

Artificial Evolution of Life History and Behavior

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ABSTRACT: We present an individual-based model that uses artificial evolution to predict fit behavior and life-history traits on the basis of environmental data and organism physiology. Our main purpose is to investigate whether artificial evolution is a suitable tool for studying life history and behavior of real biological organisms. The evolutionary adaptation is founded on a genetic algorithm that searches for improved solutions to the traits under scrutiny. From the genetic algorithm's "genetic code," behavior is determined using an artificial neural network. The marine planktivorous fish Müller's pearlside (*Maurolicus muelleri*) is used as the model organism because of the broad knowledge of its behavior and life history, by which the model's performance is evaluated. The model adapts three traits: habitat choice, energy allocation, and spawning strategy. We present one simulation with, and one without, stochastic juvenile survival. Spawning pattern, longevity, and energy allocation are the life-history traits most affected by stochastic juvenile survival. Predicted behavior is in good agreement with field observations and with previous modeling results, validating the usefulness of the presented model in particular and artificial evolution in ecological modeling in general. The advantages, possibilities, and limitations of this modeling approach are further discussed.

Keywords: individual-based model, artificial neural network, genetic algorithm, stochastic environment, habitat selection, energy allocation.

Modeling has become an important approach in behavioral ecology (Stephens and Krebs 1986; DeAngelis and Gross 1992; Krebs and Davies 1997) because of the complexity of the living world. The advent of individual-based models (IBMs; Huston et al. 1988) has provided ecologists with a flexible tool that allows populations to be simulated from their individual members. This approach has several

advantages, most notably the inclusion of individual variability, spatial detail, and easy comparisons with observational data performed on individuals (Huston et al. 1988). Another advantage of IBMs is that the approach has the same apparent unit as evolution—namely, individuals. This allows evolutionary motivation for behavior to be implemented in IBMs using adaptive models based on the genetic algorithm (GA; Holland 1975). The GA applies the principle of evolution by natural selection to search for increasingly better solutions to a given problem. Solutions are presented in the form of a numerical "genetic code" (Holland 1975) that expresses the trait(s) under scrutiny. As with the gene pool of a real population, the pool of codes evolves over time as a result of mutations, recombinations, and selection within the constraints imposed by the outer environment and the physiology of the organisms. The code may further be translated into behavior using an artificial neural network (ANN), a highly simplified model of the decision process in a nervous system (Rummelhart et al. 1986). The GA code is used in the ANN for differential weighting of the information of importance for behavioral decisions. This modeling approach is termed an individual-based neural network genetic algorithm (ING) model (Huse and Giske 1998), and we have shown that this modeling approach yields behavioral solutions similar to those of conventional optimization models (Huse et al. 1999).

Normally the solutions in a GA are evaluated and sorted according to an a priori defined fitness criterion, and only the individuals possessing phenotype(s) with the highest fitness are allowed to reproduce (Goldberg 1989). It can sometimes be valuable to avoid the use of fitness measures, which severely restrict the inclusion of stochasticity, density dependence, and games in behavioral models. Individual-based models allow the use of a different definition of fitness. Instead of rate maximization, one can simulate the entire life history of a population of organisms, including spatial movements, foraging, growth, predator avoidance, and reproduction. A simulated individual will then contribute to the "gene pool" based on its capability of reproducing its genetic code through offspring. This capability will reflect its behavioral strategies: good

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strategies are those that best promote offspring production in a given environment.

Artificial evolution as described above is commonly applied in the field of artificial life (A-life; Langton 1989). To the best of our knowledge, ING models applying emergent fitness (or “endogenous fitness”; Mitchell and Forrest 1995) have previously been applied only to simple artificial scenarios (Ackley and Littman 1991; Menczer and Belew 1996) based on imaginary “agents” and never to a complex biological model. Our main purpose is therefore to investigate whether artificial evolution is a suitable tool for studying life history and behavior of real biological organisms. This is addressed by studying the role of environmental stochasticity on behavior and life-history strategies of the mesopelagic fish Müller’s pearlside (*Maurollicus muelleri*) using an ING model. Furthermore, we discuss the pros and cons of artificial evolution compared to the traditional fitness-based approaches in behavioral ecology and life-history theory in the context of the results of the simulation model.

Model Description

Model Organism Description

Maurollicus muelleri (Stormiiformes, Sternoptychidae) is an abundant midwater fish found worldwide on continental slopes (Gjøsæter 1984; Kawaguchi and Mauchline 1987). It performs extensive diel vertical migrations (DVMs; Giske et al. 1990; Baliño and Aksnes 1993; Rasmussen and Giske 1994; Goodson et al. 1995) and feeds visually on copepods and other zooplankton (Gjøsæter 1981). It is a multiple-batch spawner (Melo and Armstrong 1991), with a spawning season that stretches from March to September in Norwegian waters. This species attains reproductive maturity after 1 yr, and the fish seldom reach an age exceeding 3 yr (Gjøsæter 1981). The local populations are subject to substantial interannual variation in recruitment (Kristoffersen and Salvanes 1998). During winter, *M. muelleri* is located in two distinct vertical layers that can be detected by acoustic methods (Giske et al. 1990; Baliño and Aksnes 1993). Juveniles constitute the upper sound-scattering layer (SSL), and adults constitute the lower SSL. The main predators of *M. muelleri* in Norwegian waters are blue whiting *Micromesistius poutassou* (Risso), saithe *Pollachius virens* L., and Atlantic salmon *Salmo salar* L. (Rasmussen and Giske 1994).

The reason for using *M. muelleri* as a model organism is the relatively broad knowledge of its life history and vertical migration behavior. This knowledge is attributed to both field observations (see, e.g., Gjøsæter 1981; Melo and Armstrong 1991; Rasmussen and Giske 1994; Goodson et al. 1995; Salvanes and Stockley 1996) and modeling

studies (Giske and Aksnes 1992; Rosland and Giske 1994, 1997). This allows us to compare the ING predictions with both observations and prior modeling predictions. Rosland and Giske (1994) modeled vertical distribution of *M. muelleri* on a single day in a western Norwegian fjord, while Rosland and Giske (1997) modeled DVM behavior through the entire life cycle. We have kept the environment and physiological properties as similar as possible to the stochastic dynamic programming models of Rosland and Giske (1994, 1997) in order to permit comparison.

The ING Concept

Genetic algorithms have been widely used in A-life theory and research to evolve behavioral rules in agent-based models (see review by Mitchell and Forrest 1995). The “agent” in agent-based models is directly analogous to an “individual” in IBMs (Uchmanski and Grimm 1996; Parrott and Kok 2000). Each type of behavior (or trait) is represented in the GA in the form of a numerical “genetic code.” An individual’s genetic code must not be confused with real biological genetic material (DNA), and therefore terminology from Goldberg (1989) will be used. The GA analogue of a biological chromosome is a “string,” the analogue of a gene is a “character,” and each alternative of a character (an allele) is a “character value.” It should be noted that the genetic strings applied here are haploid. Individuals in the populations may differ with respect to the character values on their string. During a simulation, the GA searches for increasingly better behavior over many generations, in response to the variables affecting the fitness of an individual, by adapting the numerical values in the genetic code. The adaptation in a GA model is similar to biological adaptation: organisms that survive until reproduction send their character values off to the next generation in proportion to their clutch sizes.

An ANN comprises the link between genetics and behavior. The ANN is a method that applies neurobiological principles of synaptic brain activity to calculate output behavior by differential weighting of input variables (Rosenblatt 1958; Rummelhart et al. 1986; Montana and Davis 1989). Each character value specifies the weighting of one synapse in the modeled fish brain.

The ANN applied here is a feedforward network with an input layer, a hidden layer, and an output layer. Each of the layers consists of a number of nodes that receive input data (fig. 1A). Both biotic and abiotic environmental variables together with physiological state variables may be used as information input. The input data are multiplied by allele-specific weights that connect nodes between layers. At the nodes in the hidden layer, all incoming stimuli from the input layer nodes are summed before the signal is sent toward the output node. When a GA is used

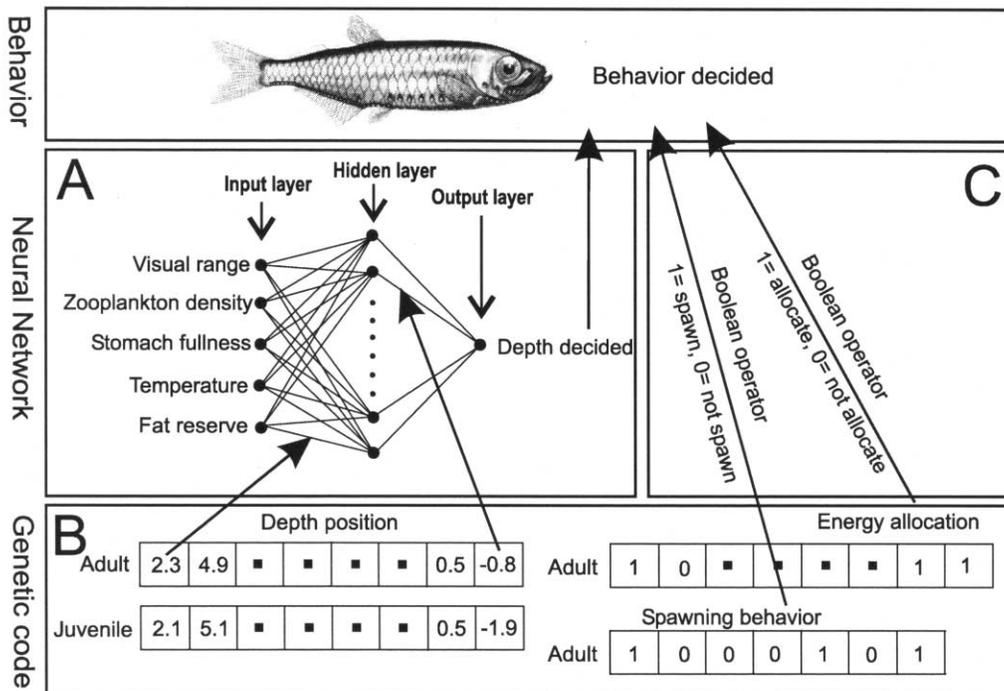


Figure 1: The relationship between the genetic algorithm’s genetic code (B), artificial neural network structure (A), and behavior. An individual uses two different strings for depth positioning, depending on its maturity status. Depth position is determined by character values and input variables experienced by the individual. The strings for energy allocation and spawning behavior are inherited Boolean operators that decide whether or not to spawn and when to allocate excess energy to fat or structural growth.

to adapt the weights of the ANN, the ANN weights are represented in the GA as the genetic code (van Rooij et al. 1996; fig. 1B). The ANN is a proximate stimulus transformer, able to generalize complex patterns of stimuli to individual responses. Described in biological terms, with analogous ANN terms in parentheses, the stimulus-response process works as follows: by receiving information (input values) at the sensory organs (input nodes), and sending these signals through the web of neurons (weights) in the central nervous system (ANN), one or several actions are made by the muscles (output node[s]). The GA genetic codes may also be used directly to determine behavior without being incorporated into an ANN. This is the case for energy allocation and spawning strategy in the present model (fig. 1C).

