

Towards a robust concept for modelling zooplankton migration

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We develop a model framework for handling some aspects of zooplankton behaviour in biophysical simulation models. The vertical behaviour of zooplankton (their diel vertical migration pattern, or DVM) is modelled as a stimuli-response process where inputs from the environment (i.e. presence of light, food, and predators) are used as decision parameters. By use of simple artificial neural networks to control behaviour and optimising these by genetic algorithms we obtain close to optimal sets of DVM strategies. We show how adding increasing levels of environmental complexity (number of stimuli, stochasticity, and seasonality) to the model affects predicted behaviour. Within 50 generations of adaptation the model strategies perform reasonable well under the levels of environmental complexity used in simulations. The performance of strategies tended to increase with the complexity level of inputs used to control behaviour. By adapting strategies to environments with a stochastic variability we show that the strategies become more plastic to unpredictable changes in environmental forcing. Also, we discuss how plastic strategies with high degree of robustness to environmental fluctuations of the magnitude encountered in nature can be derived from this method. Results are discussed in relation to the behavioural patterns observed in the field.

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INTRODUCTION

Zooplankton drift with the water masses in the horizontal plane but may regulate their position in the vertical dimension (Murray & Hjort 1912; Russel 1927). Many of these animals show ontogenetic or seasonal differences in their vertical distribution spanning more than 1000 m (Østvedt 1955). On shorter time-scales their pattern of diel vertical migrations (DVM) may result in daily displacements of the peak distribution from surface to depths of several hundred meters – and back again (Longhurst 1976; Wiebe & al. 1979). Such migrations expose the zooplankton to water masses of variable shear-velocities over daily as well as seasonal time-scales. The net transportation effect of this may add considerable complexity to the spatial dynamics of such populations (Hardy & Gunther 1935; Hardy 1936; Frassetto & al. 1962; Kaartvedt, 1993; Eiane & al. 1997; Hill 1998).

The DVM behaviour of zooplankton has been studied quite extensively over the years (Kerfoot 1985; Lampert 1989; Ohman 1990; Fiksen 1997). Today this behaviour is understood as a strategy for trading off mortality risk and energy intake over the life history of the animals (Stich & Lampert 1981; Iwasa 1982). Although the long-term optimal balancing of predation risk versus growth

offers the best ultimate explanation for DVM behaviour in zooplankton (McLaren 1963; Stich & Lampert 1981; Aksnes & Giske 1990; Houston & al. 1993), we may need to invoke multiple proximate explanations or mechanisms to fully understand the adaptiveness of the trait. A brief survey of the literature suggests that the vertical behaviour of planktonic organisms is sensitive to ontogeny (Longhurst 1976; Heath 1999), light intensity (Kampa & Boden 1954; Longhurst 1976; Baliño & Aksnes 1993), photoperiod (Miller & al. 1991) food distribution (Aksnes & Giske 1990), predator abundance (Enright & Honegger 1977; Dodson 1988; Kaartvedt 1996), and the functional types of predators present (Ohman & al. 1983). The plasticity of vertical migration strategies, observed both among and within populations (Ohman & al. 1983; Heath 1999) further suggests that selection has favoured the evolution of proximate response strategies that are sufficiently functional under the range of stimuli variation encountered in nature (Ohman 1990).

Resolving such complex and large-scaled processes solely by focusing on field efforts may prove time consuming and costly. Alternatively, further insight in the dynamics underlying the distribution of zooplankton in space and time may be sought by incorporating zooplank-

