{2a}$$

where F^* is phytoplankton concentration and N^* is copepod concentration at steady-state, respectively and γ is phytoplankton growth rate. The maximum copepod concentration for non-interference feeding is therefore

$$N^* = \gamma/C \tag{2b}$$

at steady state. Interference is induced when $N > N^*$, and individual feeding will decrease in proportion to the ratio between them:

$$f = \begin{cases} f_1 & N \leq N^* \\ f_1 \gamma/CN & N > N^*. \end{cases} \tag{3}$$

Interference is therefore a function of phytoplankton growth rate, copepod concentration and clearance rate, which is temperature dependent.

Table 1
Descriptions of symbols for parameters and variables

Symbol	Description
γ	phytoplankton growth rate
Δz	vertical extension of depth interval
θ	visual predator's field angle
ρ_j	expected instantaneous rate of increase of individual in depth j
Φ_j	instantaneous fitness of individual in depth j
Ψ	number of profitability levels to search
a	assimilation efficiency
A	prey detection area
C	clearance rate
D	depth of water column
e	predator–prey encounter rate
E_z	irradiance at depth z
f	instantaneous feeding rate
f_1	density-independent feeding rate
F	food concentration
F_{lim}	maximal F that will limit feeding rate
f_{max}	temperature-limited feeding rate
g_j	instantaneous growth rate in depth j
h	neighborhood number
H	neighborhood: sequence of depths with same V_j
I	24 h average ingestion rate of predator
j	patch (here: depth) number
K	number of utilized depths
L	total number of available depth layers
m	instantaneous metabolic rate
$M(N)$	density-dependent mortality risk
M_1	M in absence of risk dilution
M_j	instantaneous mortality risk in depth j
N_1	the lowest concentration of copepods in a depth that satisfies $S_j = S(N, z)$
N_2	the highest concentration of copepods in a depth that satisfies $S_j = S(N, z)$
N_j	concentration of competitors in depth j
N_{T}	copepod population size
P	predator concentration
r	(expected) instantaneous population growth rate
R	sensory range of predator
S_j	density-dependent habitat profitability at depth j
t	time
v	swimming speed of predator
V_j	number of possible values of N to be considered at depth j
W	copepod dry mass
X_h	number of combinations to be considered in neighborhood h
z	depth

Subscripts t and v in equations refer to tactile and visual predators, respectively. An $*$ designates minimum concentration of food or copepods for a density-dependent effect to occur.

2.1.1.3. Growth. .Metabolic costs m are temperature-dependent and described by an equation of the von Bertalanffy form, similar to clearance rate (Huntley and Boyd, 1984; Fiksen and Giske, 1995). The assimilation efficiency a is assumed constant, and the feeding surplus may then be written as

$$g = af - m. \tag{4}$$

The most important variables underlying g are temperature, food concentration, food renewal rate and competitor concentration. At very high food concentrations, feeding rates will be at maximum (Eq. (1)) and the efficiency of converting food to growth drops. At very low food concentrations and ingestion rates, metabolism will outweigh feeding, giving a negative 'growth'. This is probably common in deep waters, e.g. at the overwintering depths of the large calanoid copepods in boreal waters (Hirche, 1993; Williams and Conway, 1988; Conover and Siferd, 1993). During the non-breeding season, fitness might be maximized by locating a depth which minimizes mortality risk (Stephens, 1981; McNamara, 1990). The latter situation is, however, not covered in this model (spring growth phase) as the copepod life history in boreal waters requires an energy surplus to be gained during spring. These two situations gives contrasting motivations, and (in absence of individual state dimensions in the model) should be modelled with different motivation rules (Eq. (10) below).

Growth is at its temperature-limited maximum (Eq. (1)) at 2–12 m at competitor concentrations below 200 ind l^{-1} (Fig. 2a). Above these densities and below these depths, community filtering will outweigh phytoplankton renewal (Eq. (3)), giving density-dependent reduction in growth rate. Vertical gradients in growth are most pronounced in the deeper parts of the water column, and density-dependent changes in growth are steepest at intermediate competitor concentrations.

2.1.2. Mortality

Ingestion by the planktivores is proportional to prey concentration and predator number when predator feeding is encounter-limited (Eq. (8) below). Hence, individual copepod mortality risk will be diluted when predator–prey encounters exceed predator capacity, i.e. when copepod concentration N exceeds a critical concentration N^*. Then mortality risk is assumed to decrease proportionally (Foster and Treherne, 1981) so that

$$M(N) = \begin{cases} M_1 & N \leq N^* \\ M_1 N^*/N & N > N^*. \end{cases} \tag{5}$$

Pelagic planktivores will be handling limited only under quite extreme circumstances (Rosland and Giske, 1994). As our model describes expected depth gradients in copepod concentration, predator digestion capacity — and not handling time — will be the decisive predator variable (Giske and Salvanes, 1995).

It is fruitful to distinguish between visual and tactile predators, as the mortality risks they represent (M_v and M_t, respectively) differ in the vertical (Eiane, 1995). While the search range of a visual predator is light dependent and therefore will vary considerably with ambient depth (Aksnes and Giske, 1993; Giske et al., 1994), we represent tactile predators by a spatially invariant search field. Tactile predators accounted for half of the total mortality in the SDP model of copepod vertical distribution (Fiksen and Giske, 1995). Having two classes of predators may yield two copepod concentrations where risk may be (further) diluted by increased concentration.