If an individual grows sufficiently large and reaches maturity, it can produce offspring by a process analogous to sexual reproduction. Part of its genetic string is then passed on to its offspring (fig. 2). Individuals that produce more offspring than others will spread their character values at a higher rate, and hence their responses to biotic and abiotic stimuli will become more common in the population. Thus, the ING model is a combined ultimate and

proximate approach, where behavior determines survivorship and reproduction, which in turn impels the “course” of evolution. If desirable, the ING model may also use conventional fitness measures, by implementing a given fitness criterion and sorting individuals in relation to achieved fitness. See Huse and Giske (1998), Huse et

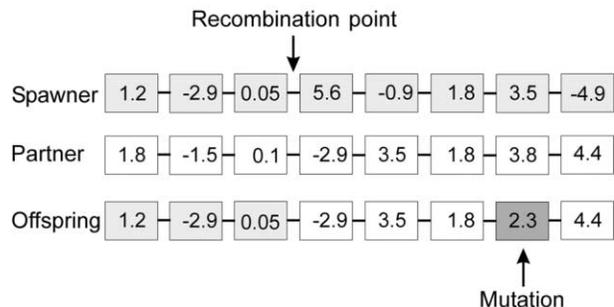


Figure 2: Exemplified structure of a genetic string. Each individual has unique strings consisting of characters that are partially inherited by offspring during sexual reproduction. Recombinations and mutations occur with a given probability at random locations on the string.

al. (1999), or the ING homepage (<http://www.ifm.uib.no/staff/huse/ing.html>) for more details on ING models. Recombinations and mutations occur with a given probability during sexual reproduction, slightly altering the offspring's genetic string and giving rise to new variation therein (fig. 2). A flowchart of the ING model is found in figure 3.

State and Adapted Traits

Each simulated individual has its present state described by the attribute vector (Chambers 1993). The attribute vector of an individual *M. muelleri* in this model is defined as

$$\begin{aligned}
 \mathbf{a} = & (\text{age, structural weight, current weight,} \\
 & \text{fat reserve, last meal, stomach} \quad (1) \\
 & \text{fullness, current depth, time),}
 \end{aligned}$$

where age is days since birth and structural weight is a measure of the skeletal size and hence not reversible (Rosland and Giske 1997). Current weight is proportional to the individual's energy density, and hence reversible. The current weight cannot exceed structural weight. Current weight divided by structural weight serves as a measure of condition. Fat reserve is excess energy stored and does not influence either structural or current weight. Last meal is the amount of food eaten during the last time step, and stomach fullness is the amount of food left in the stomach. Current depth is measured in meters below the surface, and time is measured in years, months, and minutes. All other internal state variables, except age, are measured in grams. Body length (BL) of *M. muelleri* is not included in the attribute vector and is calculated based on structural weight using weight versus length data from Masfjorden, western Norway (Rasmussen and Giske 1994):

$$BL = 46.472 \times W_s^{0.3304}, \quad (2)$$

where BL is body length in millimeters and W_s is structural weight in grams. See table 1 for parameters and variables.

The strategy vector (Huse 2001) of *M. muelleri* contains the strategy variables of the individuals:

$$\begin{aligned}
 \mathbf{s} = & (\text{vertical position, energy allocation,} \\
 & \text{spawning behavior}). \quad (3)
 \end{aligned}$$

Each strategy variable is implemented on separate strings in the GA.

Vertical Position. A dynamic depth positioning strategy is of great importance to *M. muelleri*. The fish needs to trade

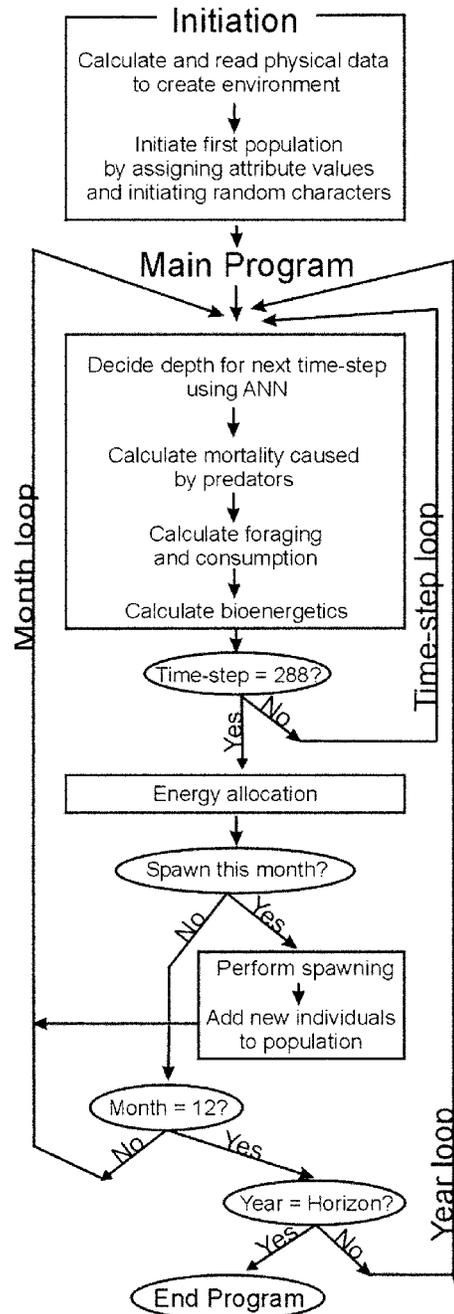


Figure 3: The structure and event flow of the presented model

off the fitness reward of foraging against the risk of predation. This trade-off is influenced by light intensity, food availability, and energy reserves (Aksnes and Utne 1997; Rosland and Giske 1997). It has also been suggested that adults and juveniles may apply different depth positioning strategies (Giske and Aksnes 1992), as growth affects fitness more for juveniles than for adults. To enable juveniles and

Table 1: Parameters and variables used in the model

Symbol	Description	Value	Unit
A_s	Annual stochasticity	.5–1.5	Dimensionless
BL	Body length of <i>Maurolicus muelleri</i>	...	mm
Δo	Total oocyte mass	...	g
Δz	Vertical migration distance	...	m
E_{pred}	Probability of a <i>M. muelleri</i> to encounter a predator	...	Dimensionless
o	Individual oocyte mass	1.4×10^{-4}	g
P_p	Predator density parameter	...	Dimensionless
r	Visual range of <i>M. muelleri</i>	...	mm
r_p	Visual range of predator	...	mm
S_s	Seasonal stochasticity	.0–2.0	Dimensionless
S_t	Condition threshold for spawning	.93	Dimensionless
θ	Reaction field half angle	30	Degrees
VM_{cost}	Vertical migration cost	...	g
W_c	Current weight of <i>M. muelleri</i>	...	g
W_s	Structural weight of <i>M. muelleri</i>	...	g
z	Current depth	1–200	m

Note: Ellipses indicate no fixed value.

adults to evolve different strategies, we constructed two genetic strings (fig. 1B) for depth positioning. An individual inherits both sets from its parents. One set will be used during the juvenile stage and the other after reaching maturity. Depth position (m) is decided each time step using an ANN. The ANN has 5 input nodes, 20 hidden nodes, 1 output node, and 20 hidden node biases. The bias values are added to the sum of incoming weights at each hidden node to improve ANN performance (Rumelhart et al. 1986). Each GA string for depth position therefore consists of 140 ($= 5 \times 20 + 20 \times 1 + 20$) characters, all evolved by the GA. The ANN input variables used to decide depth position are visual range (mm), zooplankton density (individuals m^{-3}), stomach fullness (%), temperature ($^{\circ}\text{C}$), and fat reserves (g). It is assumed that *M. muelleri* is capable of gathering this information. The output from the ANN is standardized between 0 and 200 using a sigmoid transfer function (van Rooij et al. 1996).

Energy Allocation and Spawning. Energy allocation and spawning behavior are assumed to be inherited life-history strategies, making a translation of the genetic code through an ANN obsolete. The character values, however, are evolved by the GA. The energy allocation string consists of 12 characters, one character for each month of the year, with character value 1 or 0 (fig. 1B). Character value 1 codes for excess energy to be allocated into fat, while character value 0 codes for allocation into structural growth. If, for example, character 5 has a value of 0, excess energy gained in May will be used to increase structural weight, while a value of 1 will allocate into fat reserves. The fat reserves may subsequently be used for spawning or as

additional energy in periods with negative energy intake (i.e., to increase current weight). It is assumed that only adults allocate excess energy into fat, as juveniles prioritize to increase their structural weight to reach maturity. We assume that maturation requires a structural weight of 0.6 g (Rosland and Giske 1994).

The spawning behavior string consists of seven characters, one character for each month in the spawning season (March through September) where a character value of 1 codes for spawning and 0 for no spawning.

Environment

The model has three vertical environmental gradients: zooplankton density, temperature, and light intensity. The monthly vertical profiles of zooplankton density (fig. 4) are generated by fitting a biomass production model (Giske et al. 1991) to field data of vertical zooplankton density profiles from Masfjorden on the west coast of Norway (E. Strand, G. Huse, and J. Giske, unpublished data). We do not possess detailed data on zooplankton vertical migration in the fjord over a year, and Aksnes and Giske (1993) showed that light variation, and not zooplankton distribution, is the principal factor in *M. muelleri* DVM. Zooplankton vertical profiles are therefore assumed constant during a month and throughout a day. There is currently no feedback between the foraging of *M. muelleri* on zooplankton and the zooplankton density. This assumption is justified for two reasons. First, the used zooplankton biomass numbers are based on observations and therefore have seasonal variation in zooplankton biomass incorporated. Second, Aksnes et al. (1989) showed that advective

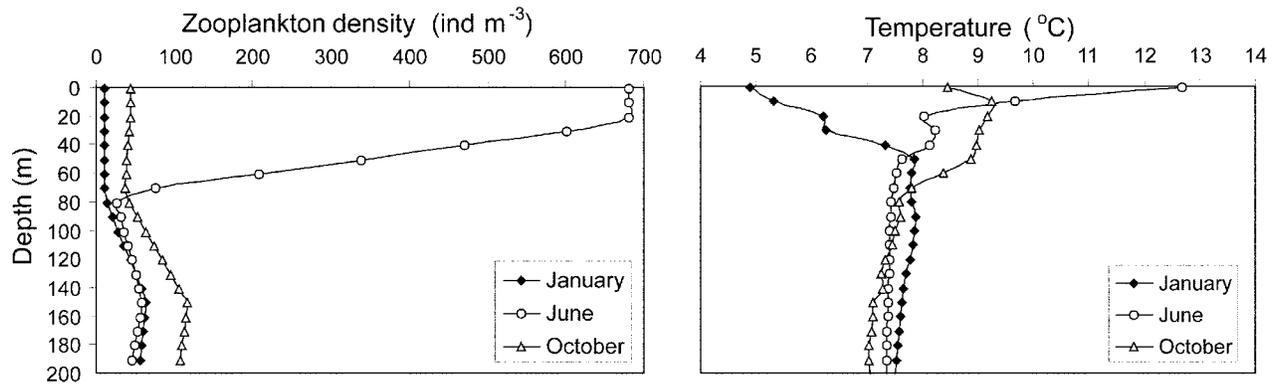


Figure 4: Vertical gradients of zooplankton density and temperature used in the simulations. Only data from January, June, and October are shown, but similar profiles exist for each month of the year. See text for material source.

tion of zooplankton into the fjord was greater than the local secondary production and hence an important factor underlying the carrying capacity of mesopelagic fish in fjords. As zooplankton biomass is renewed primarily by advection, the predation by fjordic *M. muelleri* populations has limited effect on local zooplankton biomass. Temperature data are from the nearby Herdlefjorden (fig. 4).