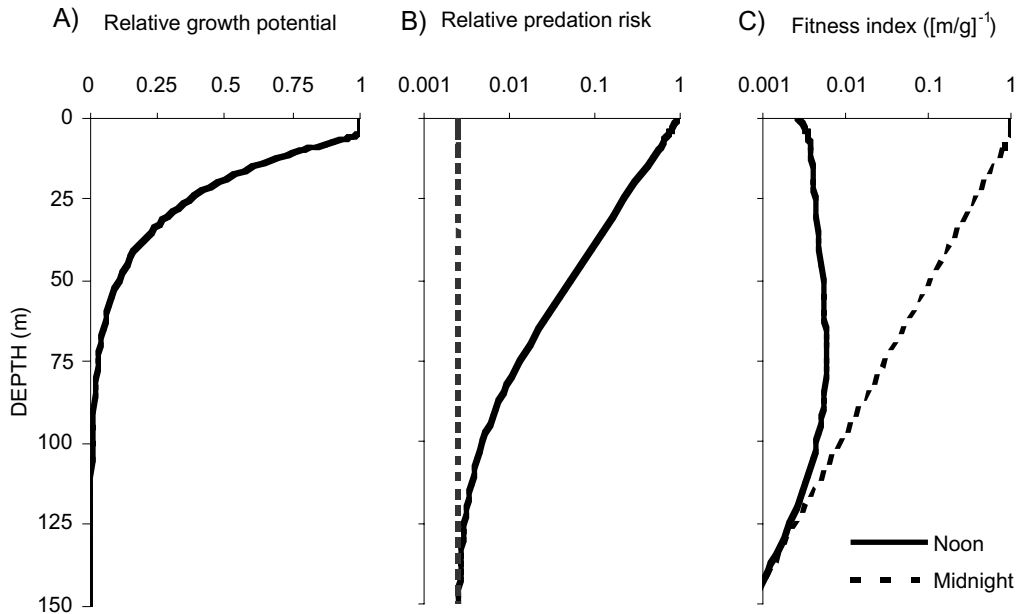


Fig. 1. The depth specific environment as represented in the model. A. Depth specific food levels are constantly high close to the surface and then drops off with depth. B. Depth specific predation risk (Eq. 1) at noon and midnight. C. Depth and time specific relative fitness values (Eq. 2) at noon and midnight.

ton behaviour into state-of-the-art models of physical oceanography (e.g. Rothlisberg & al. 1983, 1996; Bartsch 1988; Lough & Trites 1989; Tremblay & al. 1994; IGBP 1999). Models dealing with individual behaviour have been available for some time (Reed & Balchen 1982; Balchen 2000). State-of-the-art models of migrations by aquatic organisms (Rosland & Giske 1994; Fiksen & al. 1995; Giske & al. 1997; Ringelberg 1999) are too cost intensive in terms of computations for incorporations in large-scale 3D physical models. There is therefore a need for more cost-effective models for adding biological detail in such spatially resolved models.

Recent theoretical work has developed into an adaptive approach to modelling biological systems by utilising properties derived from neurology and/or genetics (Wilson 1985; Booker 1988; Keiyu & al. 1994; Nolfi & al. 1994; Menczer & Belew 1996; Dagorn & al. 1997; Huse & Giske 1998). Giske & al. (1998) illustrate the applicability of such methods in modelling complex ecological systems and the capability of handling noisy inputs associated with fluctuating environmental forcing. Here we use adaptive modelling (i.e. heuristic algorithms which explore solution spaces for optimal solutions to a problem, Giske & al. (1998)) to study how models may be adapted to optimise the behaviour of zooplankton under relatively high degree of environmental variability. We develop a methodology that enables the behavioural strategies of organisms (relating to DVM) to be

optimised solely based on the environmental information available to the individual organism at its current position in space and time. From this we build a modelling framework enabling us to search out optimal strategies for autonomous individuals that are robust to characteristic levels of environmental complexity and unpredictability. By simulations we evaluate the performance of the different strategies devised by the model to different environmental scenarios, and test for the capability of the current method to reflect some of the behavioural plasticity zooplankton show in nature.

THE MODEL

THE ENVIRONMENT

The model environment is a 200 m water column, where the model organisms are assumed to adjust their position in the vertical direction over a 24 h time period so as to optimise the trade-off between predation risk and growth. We have not parameterised the model for any particular species, but have chosen to characterise the environment by gradients in relative terms (Fig. 1). We assumed that the depth specific growth potential scales with phytoplankton standing stock. Pelagic primary production commonly decreases with depth (Fig. 1A) in response to biophysical gradients in the water column (Sverdrup 1953). Standing stock of algae, typically show a depth distribution similar to that of production, but of-

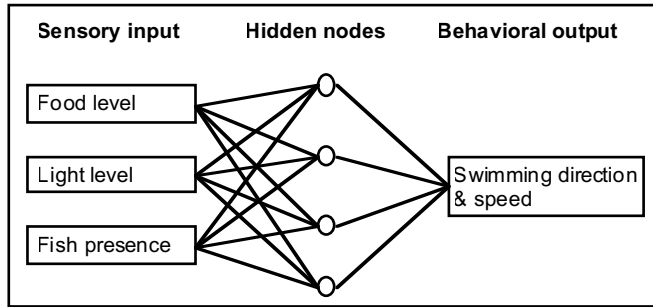


Fig. 2. The Artificial Neural Network (ANN) consisting of 3 sensory inputs (the concentration of food, the current light level, and chemical clues signifying the presence of fish), 4 hidden nodes, and the output (resulting swimming behaviour). Each connector in the network designates a weight of which the value is adapted by the use of a genetic algorithm. Mathematical operations performed in the network are described in the text.

ten are rather evenly distributed in the uppermost few meters of the water column (e.g. Melle & Skjoldal 1989). We have incorporated this in our model by characterising the growth potential ($G(z)$) for the model animals as constant in the upper 5 m of the water column, and then to decline exponentially with depth (Fig 1A). For the simplicity of this exercise we do not consider negative growth to occur.