2.1.2.1. *Visual predators.* The prey detection area of a swimming visual predator is determined by its visual range (R_v) and the search angle (θ) (Luecke and O'Brien, 1981; Dunbrack and Dill, 1984):

$$A = \pi (R_\mathrm{v} \sin \theta)^2. \tag{6a}$$

The encounter rate between a swimming planktivore and non-moving copepods is

$$e_\mathrm{v} = ANv_\mathrm{v}, \tag{6b}$$

where v_v is planktivore swimming speed. Mortality risk for a copepod from a moving visual planktivore is then proportional to the planktivore's prey detection surface, for which the visual range R_v is the only environmental variable (Giske et al., 1994). The visual range of a planktivore is influenced by depth, light regime, the planktivore and the copepod (Aksnes and Giske, 1993). According to their model, R_v^2 will be proportional to light intensity at depth (E_z), and we may therefore write (Giske et al., 1994):

$$M_1 \propto A \propto R_\mathrm{v}^2 \propto E_z. \tag{6c}$$

The proportionality factor is influenced by overall abundance of predators, predator swimming speed, the predators' feeding motivations, and by availability of alternative prey items.

In case of planktivores limited by digestion processes, predator saturation requires that prey encounters exceed stomach (or gut, whichever smallest) evacuation (Giske and Salvanes, 1995). The feeding capacity of the visual predator is therefore assumed to be constrained (Henson and Hallam, 1995), giving a maximum average ingestion rate of I_v copepods per second over its daily feeding period. Saturation occurs when $e > I_\mathrm{v}$:

$$N_\mathrm{v}^* = I_\mathrm{v} / \left(\pi (R_\mathrm{v} \sin \theta)^2 v_\mathrm{v}\right). \tag{6d}$$

2.1.2.2. *Tactile predators.* The sensory field of tactile predators is determined by their sensory capabilities (Fulton, 1982; Browman et al., 1989; Yen and Nicoll, 1990) and by the noise produced by the copepod. We make no attempt here to represent this process mechanistically, and just assume that such predators are equally efficient in near-surface water at midday as in deep water at midnight. This corresponds to setting the sensory range constant.

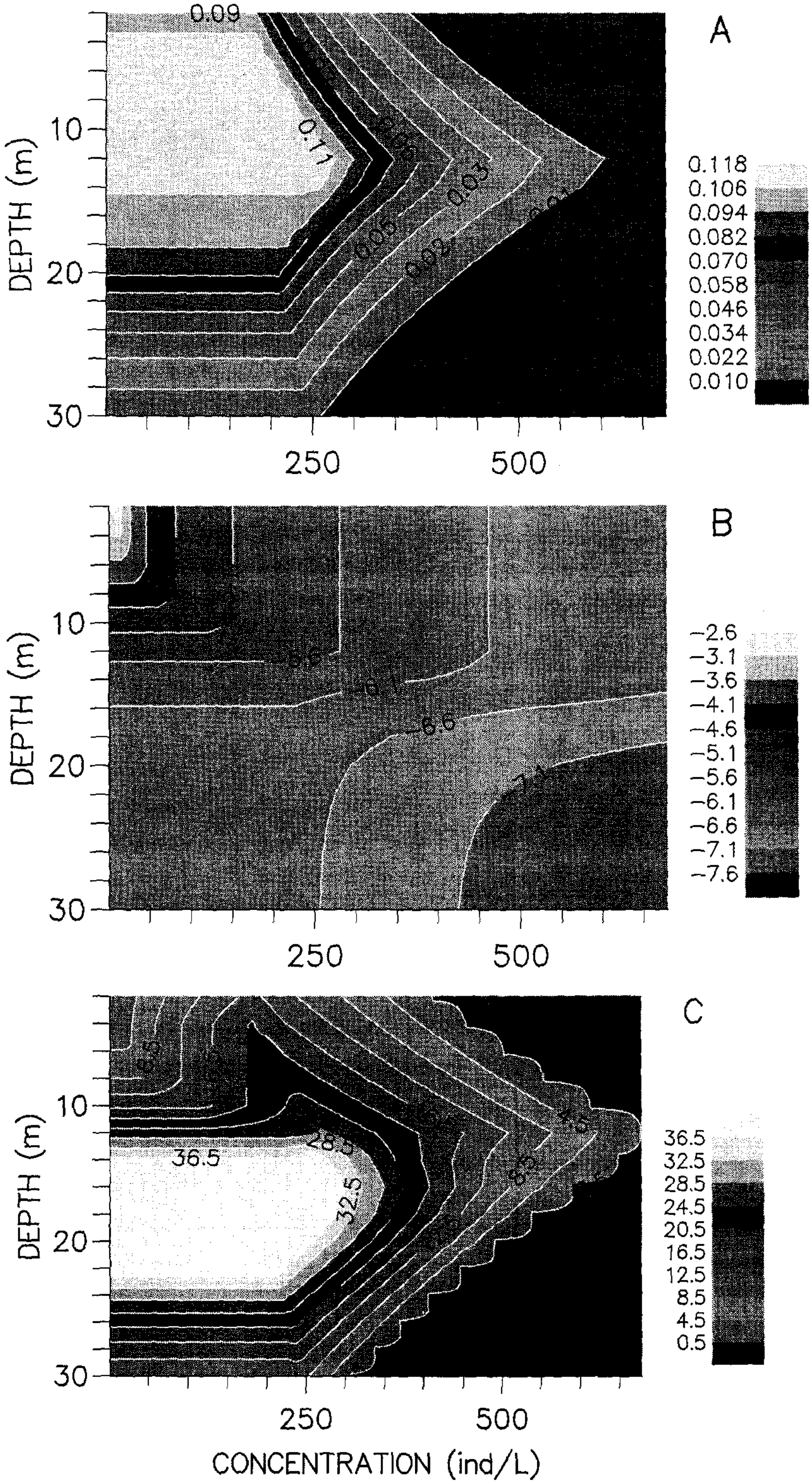
As swimming speed of tactile predators is of the same order as that of their prey, these speeds will both influence the predator–prey encounter rate. When predator and prey speeds are equal, the average relative speed between them is $4v_\mathrm{t}/3$ (Gerritsen, 1980), so we write:

$$e_\mathrm{t} = \pi R_\mathrm{t}^2 N v_\mathrm{t} \cdot 4/3, \tag{7a}$$

and saturation occurs when $e > I_\mathrm{t}$:

$$N_\mathrm{t}^* = 3 I_\mathrm{t} / \left(4 \pi R_\mathrm{t}^2 v_\mathrm{t}\right). \tag{7b}$$

We further assume that predators are not horizontally attracted to higher copepod concentrations, and


A
0.09
0.11
0.06
0.05
0.03
0.02
DEPTH (m)
10
20
30
250
500
0.118
0.106
0.094
0.082
0.070
0.058
0.046
0.034
0.022
0.010
B
−6.6
−6.1
−6.6
−7.1
DEPTH (m)
10
20
30
250
500
−2.6
−3.1
−3.6
−4.1
−4.6
−5.1
−5.6
−6.1
−6.6
−7.1
−7.6
C
28.5
36.5
32.5
4.5
8.5
DEPTH (m)
10
20
30
250
500
CONCENTRATION (ind/L)
36.5
32.5
28.5
24.5
20.5
16.5
12.5
8.5
4.5
0.5

that there is no interference between predators. Mortality risk is thus proportional to predator concentration, and the mortality rate of an individual copepod in the presence of P_v visual predators and P_t tactile predators is

$$M(N) = M_v(N)P_v + M_t(N)P_t. \tag{8}$$

Mortality risk is almost 150 times greater for a single copepod in surface waters than for an individual surrounded by 650 competitors l^{-1} at 29 m. Dilution of mortality risk has the strongest impact in near surface waters and at low copepod concentrations. In shallow waters, risk may be reduced by downward vertical migration. Opposite to growth, gradients in mortality risk are weaker at larger depths (Fig. 2b), where visual predators are less efficient.

2.2. *Fitness and spatial distributions*

The ideal free distribution (IFD) is one of a set of theoretical distributions investigated by Fretwell and Lucas (1970). The original IFD was based on five assumptions: (1) competitors are equal, (2) resources are patchily distributed, (3) the competitors incur no cost to move, (4) each individual will go to the patch with highest gain, and (5) competition between individuals is 'scramble', without any contest or combat. The IFD was developed in the era of the optimal foraging theory, and although Fretwell and Lucas (1970) stated that food was but one component of fitness, the examples provided assumed a direct relationship between feeding rate ('gain') and fitness (but see Oksanen et al., 1992). Under the IFD with equal competitors, the total number of individuals distribute among the patches so that the gain of an individual is equal in all patches utilized. If L patches are available, the IFD is achieved when individual gain S is equal among the $K \leq L$ utilized patches:

$$S_1(N_1) = S_2(N_2) = \ldots = S_K(N_K), \tag{9}$$

and cannot be increased by relocation.

It is not to be expected that copepods in a natural environment shall distribute relative to food concentrations, as (1) there are combinations of low copepod concentration and high food production where the individual feeding rate will not be influenced by a (minor) increase in competitor concentration (Eq. (3)), and more important, (2) one of the main resources for copepod development and fitness may be environmental temperature (Eq. (1)), which is a non-depletable resource and (3) predation risk will affect fitness in a density-dependent manner (Eq. (5)). Here, we will express gain directly in terms of the habitats' expected contribution to the fitness (Φ) of the animal, and assume the IFD to cause this fitness contribution equal for all individuals after the IFD is established. With this revision of the assumptions, the functional model will resemble what Gilliam and Fraser (1988) termed 'equal competitors under predation hazard'. Although Clark and Mangel (1986) discussed several peaked profitability-functions for group size, gain has never increased with competitor concentration in previous models of IFD (except in the verbal discussion of Allee curves in Fretwell and Lucas, 1970). This will be possible here, particularly where feeding and growth is suppressed by temperature and where mortality risk may be reduced by dilution.