The visual range (r) of *M. muelleri* depends on light conditions at the current depth (Aksnes and Giske 1993; Aksnes and Utne 1997). The prey encounter rate of *M. muelleri* is determined by a Holling type 2 functional response (Holling 1966; Giske and Aksnes 1992; Rosland and Giske 1994). *Maurolicus muelleri* have small stomachs and seem to cease eating when the stomach contents reach 3% of the structural weight (Giske and Aksnes 1992).

In adaptation models, individual behavior is almost haphazard during the first generations with random character values in the string. There is therefore a need to ease the difficulty of survival during the simulation until behavior is better adapted. We have chosen to adjust the predation pressure rather than some other selection factor (e.g., food density). The GA automatically increases the predation pressure (P_p) forced upon *M. muelleri* during the simulation whenever the population size exceeds 1,500 individuals. However, if the population is on the brink of extinction (<400 individuals after last spawning month), the GA lowers the predation pressure. The predation by visually feeding predators on *M. muelleri* is assumed proportional to the probability of encountering a predator (see eq. [4]). An individual dies as a result of predation if a random number drawn by Monte Carlo simulation (Judson 1994) is larger than E_{pred} :

$$E_{pred} = \pi(r_p \sin \theta)^2 \times P_p \times BL, \quad (4)$$

where E_{pred} is the probability that a predator encounters an *M. muelleri* of length BL. The variable r_p is the visual range of the predator, and θ is the predator's reactive half angle (Luecke and O'Brien 1981; Dunbrack and Dill 1984). The predator's encounter rate with *M. muelleri* is assumed to be independent of the *M. muelleri* density.

Bioenergetics

Rosland and Giske (1994) found that if vertical migration requires no energy, it would be profitable for an adult fish in winter to stay near the surface at night when predation risk is low, and where the water is cold and hence metabolic costs are low. Observations on adult *M. muelleri* show that they do not choose this strategy (Giske et al. 1990; Baliño and Aksnes 1993), indicating an energetic cost of pressure adjustment by the swim bladder (Alexander 1972; Schmidt-Nielsen 1983). We account for vertical migration costs (VM_{cost}) by assuming a linear relationship between vertical migration distance (Δz) and individual structural weight (W_s). The VM_{cost} is adjusted such that individuals will experience a net energy loss if changing habitat does not increase the encounter rate sufficiently:

$$VM_{cost} = 1.0 \times 10^{-5} \times W_s \times \Delta z. \quad (5)$$

A basic balanced energy budget is the foundation of the bioenergetics in this model (Hewett and Johnson 1992). This is a way to account for energy flow in an organism:

$$C = (R + S) + (F + U) + \Delta B, \quad (6)$$

where C is consumption, R is respiration, S is specific dynamic action, F is egestion, and U is excretion. Net

energy gain (ΔB) can be allocated to structural growth or to fat reserve. See table 2 for a detailed description of the bioenergetics equations.

Reproduction and Inheritance

Interannual differences in size at maturity have been reported for *M. muelleri* populations (Gjøsæter 1981; Rasmussen and Giske 1994; Goodson et al. 1995). The maturity threshold here is set at 0.6 g structural weight, as used by Rosland and Giske (1994). In our model, an individual (all individuals are female) may spawn once each month during the spawning season, according to its spawning behavior string. Maximum gonad weight is set to 7% of structural weight at each spawning day (Rasmussen and Giske 1994; Salvenes and Stockley 1996). If an individual's condition (current weight/structural weight [W_c/W_s]) is lower than a threshold value (S_t), no spawning occurs. Otherwise, the individual will spawn an oocyte mass of

$$\Delta o = \left(\frac{W_c}{W_s} \right) - S_t, \quad (7)$$

where Δo is the weight in grams of the total oocyte batch spawned. The number of eggs produced per spawner is $\Delta o/o$, where o the oocyte weight (Melo and Armstrong 1991).

Rosland and Giske (1997) assumed a static bell-shaped seasonal survival curve for *M. muelleri* larvae to account for seasonal variation in food availability, day length, and temperature. The maximum relative seasonal larval survival (value = 1.0) is found in June. Larval survival for other months is as follows: May and July, 0.9; April and August, 0.6; and March and September, 0.1.

During reproduction the chance of a recombination of the spawner's and partner's strings is set to 0.6, also meaning that 40% of all offspring are clones (except for mutations) of the spawner (fig. 2). This value has no real

biological foundation and is achieved after evaluation of model performance using different recombination rates. The chance of a mutation occurring on a single character in the energy allocation and spawning string of the offspring is set to 0.001. On the depth positioning string, only one mutation (probability of 0.1) affecting a random character value may occur. No mutation of an offspring character value can change the parental value by more than 100%.

Simulations

The model simulates the environmental conditions over one year. One day is simulated each month, with the assumption that this day is representative of the whole month. The calculated growth during one day is then scaled to get monthly development. Other variables are scaled in a similar fashion. This procedure is followed to keep simulation time within reasonable limits. Each day is divided into 5-min intervals so that short-term behavior can also be studied.

Gundersen (1997) found that only one of several clearly separated larval batches produced by the *Maurolicus muelleri* population in the nearby Herdlefjorden survived the larval stage and recruited to the 1995 cohort. The narrow length distribution of the one-group *M. muelleri* in Herdlefjorden also suggests that the surviving 1993 cohort was born within a short time interval (Hamre 1999). Because *M. muelleri* is a multiple-batch spawner, this indicates that in some years only one or a few batches survive. This variability in juvenile survival may be caused by horizontal advection of eggs and larvae during periods of prevailing northerly winds (Aksnes et al. 1989; Gundersen 1997; Asplin et al. 1999).

Two different model simulations were therefore carried out. The "deterministic" simulation assumes a constant environment, while the "stochastic" simulation has incorporated stochasticity in the survival success of the spawned batches both within and among years. The in-

Table 2: Bioenergetic equations used in the model

Description	Equation	Parameter (value)
Respiration	$R = R(W_s) \times f(T) \times A(v)$	
Resting metabolism	$R(W_s) = \alpha W_s^\beta$	$\alpha = .0033, \beta = -.23$
Temperature-dependent respiration	$f(T) = e^{R_q T}$	$R_q = .055$
Fish's activity level	$A(v) = e^{RT_0 v}$	$v = \text{swimming speed} = 1 \text{ BL s}^{-1}, RT_0 = .03$
Egestion	$F = F_a \times C$	$F_a = .16$
Excretion	$U = U_a(C - F)$	$U_a = .10$
Specific dynamic action	$S = S_a(C - F)$	$S_a = .175$
Gastric evacuation	$R_e = ae^{bT}$	$a = .0693, b = 1.0 \times 10^{-4}$

Note: Due to lack of parameter values for *Maurolicus muelleri*, values for herring (*Clupea harengus*) from Hewett and Johnson (1992) are used. W_s = body weight, T = temperature, BL = body length, C = consumption, F = egestion.

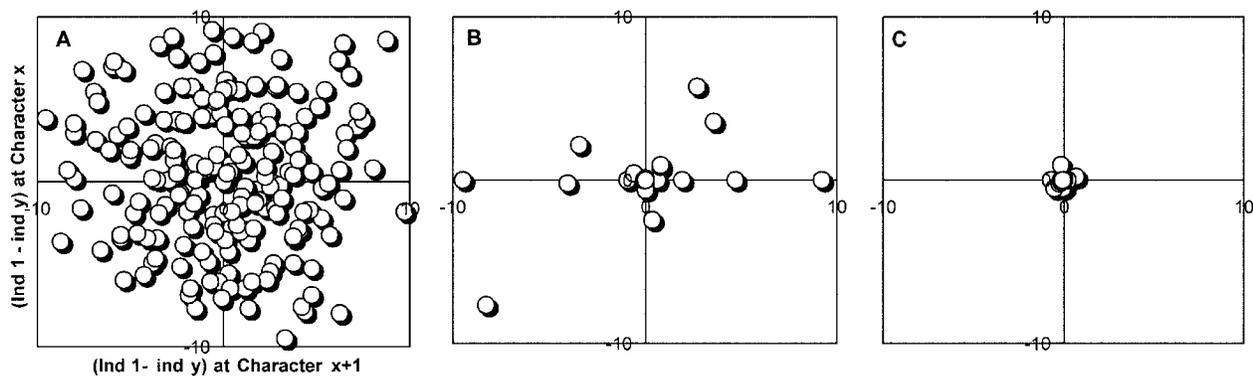


Figure 5: Character variability is obtained by subtracting the analogous character values of two individuals. The value 0 indicates identical character values. One individual's character values are compared to 200 other individuals' character values at (A) year = 1, (B) year = 250, and (C) year = 500. Data are from the deterministic environment, first replicate run.

terannual variability simulates “good” and “bad” years of juvenile prey abundance, which may affect juvenile survival (Rasmussen and Giske 1994). A uniformly distributed random number (0.5–1.5) is drawn at the beginning of each year, simulating the interannual stochasticity (A_s) in juvenile survival. Second, random numbers (0.0–2.0) are drawn at the beginning of March, May, and August to account for intra-annual stochasticity caused by advection (S_s). In the deterministic simulation both values are kept at 1.0. A female's surviving batch is found by multiplying the oocyte number with seasonal larval survival, interannual stochasticity (A_s), and intra-annual stochasticity (S_s). The juveniles are introduced to the population as 21-d-olds.

Both simulations started with an initial and maximum population of 2,000 individuals and ran for 500 years. Five replicates of both the deterministic and the stochastic simulation were performed, all initiated with different random number seeds. This was done to ensure that the adapted behavior among replicates was the same.

Results

In the presentation of results, we focus on the behavior predicted for January/February and June/July, to enable validation of our results with existing field data (see “Discussion”).