The predation risk suffered by an organism is assumed to be the sum of predation risk caused by the presence of visually guided predators (i.e. fish), and a constant “background mortality risk” (C) accounting for the sum of all other mortality risks. Zooplankton mortality risk caused by the presence of visual predators in the water column is assumed to scale with ambient light level (Aksnes & Giske 1993). Depth and temporal variations in light level was simulated by a model for theoretical diel variation in surface irradiance (Skartveit & Olseth 1988), and by applying Beer’s law for the attenuation of light with depth. The spatio-temporal specific mortality risk experienced by an individual organism ($M(z,t)$) thus scale with light intensity at depth:

$$M(z, t) = x(C + E_0(t)e^{-Kz}) \tag{1}$$

where $E_0(t)$ is surface light at time t , x is the scaling parameter, and K is the attenuation coefficient of sub-surface downward directed light (0.06 m^{-1}). Thus, the mortality risk experienced by model animals varies both with time and depth (Fig. 1B).

As an index of fitness we applied the inverse of the ratio between the mortality risk and growth potential experienced by the model animal (Werner & Gilliam, 1984). The relative fitness of an individual residing at depth z at time t ($\delta(z,t)$) may thus be described by:

$$\delta(z, t)^{-1} = \frac{M(z, t)}{G(z)} \tag{2}$$

where $G(z)$ is the depth specific growth potential (Fig. 1).

To monitor the optimality of behavioural patterns of model individuals we summed the time and depth specific fitness values of individuals (δ_{ind}) for the duration of the simulation

$$\delta_{ind} = \sum_{t=1}^T \delta(z, t)^{-1} \tag{3}$$

Where T is the temporal horizon of the simulation measured in time steps. It follows from Eqs 2 and 3 that an organism should minimise its ratio of mortality risk to growth to optimise its fitness. Eqs 1 and 2 enable the computation of optimal depth (z_{opt}) for a model animal at any time of day, thus providing a framework to evaluate the different strategies in relation to the true optimal behavioural solutions (i.e. z vs. z_{opt}), and the associated fitness relative to maximum obtainable fitness ($\delta^*(\delta_{ind})^{-1}$). Depth distributed relative fitness at noon and midnight (Eq. 2) is shown in Fig. 1C.

The chosen fitness measure is a somewhat dubious measure of optimality, as it does not take into account all aspects of behaviour and life history that relate to Darwinian fitness (e.g. effects from frequency dependence and state dependence). Models of the type described in this study functions irrespective of fitness measure used. The use of “Gilliam’s rule” in the current work is due to the analytical tractability of such an approach in that it enables straightforward computation of optimal behaviour in respect to a variable environment.

BEHAVIOUR

To control the behaviour of the model organisms, we have used a simple feed-forward Artificial Neural-Network (ANN) (Hopfield 1982; Kohonen 1984), consisting of 3 inputs, one hidden layer, and a single output (Fig. 2). The inputs constitute of three parameters that zooplankton tend to respond behaviourally to: the light regime (Kampa & Boden 1954; Longhurst 1976; Miller 1991), the food concentration (Aksnes & Giske 1990),



and whether fish are present or not in the surrounding water (Ohman 1983; Dodson 1988; Cieri & Stearns 1999).

To model DVM behaviour an ANN is given a location in a water column. At any time-step the ANN is fed by values for these three parameters corresponding to the location of the organism in space and time. The sensory inputs can be parameterised for specific organisms (Aksnes & Utne 1997). Each connection in the ANN is associated with a certain weight, which may take any real number in the interval $[-10, 10]$. Inputs are multiplied by the weight, and summed up in the nodes (or neurones) in the hidden and output layers. The excitation level (β_i) of a node (i) is based on the sum of all (j) inputs connected to the node ($\Sigma\alpha_j$), and an excitation function

$$\beta_i = \frac{1}{1 + e^{-\Sigma\alpha_j}} \quad (4),$$

which scale excitations from 0 to 1. The output of the ANN is the vertical swimming velocity of the model animal. The behavioural output (β_o) is determined by the sum of inputs from each of the hidden nodes ($\Sigma\alpha_h$), in the same way as in Eq. 4, and then scaled to fit the interval $[-10, 10]$ by:

$$\beta_o = \left(\frac{1}{1 + e^{-\Sigma\alpha_h}} - \frac{1}{2} \right) \cdot 20 \quad (5).$$

For simulations with a time step of 2 min, this corresponds to an approximate maximum vertical displacement of 1 cm s^{-1} .