Phenotypical fitness is the difference between the reproductive rate of an individual and that of its population. By denoting the expected rate of increase of an individual ρ and the corresponding rate of the population r, the fitness in habitat j is (Giske et al., 1993)

$$\Phi_j = \rho_j - r. \tag{10a}$$

Whether the population is constant, growing or diminishing, an individual will increase its fraction of the future gene pool when $\rho > r$. However, for the practical situation of determining the IFD, we see that by inserting Eq. (10a) into Eq. (9) and equating habitat profitability S with fitness Φ, we obtain

$$\Phi_1 = \Phi_2 = \ldots = \Phi_K \quad \Leftrightarrow \quad \rho_1 = \rho_2 = \ldots = \rho_K, \tag{10b}$$

as r is a population parameter constant for all habitats. As a consequence of the fitness definition in Eq.

Fig. 2. Impact of copepod concentration and depth on (A) growth rate g, (B) mortality risk (given as ln M) and (C) habitat profitability $S_j = g/M$.

(10a), an the IFD population of equal competitors will consist of individuals with fitness $\Phi = 0$, as $\rho_i = \rho_j = r$. This zero fitness can only be achieved by living an optimal life and maximizing the reproductive rate.

Individuals with an unconstrained generation time maximize their expected rate of increase ρ by maximizing the ratio of growth to mortality (Werner and Gilliam, 1984; Aksnes and Giske, 1990; Salvanes et al., 1994):

$$\max \rho \quad \Leftrightarrow \quad \max(g/M). \tag{10c}$$

We restrict our analysis to this situation, i.e. we study situations where feeding will be sufficient for growth ($g > 0$) and that reproduction can occur unhindered by seasonal and other constraints. We do not go into situations where risk of starvation must be considered, as this will make considerable changes in the individual motivation (Stephens, 1981). Then we may define the profitability of habitat j as

$$S_j(N_j) = g_j(N_j)/M_j(N_j), \tag{10d}$$

which is identical to the net reproductive ratio as employed by Hugie and Dill (1994) and similar to the 'minimize M/f' rule employed by Gilliam and Fraser (1988). The density-dependent growth rate will be found by Eq. (4) and the mortality risk by Eq. (8). For the data set used here, this habitat profitability will be at maximum for 220 copepods l^{-1} at 18–20 m depth (Fig. 2c). S_j will be reduced downward due to lower growth and upwards due to higher visual predation. In these midwater depths, a lower competitor density will not enhance individual mortality risk, but stronger competition will reduce growth more than mortality.

In IFD terms we will find the relation between the optimal competitor concentration in each habitat, so that gain is equalized by competition and predation risk dilution. The criteria we use is that (1) the number of individuals in all utilized depths shall sum up to the population size,

$$N_1 + N_2 + \dots + N_K = N_T, \tag{11a}$$

(2) that each copepod shall expect the same fitness in all utilized depths,

$$\Phi_1 = \Phi_2 = \dots = \Phi_K$$

$$\Leftrightarrow \quad S_1(N_1) = S_2(N_2) = \dots = S_K(N_K), \tag{11b}$$

and (3) that this is the solution with the highest possible habitat profitability S_j.

IFD models have been around for a while, yet they have largely been limited to small systems (but see Bernstein et al., 1988, 1991; Kacelnik et al., 1992) and diminishing return curves. To find an IFD for a large population offered a series of patches with peaked profitability curves will have tremendous computation costs, and we are forced to seek biologically sound simplifications of the problem.

2.3. Numerical solutions of the IFD

2.3.1. The continuous problem

For a given habitat profitability function $S(N, z)$ and for a population size (N_T (ind m^{-2})) we want to determine the vertical distribution that allows the largest possible habitat profitability of each individual. That is, we want to locate the largest $S_j = g_j/M_j$ that allows the identity

$$N_T = \int_D^0 N(S, z)\,dz \tag{12a}$$

to be satisfied where D is the total depth. To be able to compute the population size integral above, we must for a given density-dependent profitability function $S(N, z)$ be able to compute the inverse function $N(S, z)$. At habitat profitability S, the competitor concentration at depth z, $N(S, z)$, will be uniquely defined if $\partial S/\partial N \neq 0$ for all N. However, in general N may be a multivalued function of S for a given z. In this study we allow S to have at most one maximum, although this maximum may be a plateau. When searching for an optimal distribution, we also want for each depth to consider the possibility that there are no animals at that depth. In the one peak case without a plateau the integrand $N(S, z)$ may therefore take at most three different values: (1) $N(S, z) = 0$ and there are no animals at depth z, (2) $N(S, z) = N_1$ which is the smallest N that satisfies $S(N_1, z) = S$ and (3) $N(S, z) = N_2$ which is the largest N that satisfies $S(N_2, z) = S$.

For a given z and S there then may be 1, 2 or 3 possible values of N that must be considered. If there are no N satisfying $S(N, z) = S$, then the solution is 0. If there is one N such that $S(N, z) = S$, we get 2 possible values of N (0 and N_1). If there are 2 values of N such that $S(N, z) = S$, we get 3 possible values of N (0, N_1 and N_2) to consider in the integral. For the special case where the profitability level hits a plateau of a habitat curve, all values of N fulfilling $S(N, z) = N$ will be considered. Since $N(S, z)$ is multivalued, Eq. (12a) may take an infinite number of values.