Artificial Evolution

By keeping track of character variability, one can determine the effect of the evolutionary process. When subtracting two individuals' character values from the same point on the genetic string, 0 will indicate equal values. If the result

is positive or negative, the character values are different. The initial population was seeded with a broad range of random character values (fig. 5A), but after 250 generations the characters in the population had converged, with a cluster of equal character values (fig. 5B). There was, however, still some residual genetic variation. After 500 generations, genetic variation is reduced to a minimum (fig. 5C), indicating that there was not much room for further evolution; 500 generations was therefore a suitable time to terminate the simulation. One can also study the fixation of single character values used in the ANN by recording the value of a specific character in a randomly chosen individual during the artificial simulation. Most character values became fixed after 100–200 yr (fig. 6). All character values in the ANN were initiated between -5 and 5 . At the end of the simulation, the numerical range of characters exceeds the initiation range, indicating that the GA was able to find fit character values.

Attribute Variables

Age Structure. In the deterministic environment, most surviving individuals entered the second age group ($220 \text{ d} < \text{age} < 440 \text{ d}$) early in the spawning season, resulting in an almost discrete age structure (fig. 7A). This was clearly seen as the second age group ($220 \text{ d} < \text{age} < 440 \text{ d}$) became the major age group in April, May, and June. In the stochastic environment, however, surviving individuals entered the second age group throughout the year, making the age structure more continuous and differences between generations less noticeable (fig. 7B). This resulted in the first age group ($0 < \text{age} < 220 \text{ d}$) being the largest through the entire year. The two oldest age groups ($\text{age} > 440 \text{ d}$) were usually represented by a higher number

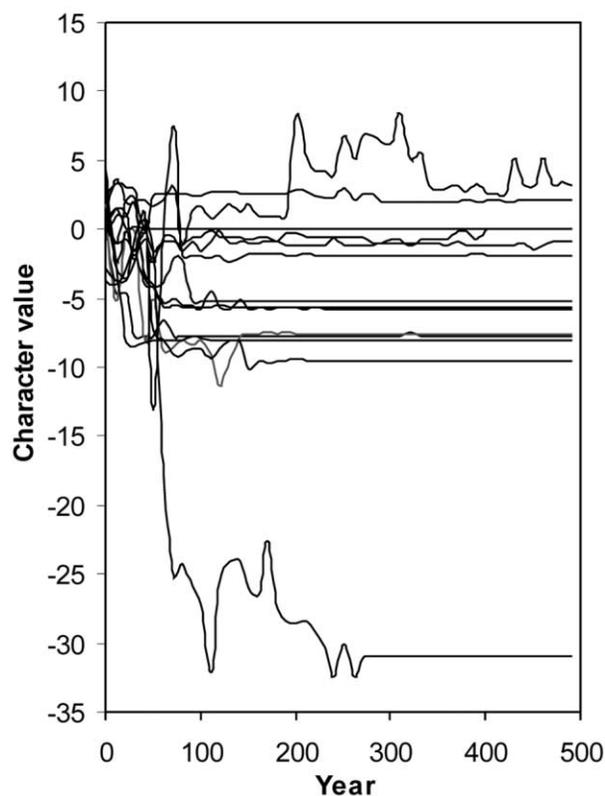


Figure 6: The adaptation of character values during a simulation. All character values are initiated randomly between -5 and 5 . After 200 generations most character values have evolved to fixed values. Data are from randomly chosen characters.

of individuals in the stochastic than in the deterministic environment.

Foraging. In the deterministic environment, juveniles in February showed a high crepuscular feeding rate at dawn (fig. 8A), with a peak at 0700 hours. Adults maintained a low feeding rate throughout the day, with a maximum foraging rate at noon (fig. 8B). In addition, juveniles foraged for a longer period at dusk compared with adults. In the stochastic environment, juveniles and adults exhibited behaviors that were more similar to each other than those found in the deterministic environment. Juveniles, though, had higher foraging rates than adults and therefore more stomach contents throughout the day (fig. 8C, 8D). In July, both simulations predicted that juveniles and adults foraged throughout the day. Juveniles in the deterministic model had an average stomach content of 70% at night, while the stochastic model predicted 20%–30%. The adults of the two models were predicted to forage quite similarly in July.

Strategy Variables

Energy Allocation and Fat Reserve. The average relationship between structural weight and fat reserves for adults is shown for each month in figure 9. In the deterministic model, adults had only a very small amount of fat during the spawning season (fig. 9A). The average adult in the deterministic model was generally heavier than the average adult found in the stochastic model and therefore had a potentially larger gonad weight. The stochastic model predicted structural growth in adults to occur mainly during March to June, with fat reserves decreasing from January to July (fig. 9B). Since there was no spawning or structural growth in January and February, the loss of fat was therefore due to a negative energy budget. This was observed in both simulations. The main difference between the stochastic and the deterministic simulation in relation to energy allocation was a greater amount of energy allocated to fat in adults that had adapted to the stochastic environment.

Energy allocation was controlled by the individual's energy allocation string. In the deterministic environment, no clear trend was seen in the period from January to August, which was probably caused by a lower energy intake and consequently little or no excess energy available for allocation. In September and October the percentage of adults allocating excess energy to fat was high (fig. 10), which corresponds to the increase in fat reserve during these months (fig. 9). In the stochastic environment the percentage of adults allocating excess energy to fat decreased from 90% to 2% during the period from January to June (fig. 10). However, from July to September, 90%–100% of the adult population allocated excess energy to fat instead of structural growth. This matches the trend seen in individual fat amount versus structural weight.

Spawning. The deterministic environment shows a bell-shaped spawning pattern, with maximum spawning occurring in July (fig. 11A). First-time spawners were dominant during spawning. Little or no spawning occurred in March, April, or May. In the stochastic model, spawning occurred in all spawning months (fig. 11B). The first three months are, however, clearly dominated by older spawners (age > 440 d), while the 1-yr-olds (age ≈ 300 d) reached maturity and commenced spawning in June.

Vertical Distribution. The diel vertical distributions of juveniles and adults in both simulations are shown for a winter (February) and summer (July) situation in figure 12. In February, the juvenile part of the population performed extensive DVM behavior, staying close to the surface at night and moving deeper during the day. The predicted behavior for juveniles differed little between the two

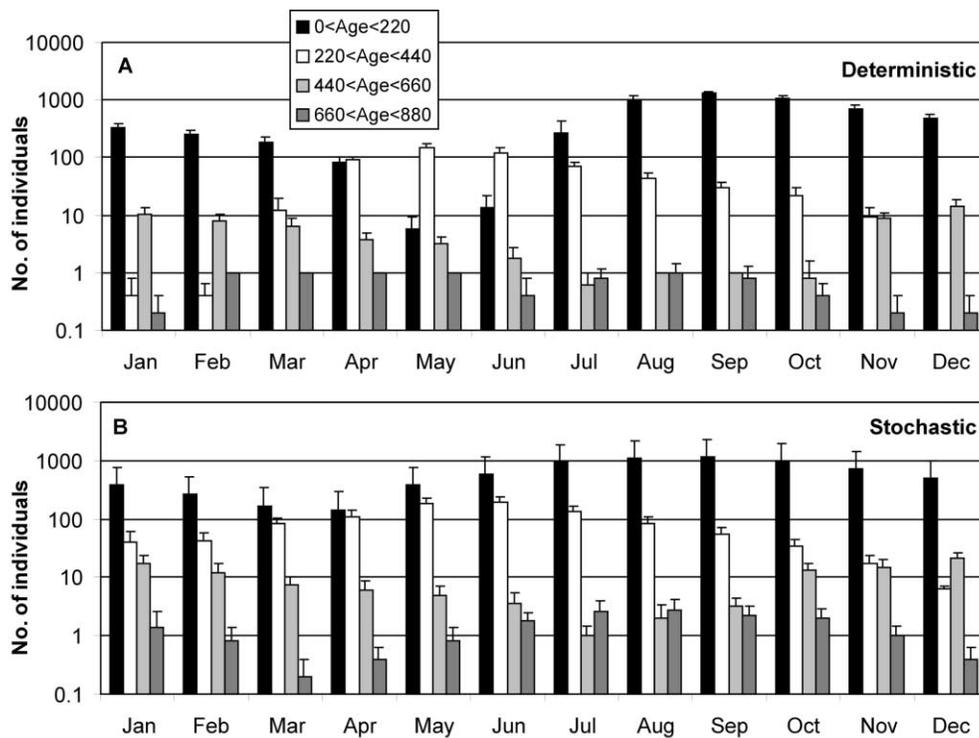


Figure 7: The population age (d) structure for *Maurolicus muelleri* in the (A) deterministic and (B) stochastic environment at year 500. Individuals are divided into four age groups. Bars are 1 SE from the five replicate runs. Note the exponential Y-axis.

simulations, except that the dawn descent of juveniles in the stochastic environment occurred 5–10 min earlier (fig. 12A, 12B). At the same time, adults performed little or no DVM. Juveniles positioned themselves higher in the water column than adults during daytime. In summer, only juveniles in the deterministic environment performed DVM, while the adults maintained a static position throughout the day (fig. 12C). Juveniles and adults in the stochastic environment behaved similarly in July, staying almost statically at depths around 75 m (fig. 12D). The greatest variation in individual behavior was found during the night, indicated by the standard error shades calculated from the five replica simulations.

Juveniles in both the deterministic and stochastic simulations showed an asymmetry in their DVM patterns in February, with a relatively late descent from the surface at dawn and a delayed ascent at dusk (fig. 12A, 12B). This resulted in conspicuous crepuscular feeding only at dawn (fig. 8A, 8C), particularly noticeable in the deterministic model. Hence, juveniles did not follow a strict isolume during the day but also took individual state into consideration. The degree of stomach fullness seemed to play the key role in explaining the asymmetric DVM pattern, as juveniles were less prone to risk in the crepuscular period

when their stomachs were fuller (fig. 13). The predation risk was proportional to visual range (see eq. [4]).