ADAPTATION OF BEHAVIOUR

To optimise behaviour we used a genetic algorithm (GA) (Holland 1975) where each ANN weight is coded for by strings of 8 binary digits. A population of 1000 ANNs are tested for their performance (Eq. 3) in the environment described above. The 50 best individuals are selected and kept for the next generation. In addition 950 new individuals are generated from the pool of binary strings of the 50 best performing individuals. This is done by standard procedures described in the GA literature involving point mutations (which happen at random with a frequency of ca. $1:10000$) and random recombination of binary strings. Holland (1975) gives a comprehensive

account on GA models, and Giske & al. (1998) discuss the practical use of combining ANNs and GAs in behavioural modelling.

ARCHITECTURE

What ANN architecture performs best at a single task, can not be known *a priori*. Given the task in question, and the desire to keep the ANN as simple as possible, 3 sensory inputs and 1 behavioural output (Fig. 2) dictates the minimum requirements of our ANN-model forced by the environmental parameters we are interested in (light, growth, and predator presence). For the sake of simplicity we have not considered the possibility of multiple sensory apparatus for one type of stimuli. Furthermore, we have confined our analysis to a sub-set of ANNs containing one hidden layer only, and without modularity in architecture. To test for the optimal number of nodes in the hidden layer a series of simulations were performed where ANNs containing from 2 to 5 nodes in the hidden layer were compared. This was done by setting up the model in a deterministic environment, and letting the population of ANNs adapt for 100 generations. Based on the performance of these runs (Table 1) we have used an ANN architecture consisting of a 4-node hidden layer (Fig. 2).

SIMULATIONS

To evaluate the performance of the model we set up a series of simulations where different aspects of environmental variability were used to force the model behaviour.

First we adapted the stimuli-response models to different levels of stimuli complexity and environmental stochasticity by adapting the behaviour of ANNs to 3 different stimuli configurations: 1) light only, 2) light and food levels, and 3) light, food, and the presence of predators. For each of these situations we adapted the ANNs both to a deterministic and a stochastic environment. In the latter, the sensory parameters were allowed to fluctuate at random (evenly distributed) between time-steps by up to $\pm 50\%$ of the value used in the deterministic runs (Fig. 1). All simulations in which ANNs were adapted were done for 50 generations, with 2 minutes time steps, and forced with a simulated light regime from 60°N at 1 May. The performance of the migration strategies adapted in this manner was then evaluated by the ratio of fitness obtained to the highest obtainable fitness ($\delta^*(\delta_{ind}^*)^{-1}$).

To test for performance to variable levels of predation pressure we adapted the model to a stochastic environment where presence of visual predators varied at random. The strategies evolved in this manner were then tested for performance against strategies evolved under high degree of stimuli complexity (light, food, and pre-

Table 1. Average fitness obtained by 4 different ANN architectures ranging from 2 to 5 nodes in the hidden layer. Values shown are the mean values for the 10 best performing individuals after 100 generations. Each value represents the average of 4 simulations.

Number of hidden nodes	2	3	4	5
Fitness ($t = 100$)	0.785	0.913	0.948	0.892



dation levels), but under variable degree of environmental stochasticity (deterministic light, food, and predator levels, and stochastic light and food levels but deterministic predator levels). To compare the performance of the strategies they were set up in a simulation over 10 days where visual predators were present at 8 days, but absent on 2 days. Performance was then evaluated relative to the highest obtainable fitness within the model setting as described above.

Finally we studied the plasticity of the model by evaluating its performance to variability in one of the input stimuli (day length) comparable to the seasonal variability at 60°N. This was done in simulations where the migration strategy adapted to an environment with stochastic light and food levels and day length ≈ 15.5 h (1 May) was compared to seasonal extremes in diel light regimes.

RESULTS

MODEL PERFORMANCE WITH VARYING STIMULI AND DIFFERING ENVIRONMENTAL COMPLEXITY

Generally the model predicts animals to stay at shallow depths for the darkest period of the day, which on the 1 May is approximately a time period of 8 h duration centred around midnight (Fig. 3 & 4). As soon as ambient light conditions start increasing the models predict animals to begin their decent travel. A maximum depth of ca. 60 m is reached after light intensities peak at noon.

Running the model for 50 generations generally produce close to highest obtainable fitness values ($< 8\%$ deviation from absolute optimal values), regardless of stimuli used and environmental representation (Table 3). In all runs the model succeeds in adapting DVM behaviour that closely follow the optimal depth trajectory over a day (Figs 3, 4). The simplest model structure used (light as the only stimuli) performed rather effectively both under deterministic and stochastic temporal variability in the light regime (Fig. 3A, B). Performance of the two

adapted strategies was equal (average relative fitness after 50 generations of adaptation (RF50) ≈ 0.953 , and 0.952 , respectively). When light is the only stimuli animals can adapt their behaviour to they tend to spend dark hours at the surface (Fig. 3), thus missing the sub-surface optimum at 5 m caused by the evenly distributed food concentrations above this depth (Fig. 1A).