2.3.2. The discrete problem (M0)

To find unique solutions to the problem stated above is in general impossible with few options and gets worse with increased choice. In the search for approximate solutions we approach Eq. (12a) with the repeated midpoint rule

$$N_T \sim \sum_{j=0}^{L-1} N(S, z_j)\Delta z, \qquad (12b)$$

where $\Delta z = D/L$, L is the number of layers in the vertical and z_j is the depth in the center of the layer. For each j $N(S, z_j)$ has up to 3 possible solutions and all permutations may be potentially interesting. Therefore, if Ψ profitability levels (determining the precision in the approximation of the true S_j) shall be considered, the computational complexity will be up to $\Psi 3^L$.

For a given depth z_j, however, there may be fewer than 3 possibilities. Let V_j ($V_j \in (1, 2, 3)$) be the number of possible values of N that must be considered in depth z_j. The total complexity then becomes $\Psi(V_1 \times V_2 \times \ldots \times V_L)$. For large values of L the computational complexity of the procedure above becomes unrealistically large. For 20 depths, $3^{20} > 10^9$ and we have to multiply this by Ψ in our search for optimal distributions. We therefore study some simplifying procedures.

2.3.3. Simplified discrete method 1 (M1)

Definition: For a given habitat profitability level S a neighborhood h is a connected sequence of discrete depths $(z_j, z_{j+1}, \ldots, z_{j+n})$ such that the number of possible copepod concentrations that must be considered in each depth is constant: $V_j = V_{j+1} = \ldots = V_{j+n}$. Thus, a neighborhood contains depths with similar-looking profitability curves that cross the current S-level equally many times.

Further, we make two restrictions to the numerical search for solutions: (1) Within a neighborhood with $V_j = 3$ we will consider only combinations of $N = 0$ and $N = N_1$ or $N = 0$ and $N = N_2$. (2) Within a neighborhood the possibility $N = 0$ will not be allowed between depths with $N \neq 0$. Thus, combinations of the type $N_j = N_1(S, z_j) \neq 0$, $N_{j+1} = 0$, $N_{j+2} = N_1(S, z_{j+2}) \neq 0$ will not be considered. The biological interpretation of these restrictions is that in a sequence of depths of similar quality, we will not allow copepods to distribute in a way that makes alternating high and low competitor concentrations, and an unexploited depth may only be found at the outer margins of exploited depths within a neighborhood.

For a neighborhood with 4 discrete depths with the possibilities $N = 0$ and $N = N_1$ the following combinations will be considered with the restrictions above: (0, 0, 0, 0), (N_1, 0, 0, 0), (0, N_1, 0, 0), (0, 0, N_1, 0), (0, 0, 0, N_1), (N_1, N_1, 0, 0), (0, N_1, N_1, 0), (0, 0, N_1, N_1), (N_1, N_1, N_1, 0), (0, N_1, N_1, N_1) and (N_1, N_1, N_1, N_1). That is $1 + (4 \times 5)/2 = 11$ possibilities.

If the current profitability level S hits the plateau of a profitability curve, then the curve will be considered a one-peak curve if the plateau is at its maximum habitat profitability (i.e. low N, e.g. depths 17–23 in Fig. 3) or a two-peak curve if not (e.g. depths 1–15 in Fig. 3).

In general for a neighborhood h with L depth levels and V_j possible values of N at each depth, the number of combinations X_h that will be considered with the 2 restrictions becomes

$$\begin{aligned} &\text{if } V_j = 1,\ X_h = 1 \\ &\quad (\text{only } (0, 0, \ldots, 0) \text{ is considered}), \\ &\text{if } V_j = 2,\ X_h = 1 + L(L+1)/2, \qquad (13) \\ &\text{if } V_j = 3,\ X_h = 1 + L(L+1). \end{aligned}$$

For a case with H neighborhoods covering the depth range, the computational complexity becomes $\Psi \times (X_1 \times X_2 \times \ldots \times X_H)$. For a case with 1 neighborhood covering the water column the complexity becomes of order ΨL^2. For an increasing number of depth levels, $L^2 \ll 3^L$, so this will be a considerable reduction in computation cost. Also with few neighborhoods the reduction will be significant.

2.3.4. Simplified discrete method 2 (M2)

Let the definition of a neighborhood be as above, but with the following restriction: For each neighborhood we consider at most the combinations (0, 0, ..., 0), (N_1, N_1, ..., N_1) and (N_2, N_2, ..., N_2). Thus, at most (if $V_j = 3$) 3 combinations will be considered.