Discussion

Artificial Evolution

Adaptation models must strike a balance in the imposed selection pressure level so that the simulated population remains alive and, at the same time, exert a selection pressure significant enough to ensure evolution of desired traits. At model initiation, the first generation's strings are seeded at random (Goldberg 1989). This means that individuals have random behavior and are unable to cope with a high selection pressure. Gomez and Miikkulainen (1997) showed that it was profitable to simulate evolution by starting with a simple task and gradually making it more challenging, as opposed to constant environmental forcing. In the present model, the selection pressure is adjusted by tuning the imposed predation risk. Huse and Giske (1998) also used this approach with a stepwise increase in predation risk, decrease in food availability, and a reduced area for successful reproduction to allow a grad-

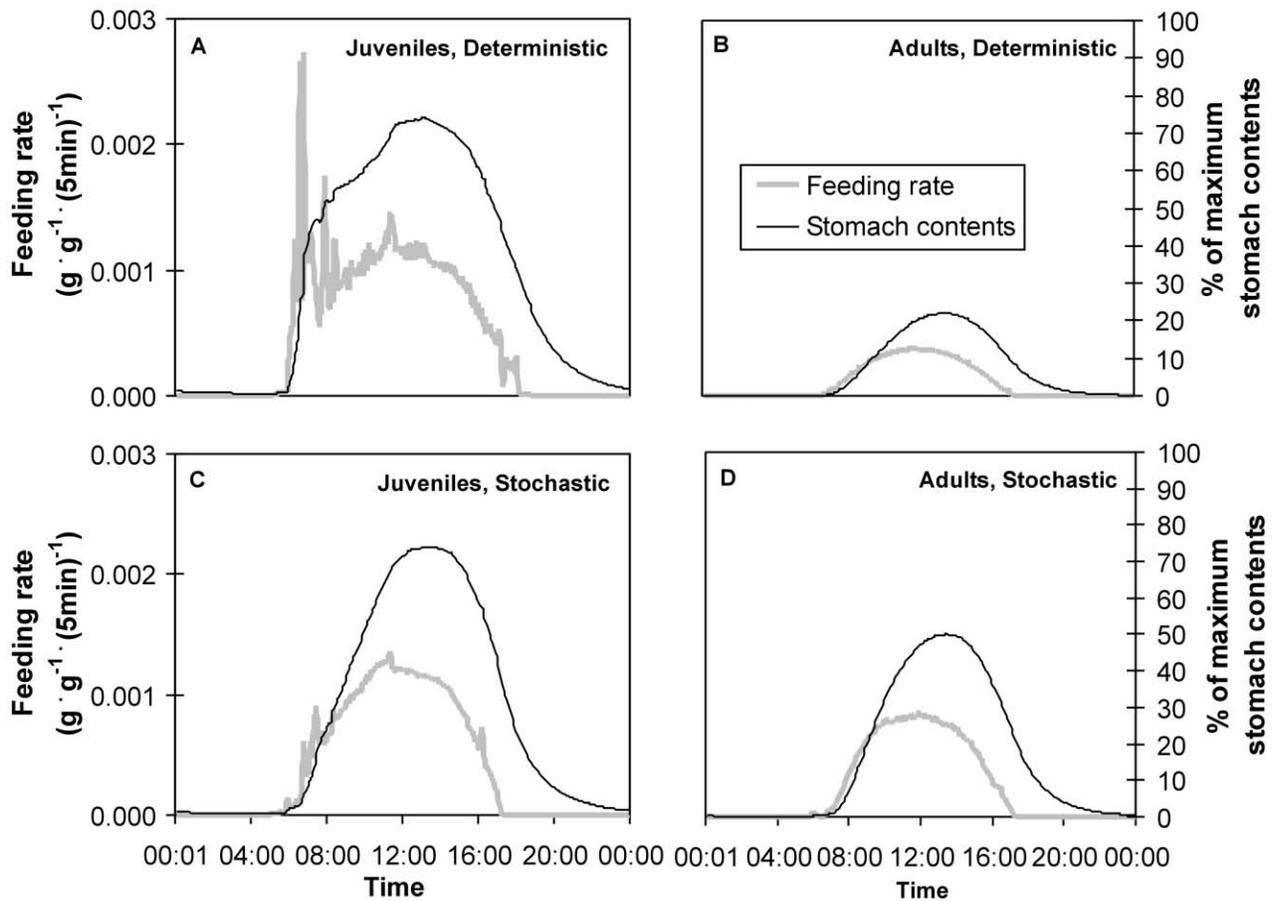


Figure 8: Average feeding rate ($\text{g g}^{-1} [5 \text{ min}]^{-1}$) and stomach contents (%) in February for adults (B, D) and juveniles (A, C) in the deterministic (A, B) and the stochastic (C, D) environment.

ual increase in the difficulties of adaptation to the environment.

Genetic control of phenotypic variation among individuals is the basis for natural selection (Maynard Smith 1993). In constant environments, natural selection works to reduce variability while other events such as mutations, recombinations, and genetic drift increase variability (Lande and Shannon 1996). Similarly, selection processes in the GA reduce the variability of the initially random character values, while recombinations and mutations during sexual reproduction create new variation.

The character values among individuals used in the ANN to control depth position evolved toward the same values, indicating a “genetically” homogeneous population converging to a single best strategy in each replicate run. Between the replicate runs, the evolved phenotypical vertical position strategies were similar, signifying that the same optimum was found in each run. However, when comparing specific character values in replicate runs, the

numerical values are not the same. This is due to the polygenic influence of characters on ANN behavior. Hence are there many different genotypes able to produce virtually the same phenotype in an ANN. Dissimilarly adapted character values further stem from the initiation procedure, where the first generation was assigned random character values, hence making the “genetical” starting point for evolution different in each replicate. The low character value variability at the end of simulations and the fixation of character values during simulations confirm that a significant selection caused by individual variation in fitness has taken place.

Genetic Algorithm and Population Genetics

In nature, as in the current model, evolution is driven mainly by natural selection, mutation, and recombinations. There are, however, other forces at work that can affect evolution.

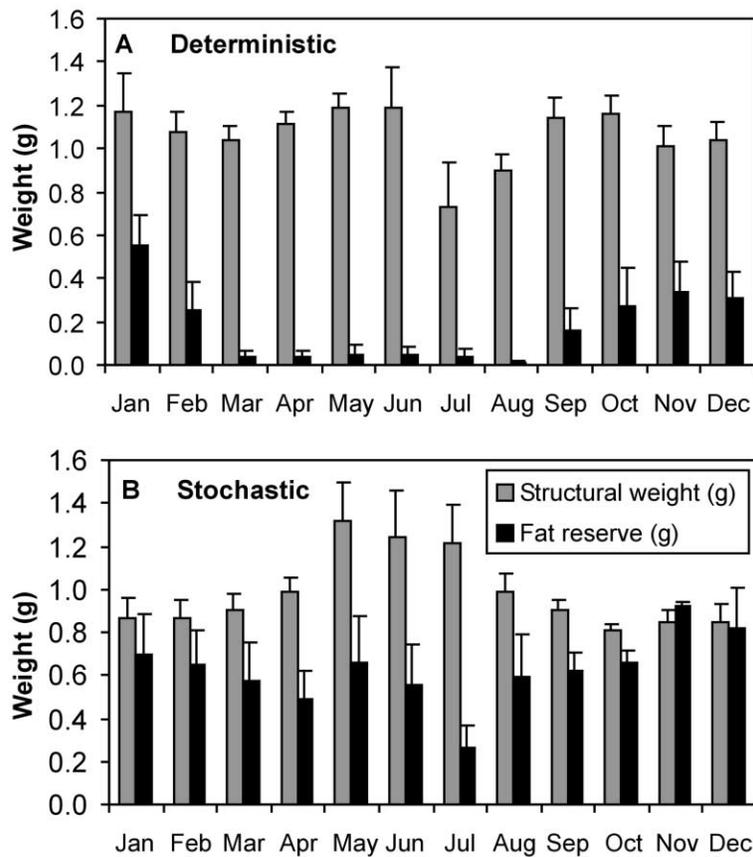


Figure 9: Seasonal changes in average fat reserve and structural weight for adults. In both environments, fat reserves decrease during spring and increase during autumn. Structural weight is greater and fat reserves smaller in the deterministic environment, as compared to the stochastic environment. Bars are 1 SE of the five replicate runs.

Since the genomes in the current model are haploid and thus without Mendelian segregation, the effect of genetic drift is rather small. Genetic algorithms can be made diploid (Calabretta et al. 1996), in which case genetic drift and dominance relations between character values could influence artificial evolution. Currently mating is completely random. This system could certainly be replaced by other schemes such as, for example, assortative mating (preference for same genotype as self) or preferences for certain other features such as size or condition. Different mate selection schemes could have an impact on results and increase the selective pressures for certain phenotypes.

Because of the recombination mechanism, characters that are far apart on the string have a lower probability of being passed on together than characters close together. This is parallel to the way recombinations work in biology. The complex linkage between characters and phenotype is one of the reasons for labeling neural networks “black box” models. There are, however, ways to examine an

ANN, and an analysis of the input weights usually reveals what input factors are most important in determining the phenotype (Aoki and Komatsu 1997).

Model Validity

Attribute Variables. The predicted feeding pattern of juveniles in February indicates low feeding at night and a relatively high feeding rate during the day. This matches the patterns observed by Giske and Aksnes (1992) and the model results from Rosland and Giske (1994). The significant crepuscular feeding at dawn seen in the deterministic environment was also predicted by Rosland and Giske (1994) and fits well with the theory of antipredator windows (Iwasa 1982; Clark and Levy 1988). The adults showed no crepuscular feeding, which can be explained by the absence of vertical migration behavior at dusk and dawn. Skagseth (1999) found that only 18% of juveniles (upper SSL) had empty stomachs in Herdlefjorden in Jan-

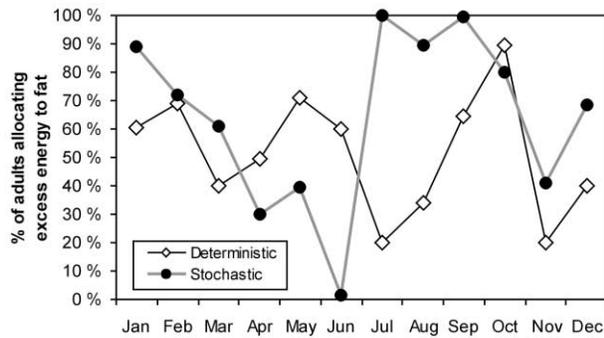


Figure 10: The adapted energy allocation rule for the stochastic and the deterministic environment. Dots and diamonds represent the average value of the five replicate runs.

uary, compared to 74% of adults (lower SSL). These findings match well with the present model, and especially the deterministic model, where there is significant difference in stomach contents between juveniles and adults. In June, about 75% of both adults and juveniles have full stomachs (Skagseth 1999). Both the deterministic and the stochastic simulations predict an average stomach fullness of approximately 90% for both juveniles and adults in the same period.

The stochastic environment explains the observed longevity of *Maurollicus muelleri* populations (Gjøsæter 1981) better than the deterministic environment, which predicts maximum longevity to be only 2 yr. Generations become increasingly separated in the deterministic environment as a result of the shorter spawning season.