Model performance is significantly higher in simulations of a deterministic environment where model animals are offered more detailed information about the environment (light and food at current depth) (RF50 ≈ 0.996 ; Fig. 4A and Table 3). The model predicts a behavioural pattern capable of tuning the night-time depth to fit the fitness maximum at 5 m depth, although individual variability in depth is quite high (Fig. 4A).

Lowest levels of performance, and highest variability (RF50 \pm standard deviation of the mean $\approx 0.931 \pm 0.005$) were observed for strategies adapted under low environmental stability (Fig. 4B; Table 3). In these simulations the model predicts night-time depth to be kept consistently deeper in the water column at a depth of about 20 m (Fig. 4B).

MODEL PERFORMANCE UNDER VARIATIONS IN PREDATOR PRESSURE

The performance of ANNs when the presence of predators differs on a daily scale is sensitive both to the sensory capabilities of the ANN and to the environmental regime strategies were adapted to (Fig. 5). When tested over 10 days under stochastic light and food conditions, and with predators being absent on two of the days the ANNs adapted to a deterministic environment performed poorly (average relative fitness \pm standard deviation = 0.65 ± 0.16) (Fig. 5A). Population adapted to stochastic light and food, but with deterministic predation pressure performed slightly better in terms of relative fitness (0.72 ± 0.09) (Fig. 5B), while populations adapted to stochastic light, food and predation pressure had the highest performance in terms of relative fitness (0.87 ± 0.05) (Fig. 5C).

Table 2. The sensory system and environmental variability that strategies were adapted for in the model runs. Input stimuli refers to the environmental parameters the ANN were allowed to tune its behaviour to: Light denotes light at the current depth of the model animal in each time step, food denotes the food concentration encountered at the given depth of the model animal, predators denotes whether visual predators are present in the water column. See text for details.

Number of active input nodes, and input stimuli	Environment
1, Light	Deterministic and Stochastic
2, Light, food	Deterministic and Stochastic
3, Light, food, predators	Stochastic

Table 3. Mean relative fitness achieved after 50 generations of simulation by adapting the model organisms to variable levels of environmental complexity (input stimuli and stochasticity of environment). Values shown are the averaged values obtained by the 5% of each generation closest to global optimum (1.00) for 10 different simulations where the random seeding is held constant between simulations to control for any chance effects. See text for details.

Stimuli adapted for	Deterministic environment	Stochastic environment
Light	0.953 ± 0.002	0.952 ± 0.001
Light and Food	0.996 ± 0.002	0.931 ± 0.005

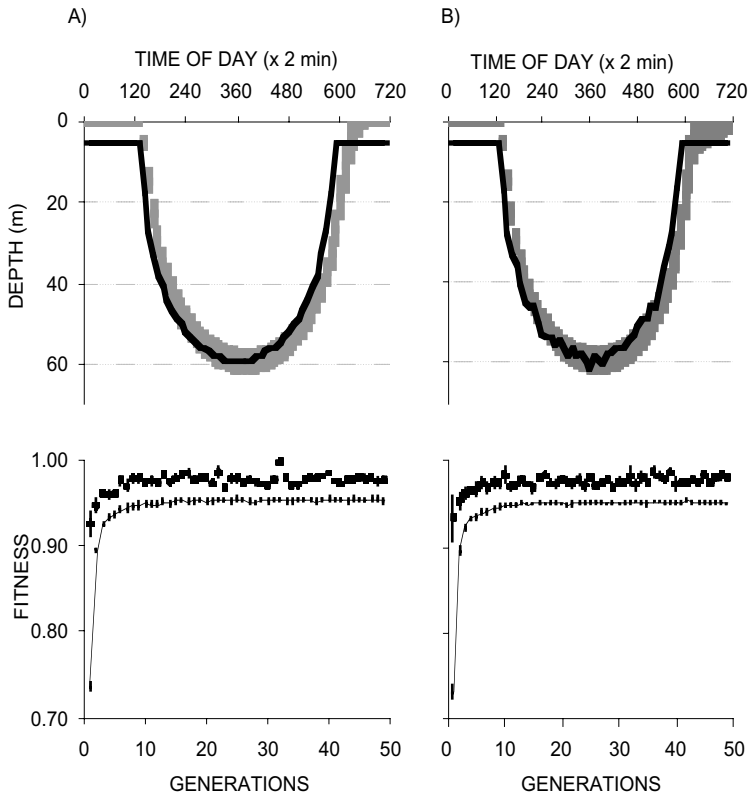


Fig. 3. Model output from simulations where only the light level at depth is used as input stimuli used to control behaviour. A. Deterministic light regime. Upper panel: Black curve shows the globally optimal depth track over a 24 h time period (1 May) as predicted directly from the fitness function (Eq. 2). Grey bars denote the mean depth ± 1 standard deviation of location of individuals. Lower panel: Fitness (Eq. 3) obtained in the model during 50 generations of adaptation. Black line denotes the average fitness of the selected proportion of individuals in each generation (0.05), and black circles denote fitness of best individual in each generation. Bars denote 95 % confidence limits of the means for 10 simulations. B. As for part A, but with random fluctuations on the light flux.