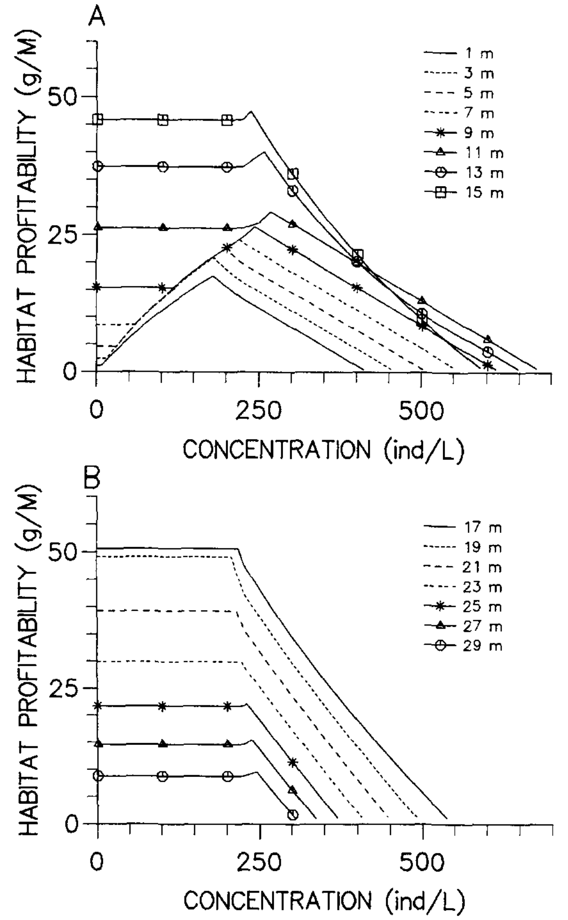


Fig. 3. Density-dependent habitat profitability curves ($S_j = g/M$) for all depths at daytime. All depths show constant S_j at low copepod concentration N. The first increase in profitability in shallow depths is due to satiation of visual predators. Tactile predators with constant search volumes are satiated at $N = 217$ ind m^{-3} at all depths.

For a case with H neighborhoods covering the depth range, the computational complexity again becomes $\Psi \times (X_1 \times X_2 \times \ldots \times X_H)$, but now with $X_h = 1$, 2 or 3. For a case with 1 neighborhood covering the whole water column, the complexity becomes of order Ψ.

3. Results

3.1. Ecology

All habitat profitability curves do initially show a plateau where $\partial S/\partial N = 0$ (Fig. 3). At shallow depths S_j will increase due to satiation of visual predators (at daytime). However, influence of visual predators is not visible at 13 m and below. Tactile predators with a constant sensoric field are satiated at all depths (both day and night) at 217 ind m^{-3}. This is visible as a weak or moderate improvement of all curves in Fig. 3.

Density-independent effects of temperature-limitation of feeding at high food concentrations affect habitat profitability at low competitor densities (Fig. 2a). Then individual profitability will be maximized by individuals concentrating to achieve risk dilution, and to seek the deeper depths where visual predation risk is lower but food is still plentiful. At intermediate copepod stock size, the largest concentrations should be found at 16–20 m, while at 10–12 m at larger population size (Fig. 2c and Fig. 3). The resulting ideal free distribution is quite stable in the sense that small alterations in overall copepod population size do not cause major shifts in the spatial distribution (Fig. 4).

The impact of light intensity on the visual range of the predators gives diel variation in the vertical distribution (Fig. 5). Except at very high copepod population size, the model predicts shallower distribution at nighttime. The difference between day and night reflects the relative impact of visual predation versus food and temperature upon vertical distribution, and it is seen that this influence diminishes with increasing copepod population size.

The nighttime optimal distributions are very similar to distributions based on maximization of g (Fig. 5). At low copepod stock sizes, concentrations in occupied depths will be lower than N^* for tactile predation, and only growth potentials will influence distributions. At higher copepod stock sizes, nighttime maximization of g/M yields heavier utilization of the best habitats and weaker utilization of marginal habitats than by the max g rule. By doing so, individuals in crowded depths obtain reduced mortality risk, while concentrations in less used habitats are too low to satiate tactile predators.

3.2. Methodology

The predicted vertical distributions from the simplified methods M1 and M2 will in most circumstances be quite similar to M0. M0 always finds the spatial distribution that gives the higher habitat prof-

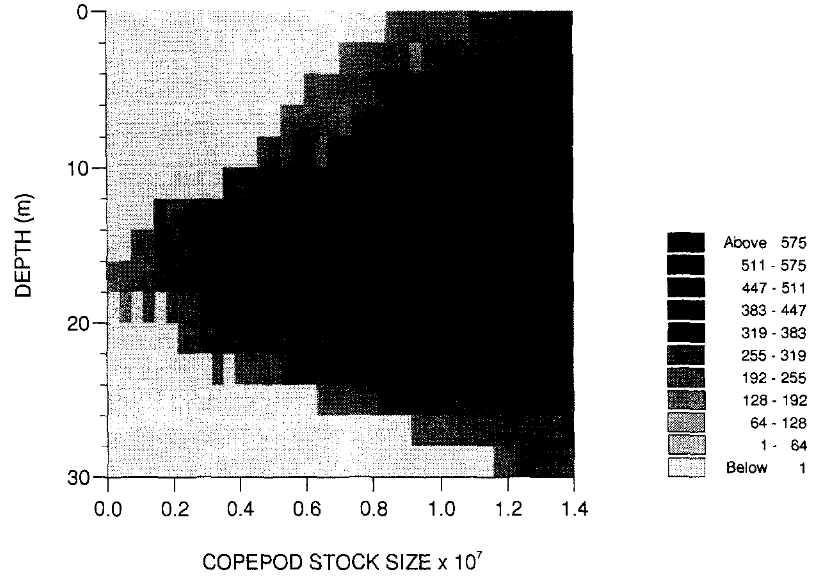


Fig. 4. Ideal free distribution of the copepods as a function of stock size N_T.

itability (Fig. 6). The differences in terms of profitability are largest at low copepod population size N_T. When N_T exceeds 10^7 ind m^{-2}, there are no differences between the solutions. At such a large copepod population size, all depths are utilized so that the simplifying restrictions will be valid. With the current data set (Figs. 1 and 2), the profitability obtained by these restrictions is never more than 4% lower than with the unsimplified method.