Strategy Variables. Our model predicts that the daytime vertical distribution of juveniles and adults in February would be around 60–65 m (upper SSL) and 70–75 m

(lower SSL), respectively. Our results also show that the adults did not ascend to the surface to feed during the night, as juveniles did (fig. 12). Giske et al. (1990) and Baliño and Aksnes (1993) reported an equivalent distribution for juveniles and adults in Masfjorden in winter (fig. 14). However, both studies found the SSLs to be positioned deeper (100 and 140 m, respectively). Similar patterns have been found by Goodson et al. (1995) in Herdlefjorden and by Kaartvedt et al. (1996) off the Norwegian coast. A test of the current model, where individuals were forced to position themselves at 150 m, resulted in 100% mortality by starvation. We believe incorrect values of eye sensitivity in the visual model or excessive metabolic rate, caused by the use of bioenergetic parameters for herring, to cause the variation between observed and predicted depth positions.

Giske et al. (1990) hypothesized that juvenile *M. muelleri* forage extensively in autumn, winter, and spring to reach maturity the following spawning season, while adults maximize survival during the nonspawning season. Rosland and Giske (1994) also found the “maximize growth” strategy for juveniles, and a “maximize survival” strategy for adults, to be optimal in winter. Our simulations show that the juveniles reach maturity during spring or early summer. The two vertical layers then merge at a depth (75–80 m) that allows visual foraging during the spawning period. This is also consistent with observations (Rasmussen and Giske 1994; Goodson et al. 1995).

Crepuscular migration extends the daily period of potential foraging without significantly increasing the feeding rate to mortality risk ratio because of the intermediate light levels (Clark and Levy 1988) and the optical properties of the surface water (e.g., high turbidity and beam attenuation; Giske et al. 1994; Rosland and Giske 1994). Since juveniles in winter empty their stomachs during the night, the feeding rate in the crepuscular period is poten-

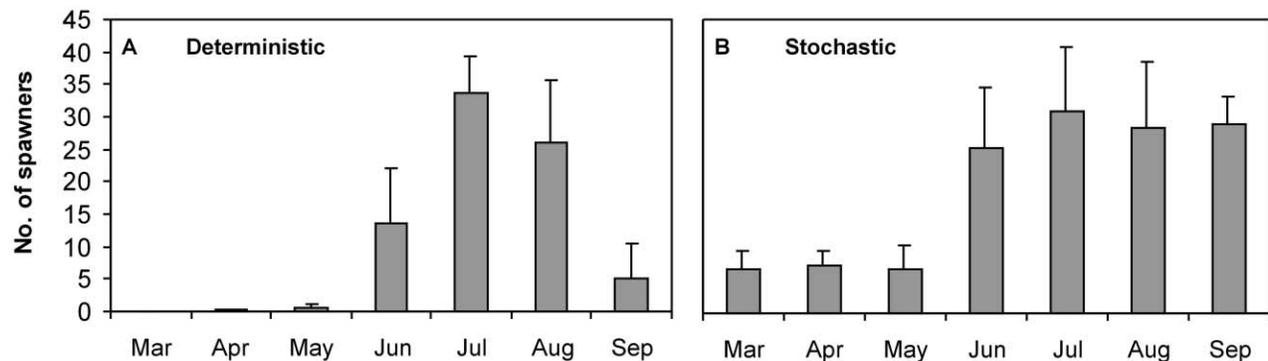


Figure 11: Number of spawners each month in year 500 (± 1 SE). The spawning occurring from March to May is performed mainly by second- and third-season spawners (age > 440) in the stochastic environment (B) and by first-time spawners in the deterministic environment (A).

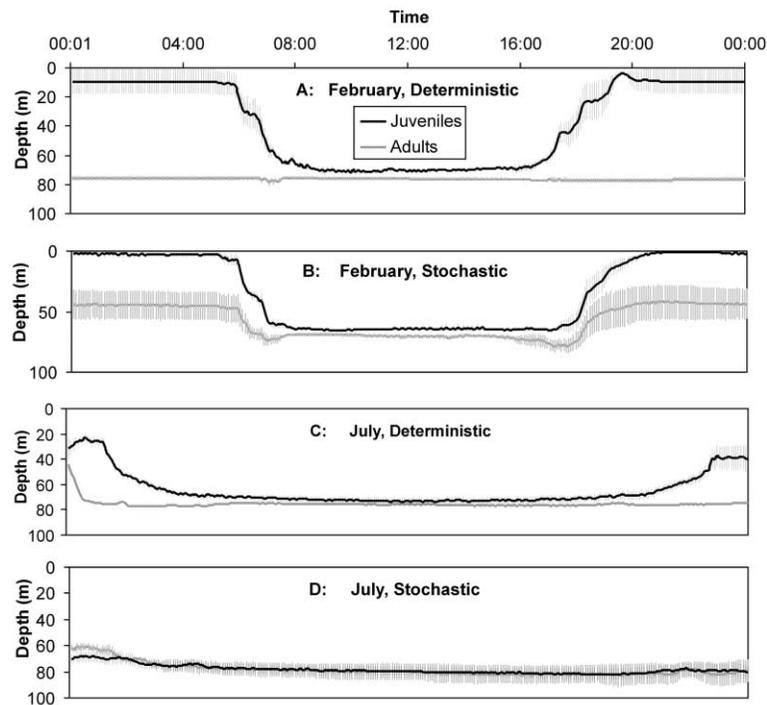


Figure 12: Average vertical position for juveniles (*thin black lines*) and adults (*gray lines*). Vertical bars indicate 1 SE of the five replicate runs. Distributions are from February (A, B) and July (C, D) for both the deterministic environment (A, C) and the stochastic environment (B, D).

tially greater at dawn than at dusk, as juveniles have some stomach contents after daytime feeding (Rosland and Giske 1994). However, that this variation in potential feeding rate results in an asymmetric DVM pattern (fig. 13) has not, to the best of our knowledge, been reported previously. When reexamining the field results of Baliño and Aksnes (1993; fig. 14) and the model predictions of Rosland and Giske (1994), the same pattern is observed. In the present model this asymmetric DVM pattern is triggered by the amount of stomach contents.

Observations show that juveniles reach maturity and commence spawning in May/June (Goodson et al. 1995) as 1-yr-olds (see, e.g., Gjørseter 1981; Rasmussen and Giske 1994). This is predicted in both simulations. There is, however, one major difference between the two environments. In the deterministic environment, very few or none of the individuals spawned in two consecutive years. Goodson et al. (1995) found a difference in seasonal fecundity between age groups and suggested that repeat spawners spawn earlier in the season and with greater intensity than first-time spawners do. This spawning strategy is found only in the stochastic environment, and is thought to be a result of the interannual variation in larval survival (S_a).

There are significant differences in fat reserves between

adults adapted to the deterministic and those adapted to the stochastic environment. Hamre (1999) found that fat reserves reach a minimum in adult *M. muelleri* in June and July (fig. 15). In the period from August to January, adults allocate net excess energy to fat, probably to cope with a period of negative growth during winter/early spring (see, e.g., Giske et al. 1990; Goodson et al. 1995). The same seasonal pattern in fat content is found in both of our simulations, although the amount varies significantly. We believe this to be related to the adapted longevity and the second spawning season in the stochastic environment. In the deterministic environment, energy is allocated to structural growth, thereby maximizing the possible gonad weight. In the stochastic environment, adults traded increased structural weight for increased fat reserves and gained the possibility of a second spawning season. Most of the fat allocation took place during July to September (fig. 9). In the same period, the adults in the stochastic environment positioned themselves deeper (85–90 m) than in the deterministic environment (75 m). This descent doubled their survival probability. In the stochastic environment, no structural growth occurred during this period.

Stochastic versus Deterministic Environment. The effect of

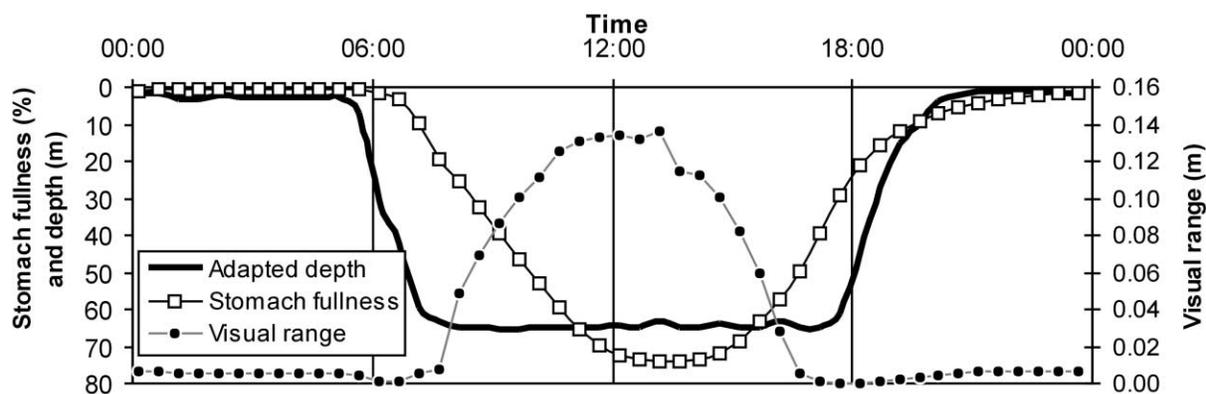


Figure 13: The relation between depth position, visual range, and stomach content throughout the course of one day in February. Juveniles show a delayed ascent at dawn that results in an asymmetry in the experienced visual range. This behavior is caused by higher stomach content at dusk than at dawn. Data are from the stochastic environment.

environmental fluctuation on a population's life-history strategy has been studied in detail (see, e.g., Southwood et al. 1974; Stearns 1976, 1992; Roff 1992). In the above section we compared our model's predictions with other model simulations and with field observations. We have found that the stochastic environment better explains some life-history traits (e.g., age structure), while others are better explained by the deterministic environment (e.g., depth positioning and foraging).

To the best of our knowledge, there exists no numerical value of the effects of intra-annual (S_t) or interannual (A_t) variation on recruitment in *M. muelleri* populations. The values applied are therefore only approximations in strength, pattern, and frequency. We believe, however, that stochastic events have been a major factor in shaping the life history of *M. muelleri*. Kristoffersen and Salvanes (1998) compared *M. muelleri* populations in oceanic and fjordic environments and found individuals inhabiting fjords to have a longer spawning season and a greater reproductive life span than oceanic populations. They also found indications of higher recruitment variation in fjordic populations and suggested that the spawning pattern of the fjordic population is a bet-hedging strategy. The "bet-hedging" theory (Murphy 1968; Schaffer 1974) concerns individuals that reduce their variation in fitness caused by environmental variability in mortality at the expense of their expected total fitness (Seeger and Brockmann 1987). Among the predictions derived from environments with varying juvenile mortality are increased longevity, more broods, and smaller brood sizes (Stearns 1976). This is in accordance with the difference in our predictions for deterministic and stochastic environments. We believe interannual variation in larval survival to be the main selection factor for the increased longevity seen

in the stochastic environment. This strategy will be favored over other strategies by enabling successful spawning the following year if conditions have been unfavorable.