PLASTICITY TO SEASONAL CHANGES IN LIGHT REGIME

Strategies evolved under a stochastic light and food regime at 1 May performed equally well when tested on the light regime of mid-summer (average relative fitness \pm standard deviation = 0.91 ± 0.02 and 0.90 ± 0.02 , respectively, but proved less effective on a mid-winter situation (0.81 ± 0.02) (Fig. 6).

DISCUSSION

Compared to other models available (e.g. Mangel & Clark 1988; Fiksen 1997) the model presented in this work provides a relatively cost-effective way of adding this biological detail to ocean models with spatial resolution. The ANN used to control behaviour (Fig. 2) may be adapted to describe the model organism in question based on its biology and the characteristic variability of the model environment. By optimising strategies for ver-

tical migration in advance, the ANN reduces to a compact mathematical function once the optimal weights are found (by substitution of Eq. 4 into Eq. 5). Its incorporation in large-scale models thus carries with it only a slight increase in computational effort. We believe this property makes the model well suited for increasing the biological detail in particle tracking studies. The input stimuli used in the model are obtainable by relatively low cost field efforts (remote sensing, acoustic surveys), or from simulation studies. Parameterisation of the model for a given species may prove more complicated but stimuli thresholds for proximate triggering of behaviour is starting to become available for a range of planktonic animals (e.g. Dodson 1988; Bollens & Stearns 1992; Tande & Slagstad 1992; Balinño & Aksnes 1993; Cieri & Stearns 1999; Ringelberg 1999).

Any model of behaviour of autonomous agents which aim at reflecting the basic properties of living organisms

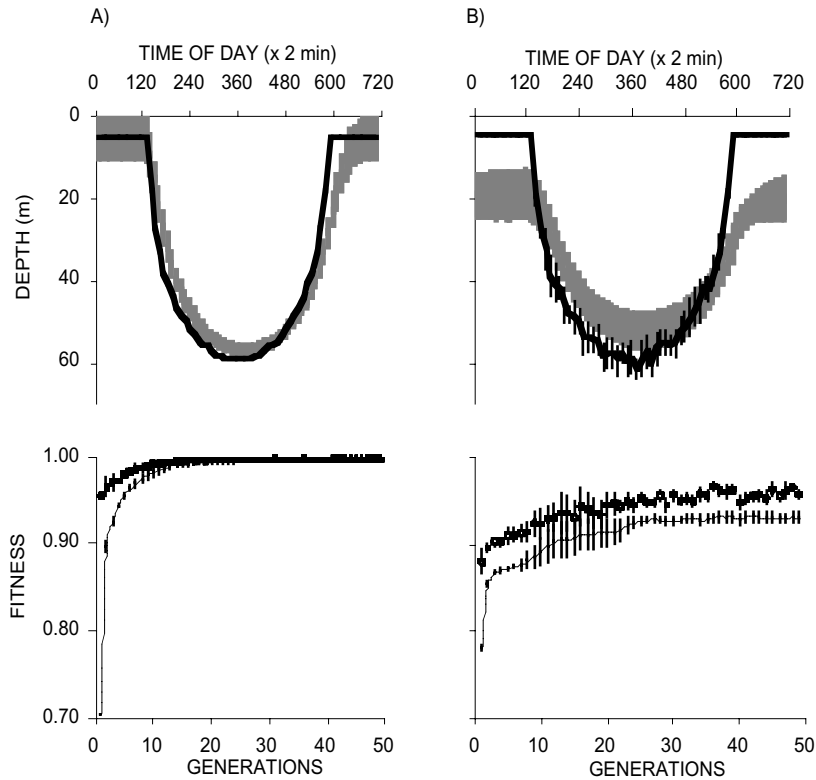


Fig. 4. Model output from simulations where both light level and food concentration are stimuli offered to control behaviour by. A. Deterministic light and food regime. B. Randomly fluctuating light and food regime. See Fig. 3 for further details.

must involve parallelism and distributed processing of stimuli (Langton 1988; Wilson 1991). If, as in the present work, one wishes to model behaviour as a stimuli-response process under the high degree of stochastic environmental unpredictability encountered in nature, the ANN approach (Hopfield 1982; Kohonen 1984) presents itself as the only obvious solution. However, the postulate that ANNs will only function for a problem that are well defined in a statistical sense (Keiyu & al. 1994), undoubtedly have much hampered the use of ANNs in behavioural ecology. Our result (Figs 3-6 and Table 3) shows this view to be too pessimistic. By applying a GA for optimising the connector weights in the ANN, instead of the more traditional backward propagation technique, we omit the problems specified by Keiyu & al. (1994). Furthermore we invoke an optimisation procedure harbouring more ecological and evolutionary tractable dynamics (Holland 1975) than the backward propagation routine. This result is achieved even though we have applied an evenly distributed random term to describe environmental variability, thus avoiding a statistical peak in signal for the ANN to operate on. The use

of a simple fitness measure (Eqs 2 & 3) enable us to monitor the deviation between adapted behaviour and global optimum in simulations, and obtained performance shows our method to be effective (Table 3).