All three cases where M2 predicts suboptimal distributions (Fig. 6) are caused by the neighborhood restriction. In the first two instances M0 fills a depth

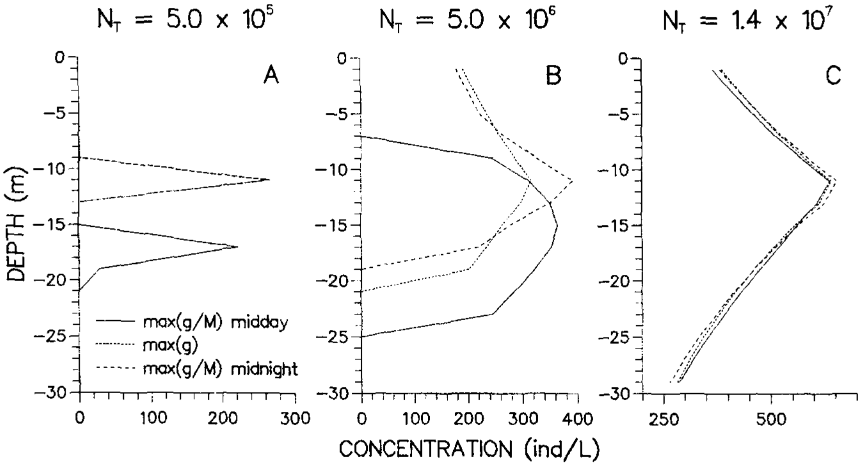


Fig. 5. Vertical distributions of copepods maximizing $S_j = g/M$ (at midnight and midday) and copepods maximizing $S_j = g$ (midday and midnight equal) at low ($N_T = 5 \cdot 10^5$ ind m^{-2}, left), medium ($5 \cdot 10^6$ ind m^{-2}, center) and high ($1.4 \cdot 10^7$ ind m^{-2}, right) copepod stock sizes.

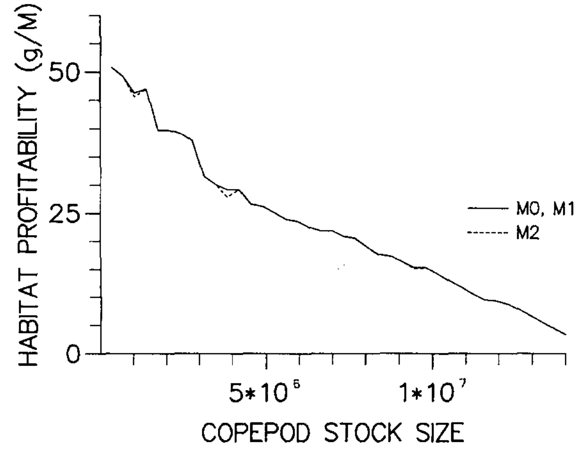


Fig. 6. Habitat profitability (g/M) achieved under the three methods used at low copepod stock sizes. M0 is the unsimplified, and M1 and M2 are the simplified methods. M1 always gave the same fitness as M0.

with N_2 individuals adjacent to N_1 depths, and in the third case M0 fills N_1 individuals into an area where other depths have N_2 concentrations.

As the simplified methods allow reductions in the total number of possible solutions, the computation time is also strongly reduced. For the runs presented here with 15 depth intervals ($\Delta z = 2m$), M0 used 101 min, M1 used 4.6 min, and M2 used only 14 s to find the solution to Fig. 4 on our UNIX machine, i.e. an increase by a factor of 20 from M2 to M1 and from M1 to M0. Solutions predicted by M1 and M2 at increased depth resolution ($\Delta z = 1m$) did not differ much from the runs with 15 depth intervals, indicating little sensitivity for the depth resolution with the present data set. The doubling of depth intervals did, however, have great effects on the run time of the models.

4. Discussion

4.1. Ecology

The main difference of the model presented here compared with traditional IFD models (Fretwell and Lucas, 1970) is the inclusion of density-dependent predation risk and the possibility of density-independent regulation of the feeding rate in the profitability function. Such curves yield the prediction that if competitor concentration is so low that the feeding rate is not or only weakly impaired, individuals should join groups to avoid predation in stead of spreading out to match the resource input. We have modelled the growth phase of copepods, where feeding motivation will be high. Under other circumstances (Aksnes and Giske, 1990; Giske and Aksnes, 1992; Utne and Aksnes, 1994; Utne, 1995), predation risk dilution may be even more important and expected matching with resources even poorer.

Hugie and Dill (1994) modelled the ideal free distribution of predator and prey fishes where both trophic levels were dynamically represented. They found that the prey density was independent of both predator density and resource level, and only affected by the inherent riskiness of the habitat. Like them, we assume that predators may relocate, so that predator concentration is no cue for habitat profitability. Contrary to them, we found that the predation risk has decreasing importance with increasing prey population size, and that the resource input rate eventually becomes the dominant environmental signal ('input matching' (Parker, 1978; Milinski, 1979) or 'habitat matching' (Pulliam and Caraco, 1984)). The difference in results stems from our formulation of density-dependencies in feeding rate and mortality risk. Our formulations contain the possibilities of resource deprivation under intensive competition and risk dilution by predator satiation. As the deep and safer depths also are the poorer depths, both these factors will lead to a gradual shift towards higher sensitivity to food input ratio at the expense of habitat riskiness at increased copepod concentration.