ING Perspectives

Railsback (2001) proposed that ecological individual-based models would profit by adopting key elements from the field of complex adaptive systems, a field of research that shares a lot with the A-life community. The present model supports this view by showing that fit behavior can emerge as individuals are adapted to various environments. Individual-based models may and should be used for experimental purposes, to test existing biological theories and search for new ones (Grimm 1999). The ING approach is able to solve a series of biological problems where conventional approaches in evolutionary ecology, such as life-history theory (LHT), game theory (GT), and stochastic dynamic programming (SDP), may not be adequate. However, the ING tool also comes with its own limitations, and below we discuss some pros and cons of ING and how it compares to these traditional modeling approaches.

Unstable Environments. The Euler-Lotka equation and life-history models based on this equation require a stable age (or stage) distribution to find the solution that returns maximum reproductive rate (Roff 1992; Stearns 1992). The stable age distribution appears when conditions are repeated exactly for each generation, so that mortality and fecundity depend on age (or stage) alone. Life-history theory therefore addresses rather idealized worlds, where fluctuations and instabilities may be ignored. In GT (Sigmund 1993; Dugatkin and Reeve 1998), time is not a variable at all, and consequently solutions that are found describe

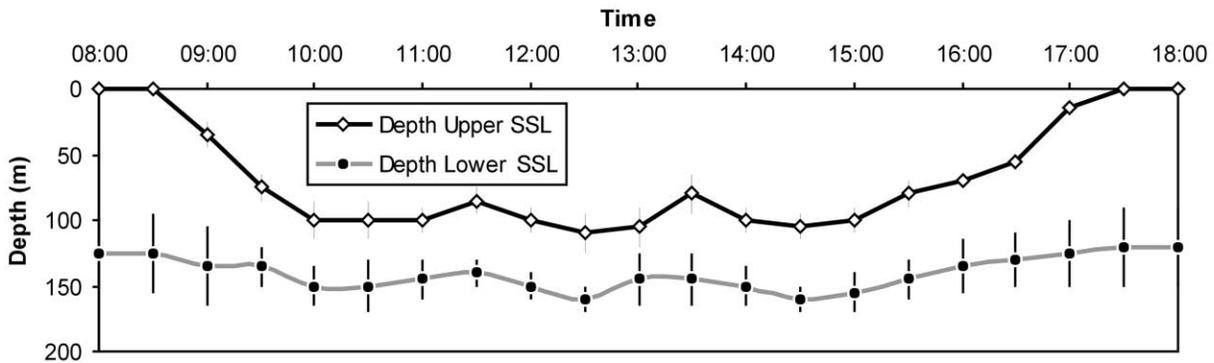


Figure 14: Observed vertical position of *Maurolicus muelleri* in Masfjorden, western Norway, modified from an echogram by Baliño and Aksnes (1993), showing the two sound scattering layers (SSLs) and their vertical position during the visual and crepuscular period of one day in late January. Vertical bars indicate the width of the SSLs.

only steady state situations. In SDP models, variation can occur at several time scales, but the method requires that the future (i.e., the modeling horizon) is known or can be estimated (Houston and McNamara 1999; Clark and Mangel 2000). The ING model is not restricted by any of these demands. The present model is run for both a deterministic and a stochastic environment, and in the stochastic environment, conditions are never repeated exactly for two generations. This allows the study of behavioral adaptation under stochastic population dynamics (Yoshimura and Clark 1993), which vastly increases the biological realism of evolutionary models of behavior.

Complex Interactions. The model presented here is notably elaborate, with the use of three strategy variables, a detailed description of the environment and the organisms' phys-

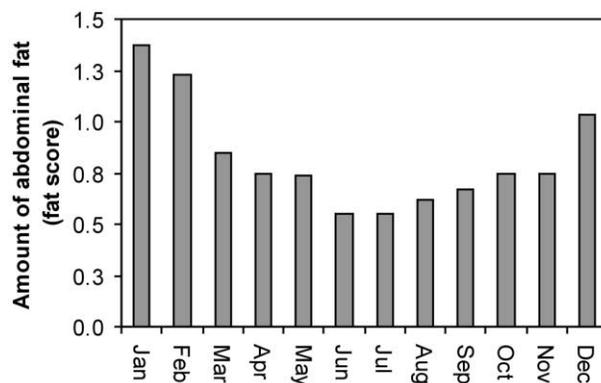


Figure 15: Average abdominal fat index for adult *Maurolicus muelleri* in Herdlefjorden, western Norway (modified from Hamre 1999). Fat scores for individuals were assigned as follows: 0 = none, 1 = some, 2 = much, and 3 = abnormal. Data are pooled for adult males and females.

iology, and a high time resolution. Hence, one of the major strengths of the ING approach is its potential for solving complex problems. In SDP models, the optimal solution is found by backward induction. This means that decisions taken early in life (i.e., late in the backward decision procedure) cannot be allowed to impact the future in a way that invalidates the solutions already found. Strong trophic interactions can be studied by dynamic games (Houston and McNamara 1999), but this method is still limited to a lower level of complexity than in the ING approach. Game theory is also limited to two or at most a few classes of interacting agents. Giske et al. (1997) modeled the vertical distribution of a copepod population by ideal free distribution (IFD; Fretwell and Lucas 1970) in a complex landscape with density-dependent mortality risk and growth rate. They concluded that inclusion of individual variation in this landscape would not be feasible because of the IFD demand on equal fitness for all actors. Further, as SDP compares all possible solutions and picks the best, it is limited by the “curse of dimensionality.” As the GA performs only a local search for increasing peaks in the fitness landscape, and as the fitnesses of suboptimal solutions are not stored, the ING can describe the organisms with more biological detail than SDP.

Two common types of complex interactions are density dependence and state variation. Stochastic dynamic programming can explore state variation, while density dependencies can only be investigated to some degree by dynamic games. Game theory, and in particular IFD, can handle density dependencies, though only at the expense of state description and time variation. Individual-based neural network genetic algorithm models can include simultaneous variation in environment, state, and densities. This was done in the model of capelin (*Mallotus villosus*) distribution in the Barents Sea (Huse and Giske 1998).

Their model was based on the same description of the physical and biological environment as in the SDP model by Fiksen et al. (1995). Both models captured the major seasonal horizontal migration routes for all age groups. However, the backward induction in the SDP model did not enable it to incorporate density-dependent interactions in feeding and mortality risk. Therefore the SDP model predicted the entire population of Barents Sea capelin to aggregate in a few horizontal cells each month, while the ING model predicted a wider spatial distribution as a result of food competition.

Games between predators and prey are an additional kind of complex interaction with which the ING approach is in principle able to deal. However, since the method has only been applied to simple predator-prey problems (Huse et al. 1999), it is premature to draw conclusions about its applicability in this field.

Linking Proximate and Ultimate Explanations. Ethologists and ecologists have, since Tinbergen (1963), distinguished between ultimate and proximate explanations. While ultimate models focus on the fitness consequences of actions, and on the evolvability and evolutionary stability of the trait, proximate models concentrate on the environmental and physiological triggers of a response. Tinbergen (1963) called them survival value and causation, respectively. The ING is simultaneously an ultimate and proximate approach. The GA works by finding differences in fecundity and survivorship, while the ANN performs decisions based on local knowledge. The ING can thus work to bridge the perspectives of ultimate explanations in behavioral ecology and proximate explanations in ethology. While the GA ensures that the decisions made by the ANN are adaptive, the ANN is also able to make decisions in the absence of fitness gradients. Individuals are also able to make mistakes, and once led astray, a locally informed ING individual may have serious trouble getting back on track. (This may also remind one of real animals.) The evolved individuals will respond to the information they receive, irrespective of their lack of immediate link to growth or survival. According to the fundamental theorem of natural selection (Fisher 1930), the speed of the GA will depend on the steepness in the fitness gradients and the amount of genetic variation available. The weaker the link between a series of decisions or ANN genes and fitness, the lower the credibility their adapted values will have.

Genetics. The genetics of the evolving ING population remains the key to understanding the ING approach. In ING models with emergent fitness, the gene pool is completely explained by the surviving reproducers of the previous generation(s). As in real biological evolution, the evolution of the ING gene pool is forced by mutations, recombi-

nations, surplus reproduction, and natural selection due to mortality and variation in fecundity. Several of these forces contain a substantial random component. Unlike optimization tools such as SDP, the GA does not search the entire solution space for potentially superior solutions. The hill-climbing procedure of a local search allows much quicker localization of the peaks in the fitness landscape. In addition, it allows for searching in far more complex solution spaces. However, the structure of the landscape also impacts the ability of the GA to arrive at the globally optimum solution (Kauffman and Levin 1987; Goldberg 1989). There is a trade-off in complexity of the genome: too few genes may hinder the exploitation of the entire fitness landscape. Too many genes may require a very long adaptation period. The genome size chosen in this model has struck the right balance, as genomes stabilize before the end of the simulation period (fig. 6), and as repeated computer runs arrive at the same behavior (e.g., figs. 7, 9, 12). However, allele frequencies differ between replicate runs. The genome used in the ANN can be seen as an equation set with 140 variables (number of characters on the depth position string), for which there may exist more than one biologically possible solution. The repeated simulation runs show that several equally fit structures of the ANN exist with regard to the environment and the decisions the organism must make. If the goal is to understand the resulting behavior, then this variation is unproblematic. If, however, the goal is to analyze the ANN, then it may be fruitful to consider simpler brain structures that are more likely to repeat.

A-Life and B-Life. As pointed out by Toquenaga and Wade (1996), there has been little interaction between A-life and conventional biology (B-life) as a result of sparse communication between the two fields. While the exploration of B-life is conducted by biologists, A-life is the creation of computer scientists and mathematicians (Levy 1993). The number of conventional biologists interested in A-life remains rather low (but see Belew and Mitchell 1996).

By incorporating a GA into an IBM, the aspect of evolution can be included as is shown here. The IBM then becomes a robust tool for calculating fit life histories and behaviors. No theory, be it verbal, analytical, or numerical, can incorporate everything that we consider being reality. In this sense, theories necessarily describe artificial worlds, something that is made explicit in A-life. In this article, techniques that have been successful in A-life are applied to simulate real life. Through simulation of artificial systems that resemble the basic properties of an ecosystem, A-life may provide a direct conceptual understanding of how complex systems function and behave. This study shows the possible continuum between A-life, a minimal model for proving a point, and B-life, a complex model

of a specific species at a given location. One problem with simulating “realistic” ecology, as compared to the abstraction of an A-life model, is that the evolutionary constraints acting on the target species must be recognized and quantified. If realistic behavior is to be expected, the model should be forced in a restrictive manner to follow an evolutionary trajectory similar to that of the particular animal. By imposing such constraints, however, the model loses some of its explanatory power (Loehle 1983). The degree to which one should try to force the adaptive system in a specific direction should therefore depend on the nature of the problem one is trying to solve.