A critical assumption for the model presented here is that planktonic animals optimise their behaviour in responses to the changes in some environmental stimuli, and not in accordance to some pre-programmed endogenous scheme. We rest this assumption on the growing numbers of studies of the nature of proximate stimuli and the behaviour responses they invoke in planktonic animals. For instance, Tande & Slagstad (1992) found that DVM in various developmental stages of *Calanus finmarchicus* in Arctic waters was most accurately described by avoidance of some stage specific upper threshold in ambient light level and to be modified by the degree of individual food requirements. Similarly the daily vertical displacements of planktonic organisms in a fjord on the south-western coast of Norway apparently track an isolume over the course of a winter day (Baliño & Aksnes 1993). DVM in *Daphnia* spp. may effectively be modelled as a proximate response to light intensity at

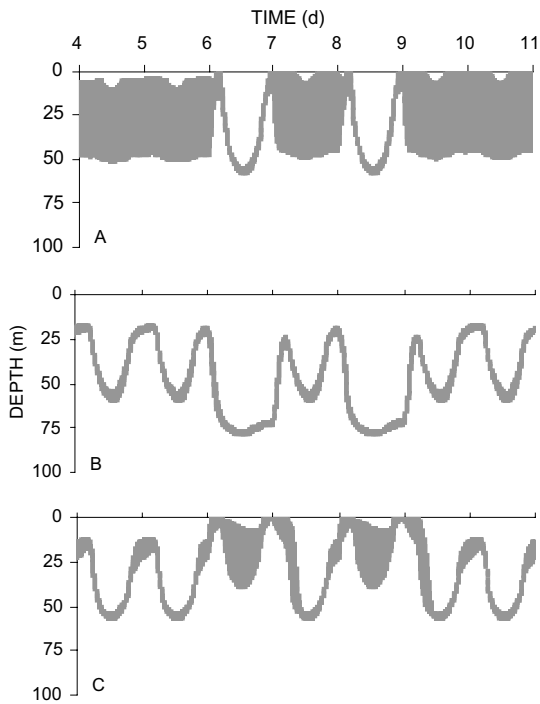


Fig. 5. Behaviour of differently adapted models over the 7 last days of a 10 day simulation where predation risk is low at 2 days (days 6 and 8), but high on other days. A. Model adapted to deterministic food and light levels. B. Model adapted to stochastic light and food levels. C. model adapted to stochastic light, food, and predator levels.

depth (Ringelberg 1999), but may be altered if fish mediated chemicals are induced in the water (Dodson 1988; Ringelberg 1999). Behavioural responses to fish exudates is described for the marine copepods *Acartia hudsonica* and (Bollens & Stearns 1992), and Cieri & Stearns (1999) show that the functional proximate stimuli utilised by *A. hudsonica* and *A. tonsa* is a combination of light level and chemical fish exudates. Furthermore, Unstad & Tande (1991) found *C. finmarchicus* to aggregate vertically at a narrow depth stratum with high standing crop of phytoplankton, indicating that copepods are capable of responding behaviourally to food concentrations in the field. A general result obtained by modelling DVM as a “stimuli–response” process is the predicted time lag between the globally optimal depth and the depth obtained by model organisms (Figs 3-6). Control simulations were performed to check that this effect was not an artefact introduced indirectly through some other factor (e.g. the swimming speed). The temporal offset is directly linked to modelling behaviour as requiring a stimulus, which must be introduced to the animal before it,