Life history decisions as allocation to growth, storage or reproduction and risk-willingness can only be understood in the context of how these decisions influence the maximization of ρ. Ultimately, vertical migrations must also be evaluated by this measure. For this purpose SDP and individual state are needed. However, copepods generally lag behind their algal resources, such that mismatch may be a common feature (large population – low food availability). Thus they are likely to be regulated by density-dependent mechanisms at least at some times of the year. On the other hand, the lack of food will affect their state, and actions like entering diapause or modifying activity to increase survival can be induced. In an IFD model the action can be to spread out, while the SDP model could predict other behaviors. The different models may therefore complement each other, as individuals in nature will rely on a range of actions simultaneously, which we currently only are able to study separately.

If both the current IFD and the SDP model by Fiksen and Giske (1995) captured the essence of habitat profitability, then the conclusions from one model should be modified in the light of the results from the other. In essence, it is clear that at high population densities the predictions from the SDP-model will be mistaken, while SDP may be superior (provide more information) at low population densities or at high resource levels. Also, when predators are dense or can operate efficiently, the SDP model may predict a too deep distribution, because it does not consider the option of clumping, or the IFD model will predict a too deep distribution when food is scarce, because it does not include the risk of starvation.

Theories and models are imperfect abstractions of reality, lacking some essential features of the individual or the environment. Predictions based on only one modelling approach should therefore be treated with caution. The two models discussed (SDP and IFD) illustrate why we to a larger extent should apply several and different approaches to study the same phenomena. Hopefully, future approaches may be able to capture more of these abilities within one framework.

4.2. Methodology

The IFD theory has usually been applied to situations with few habitats and few individuals. With intentions of modelling population dynamics including density-dependent processes in natural systems it will inevitably be necessary to include far more habitat options and individuals, which makes computations far more difficult.

Discretization of a continuous system always includes the danger of creating unnatural border lines that might affect the model predictions, and the need for good resolution will certainly depend on environmental properties as well as the organism in study.

With the current settings, the two simplified procedures produce almost identical distributions as M0 does. However, in another scenario not documented here, where risk dilution occurred at far lower copepod concentrations (e.g. by better vision and lower digestion rate of the visual predators), we have seen that both simplified methods may fail to find the optimal distributions when stock size N_T is small, and the resulting habitat profitability may be as much as 25% lower by M2 than by M0. This potential difference in precision of the simplified approaches at high and low population sizes is caused by more switches between empty ($N(S, z) = 0$), low-concentration ($N(S, z) = N1$) and high-concentration ($N(S, z) = N2$) depths at lower population sizes. These switches are not always discovered under the simplifying restrictions. In a situation where many habitat profitability curves resemble the 1 *m* curve in Fig. 3, M2 will match the original only when all depths are utilized, and the competitor concentrations in all depths are on the falling right-hand side of the habitat profitability curve. The technical process of finding the IFD is then identical to the classical IFD with monotonically decreasing habitat profitability. M2 thus resembles the methods of Bernstein et al. (1988, 1991) and Kacelnik et al. (1992) who sought for solutions in a multi-patch landscape with strictly negative effects of competition. M2 may also find the IFD at very low competitor abundances, so that all depths are utilized in the rising left-hand side of the profitability curve. However, the probability that optimal competitor density in all depths shall be on the left-hand side is quite small, and the simplifying restrictions should be applied with caution under weak competition. We regard this paper as a first attempt to find simplified solutions, and other methods — that can allow more spatial patchiness at low computing cost — should be investigated.

As long as the habitats differ in quality, there is a general trend that for low abundances, only the few best depths will be occupied (yielding relatively few possible solutions), and as abundance increases more of the less profitable depths will be included (yielding relatively many possible solutions). Thus for low N_T (when computational costs are low), M0 or M1 may be applied to search the optimal distribution, while for high N_T (where computational costs are high) M2 will almost always be valid and may be applied.

Applying the IFD framework on zooplankton in a vertical system is somehow unrealistic as it can hardly perceive the concentrations of conspecifics several meters away. Neither is it free to relocate without costs in energy and time. The same problem would occur on large scale systems like a horizontal distribution of fish populations, where the IFD assumptions of free movement and total knowledge of other habitats and competitors are broken. For such situations, movement rules allowing relocation related to normal swimming speeds of the individuals (Rosland and Giske, 1994; Fiksen et al., 1995), and a (fading) memory (or reliability) of the quality of habitats visited (Milinski and Regelmann, 1985; Milinski, 1994), can increase the realism of the model. It may also reduce computer costs, as not all habitats need to be considered for all individuals. Further, a slight turbulence would ruin most patterns of zooplankton distribution, e.g. the pattern in Fig. 5a where risk dilution forces all individuals into one thin vertical layer. Some of the predictions yielded by this model will therefore apply more to organisms (e.g. fish) that may overcome the chaotic power of turbulence.

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