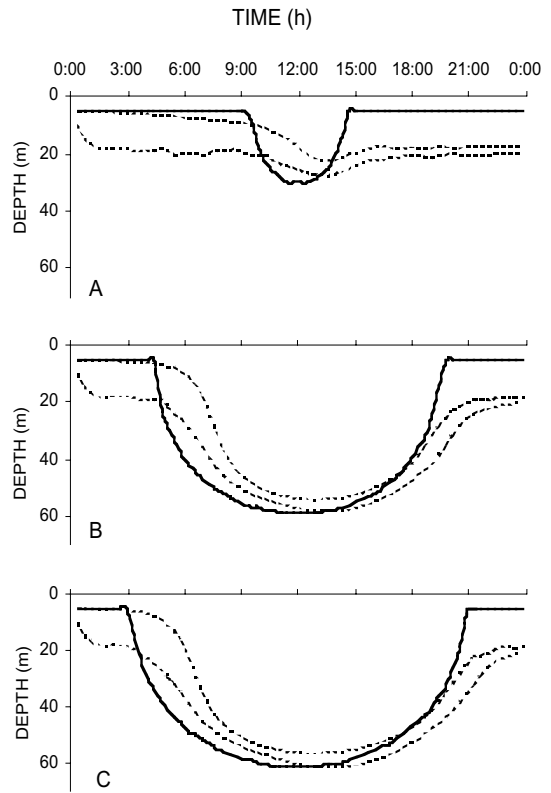


Fig. 6. The behaviour of the model under seasonally difference in light regime. Model adapted to random variations in light and food, but constant predation risk and to the light regime and photoperiod from 1 May (B). A. Predicted behaviour when the model is run under the light regime from mid winter. C. The model predictions from runs forced by light regime from mid summer. Solid lines denote optimal depth (by Eq. 2), broken lines denote upper and lower distribution of the mean depth ± 1 standard deviation of the population.

can operate on it. Furthermore, our model only offers model organisms information about the environmental states from their immediate surroundings. The behavioural strategies adapted in model organisms therefore are limited in terms of search techniques for the globally optimal location to a directional movement (up or down) by a certain speed. Adapting to a changing environment thus involves trial and error, and should be expected to be time consuming.

We do not know of any study reporting this modelled trait in nature. But the predictions suggested by all model runs: That animals are expected to reach their night-time depth at lower light intensities than the intensities at which they start the descent migration at dawn, is testable. We suggest further work should focus on this prediction to



validate model predictions. Applying high resolution sampling devices (high-frequency acoustics or optical instruments) should enable such an analysis.

Planktonic organisms differ in the strategies they have adapted in order to optimise their fitness under the unpredictable and ever moving water column. While some organisms are capable of maintaining their position, others are not and drift with the water masses in which they live (Kaartvedt 1993). Ocean water transport is highly complex and planktonic organisms will be subject to unpredictable spatial relocation on a time scale corresponding to a few generations. Key environmental characteristics for planktonic organisms as food and the risk of falling prey are not evenly distributed in space and time, and vital rates of planktonic populations generally are highly variable (Ohman & Wood 1996). Observations of differences in vertical behaviour attributed to differences in environmental stimuli are often made for a given species of zooplankton (Ohman & al. 1983; Eiane & al. 1999). Thus, while there is a fair chance that a given planktonic organism over its life span will experience an environment comparable to that of its mother, this probability may decline rapidly for successive generations of offspring originating from a given mother individual. Indeed, recent surveys report indications of considerable genetic exchange between local strains of *C. finmarchicus* throughout much of the Northern Atlantic Ocean (Bucklin & al. 1996), an area of considerable spatio-temporal variability in environmental forcing. The strategic behavioural decisions so successfully made in one generation therefore, may not be suitable for the later generations. This implies that the palette of behavioural strategies evolution has made available to a panmictic planktonic organism are confined by what have proven robust to environmental fluctuations characteristic of the range of habitats the species has occupied

successfully over its evolutionary history. The globally optimal strategy in one specific situation may be catastrophic under different conditions and therefore, organisms should be expected to have adapted towards strategies that carry with them the highest fitness reward over long time (Yoshimura & Clark 1993; Tuljapurkar & Caswell 1997).

To model large-scale behavioural processes as DVM it is crucial to understand how the associated fitness effects act on the individual organism (Tuljapurkar & Caswell 1997). This is the underlying fundamental assumption behind most of the theoretical tools developed to understand behaviour over the past decades (e.g. Fretwell & Lucas, 1970; Charnov 1976; Mangel & Clark, 1988). Undoubtedly, this approach has led to a vast amount of research, particularly on the theoretical area, which has developed into a highly efficient way of analysing behaviour and life history in an ecologically and evolutionary sound framework. However, biological realism is not perfect in any model and Giske & al. (1998) lists several potentially important ecological mechanisms adaptive models are capable of handling better than traditional models (e.g. density dependence, temporal variable environments). In addition the current work suggests that modelling behaviour as an adaptive stimulus-response process is a useful tool for producing plastic and robust strategies (Figs 6-7). However, adaptive modelling (at least as presented here) does not assure that global optimums are reached in the same way as is done by some other model tools (Mangel & Clark 1988). Perhaps a problem of even greater importance arises from using an ANN to control behaviour. Constructing, and optimising ANNs are rather straight forward, but extracting significant information from such models is not trivial, and must typically be done by indirect (correlative) analysis.

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