Limitations. Every new offer on the market comes with additional costs. We will try our best to articulate the most serious of these. The most obvious cost in using an approach based on the GA is that one cannot easily ascertain that the solution arrived at is the best solution globally. If the problem to be solved is very simple, then alternative methods like SDP, LHT, or GT may be used to verify the likelihood of the ING solution. However, in situations where these other methods are not easily applicable, there may not be alternative methods with which to compare the solution. We cannot then readily know that the ING solution found is biologically plausible. One solution to this problem is to conduct several simulation runs (as done here) with differing random seeds, in order to check whether the solution arrived at a local or global maximum. But again, several different gene pools may exist that are of similar fitness values.

The adaptation process will also require attention. No standard mutation or recombination rates exist; instead these must be found by trial and error. Rates that are too low may lead to stranding on suboptimal local fitness peaks, while rates that are too high may hinder the adapted string from being maintained at the global maximum (Sumida et al. 1990). Neither is there yet a standard procedure for selecting a structure of the ANN. Alternatively, these rates can be implemented as characters and adapted in the same way as other traits.

In models with emergent fitness, the whole life cycle of the organism must be modeled. However, if a fitness criterion is chosen (see Huse et al. 1999), the ING model will find itself in the same situation as models with explicit fitness formulations: the credibility of the emerging behavior will depend on the quality of the fitness measure.

Conclusions

We have shown that the ING modeling approach and artificial evolution has a great potential outside the realm of A-life and provides realistic predictions about the behavior

of natural populations. There is, however, no such thing as a final modeling approach in ecology.

Each method will have its own simplifying assumptions and restrictions on validity. These restrictions are not as obvious in ING and other adaptation tools as they are in the optimization tools (Giske et al. 1998). However, ING (or SDP) approaches cannot match the intuitive mathematical elegance of a simple LHT-based model. In addition, ING is a laborious method and should not be undertaken unless standard optimization methods are incapable of answering the scientific issue in question. As such issues appear more and more frequently, we believe that a tool that can direct individual behavior in fluctuating or stochastic environments, under complex selection pressures, and in the absence of strong fitness gradients will be a valuable addition to the ecologist’s tool kit.

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Literature Cited

- Ackley, D., and M. Littman. 1991. Interactions between learning and evolution. Pages 487–509 *in* C. G. Langton, C. Taylor, J. D. Farmer, and S. Rasmussen, eds. *Artificial life II*. Addison-Wesley, Redwood City, Calif.
- Aksnes, D. L., and J. Giske. 1993. A theoretical model of aquatic visual feeding. *Ecological Modelling* 67:233–250.
- Aksnes, D. L., and A. C. W. Utne. 1997. A revised model of visual range in fish. *Sarsia* 82:137–147.
- Aksnes, D. L., J. Aure, S. Kaartvedt, T. Magnesen, and J. Richard. 1989. Significance of advection for the carrying capacities of fjord populations. *Marine Ecology Progress Series* 50:263–274.
- Alexander, R. M. 1972. The energetics of vertical migration by fishes. *Symposia of the Society for Experimental Biology* 26:273–294.
- Aoki, I., and T. Komatsu. 1997. Analysis and prediction of the fluctuation of sardine abundance using a neural network. *Oceanologica Acta* 20:81–88.
- Asplin, L., A. G. V. Salvanes, and J. B. Kristoffersen. 1999. Nonlocal wind driven fjord-coast advection and its potential effect on plankton and fish recruitment. *Fisheries Oceanography* 8:255–263.
- Baliño, B. M., and D. L. Aksnes. 1993. Winter distribution and migration of the sound-scattering layers, zooplankton and micronekton in Masfjorden, western Norway. *Marine Ecology Progress Series* 102:35–50.
- Belew, R. K., and M. Mitchell, eds. 1996. *Adaptive indi-*

- viduals in evolving populations: models and algorithms. Addison-Wesley, Reading, Mass.
- Calabretta, R., R. Galbiati, S. Nolfi, and D. Parisi. 1996. Two is better than one: a diploid genotype for neural networks. *Neural Processing Letters* 4:149–155.
- Chambers, C. R. 1993. Phenotypic variability in fish populations and its representation in individual-based models. *Transactions of the American Fisheries Society* 122: 404–414.
- Clark, C. W., and D. A. Levy. 1988. Diel vertical migration by juvenile sockeye salmon and the antipredation window. *American Naturalist* 131:271–290.
- Clark, C. W., and M. Mangel. 2000. *Dynamic state variable models in ecology: methods and applications*. Oxford University Press, New York.
- DeAngelis, D. L., and L. J. Gross, eds. 1992. *Individual-based models and approaches in ecology*. Chapman & Hall, London.
- Dugatkin, L. A., and H. K. Reeve. 1998. *Game theory and animal behavior*. Oxford University Press, New York.
- Dunbrack, R. L., and L. M. Dill. 1984. Three-dimensional prey reaction field of juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:1176–1182.
- Fiksen, Ø., J. Giske, and D. Slagstad. 1995. A spatially explicit fitness based model of capelin migrations in the Barents Sea. *Fisheries Oceanography* 4:193–208.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford.
- Fretwell, S. D., and H. J. J. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. 1. Theoretical development. *Acta Biotheoretica* 19:16–36.
- Giske, J., and D. L. Aksnes. 1992. Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*. *Sarsia* 77:253–261.
- Giske, J., D. L. Aksnes, B. M. Baliño, S. Kaartvedt, U. Lie, T. J. Nordeide, A. G. V. Salvanes, S. M. Wakili, and A. Aadnesen. 1990. Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia* 75:65–81.
- Giske, J., D. L. Aksnes, U. Lie, and S. M. Wakili. 1991. Computer simulation of pelagic production in Masfjorden, western Norway, and its consequences for production of released 0-group cod. *ICES Marine Science Symposia* 192:161–175.
- Giske, J., D. L. Aksnes, and Ø. Fiksen. 1994. Visual predators, environmental variables and zooplankton mortality risk. *Vie et Milieu* 44:1–9.
- Giske, J., R. Rosland, J. Berntsen, and Ø. Fiksen. 1997. Ideal free distribution of copepods under predation risk. *Ecological Modelling* 95:45–59.
- Giske, J., G. Huse, and Ø. Fiksen. 1998. Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries* 8:57–91.
- Gjøsaeter, J. 1981. Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in Norwegian waters. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 17: 109–131.
- . 1984. Mesopelagic fish, a large potential resource in the Arabian Sea. *Deep-Sea Research* 31:1019–1035.
- Goldberg, D. E. 1989. *Genetic algorithms in search, optimization and machine learning*. Addison-Wesley, Reading, Mass.
- Gomez, F., and R. Miikkulainen. 1997. Incremental evolution of complex general behavior. *Adaptive Behavior* 5:317–342.
- Goodson, M. S., J. Giske, and R. Rosland. 1995. Growth and ovarian development of *Maurolicus muelleri* during spring. *Marine Biology* (Berlin) 124:185–195.
- Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115:129–148.
- Gundersen, G. 1997. Impact of birth-date on early life growth and survival of Müellers pearlside (*Maurolicus muelleri*) larvae. Cand. scient. thesis. University of Bergen, Bergen, Norway.
- Hamre, L. A. 1999. Growth and mortality of *Maurolicus muelleri* (Gmelin): do parasites matter? Cand. scient. thesis. University of Bergen, Bergen, Norway.
- Hewett, S. W., and B. L. Johnson. 1992. *Fish bioenergetics model 2*. University of Wisconsin Sea Grant Institute, Madison.
- Holland, J. H. 1975. *Adaptation in natural and artificial systems*. University of Michigan Press, Ann Arbor.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* 48:1–86.
- Houston, A., and J. McNamara. 1999. *Models of adaptive behaviour: an approach based on state*. Cambridge University Press, Cambridge.
- Huse, G. 2001. Modelling habitat choice in fish using adapted random walk. *Sarsia* 86:477–483.
- Huse, G., and J. Giske. 1998. Ecology in Mare Pentium: an individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* 37:163–178.
- Huse, G., E. Strand, and J. Giske. 1999. Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* 13: 469–483.
- Huston, M., D. DeAngelis, and W. Post. 1988. New computer-models unify ecological theory—computer-simulations show that many ecological patterns can be explained by interactions among individual organisms. *BioScience* 38:682–691.
- Iwasa, Y. 1982. Vertical migration of zooplankton: a game

- between predator and prey. *American Naturalist* 120: 171–180.
- Judson, O. P. 1994. The rise of the individual-based model in ecology. *Trends in Ecology & Evolution* 9:9–14.
- Kaartvedt, S., W. Melle, T. Knutsen, and H. R. Skjoldal. 1996. Vertical distribution of fish and krill beneath water of varying optical properties. *Marine Ecology Progress Series* 136:51–58.
- Kauffman, S., and S. Levin. 1987. Towards a general theory of adaptive walks on rugged landscapes. *Journal of Theoretical Biology* 128:11–45.
- Kawaguchi, K., and J. Mauchline. 1987. Biology of Sternoptychid fishes in the Rockall Trough, northeastern Atlantic Ocean. *Biological Oceanography* 4:99–120.
- Krebs, J. R., and N. B. Davies, eds. 1997. *Behavioural ecology: an evolutionary approach*. 4th ed. Blackwell Scientific, Oxford.
- Kristoffersen, J. B., and A. G. V. Salvanes. 1998. Life history of *Maurolicus muelleri* in fjordic and oceanic environments. *Journal of Fish Biology* 53:1324–1341.
- Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50:434–437.
- Langton, C. G., ed. 1989. *Artificial life*. Addison-Wesley, Reading, Mass.
- Levy, S. 1993. *Artificial life: a report from the frontier where computers meet biology*. Vintage Books, New York.
- Loehle, C. 1983. Evaluation of theories and calculation tools in ecology. *Ecological Modelling* 19:239–247.
- Luecke, C., and W. J. O'Brien. 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1264–1270.
- Maynard Smith, J. 1993. *The theory of evolution*. Canto ed. Cambridge University Press, Cambridge.
- Melo, Y. C., and M. J. Armstrong. 1991. Batch spawning behaviour in lightfish *Maurolicus muelleri*. *South African Journal of Marine Science* 10:125–130.
- Menczer, F., and R. K. Belew. 1996. From complex environments to complex behaviors. *Adaptive Behavior* 4: 317–363.
- Mitchell, M., and S. Forrest. 1995. Genetic algorithms and artificial life. Pages 267–289 in C. G. Langton, ed. *Artificial life: an overview*. MIT Press, Cambridge.
- Montana, J., and L. Davis. 1989. Training feedforward networks using genetic algorithms. Pages 762–767 in N. S. Sridharan, ed. *Eleventh international joint conference on artificial intelligence*. Morgan Kaufman, Detroit.
- Murphy, G. I. 1968. Patterns in life history and the environment. *American Naturalist* 102:391–403.
- Parrott, L., and R. Kok. 2000. Incorporating complexity in ecosystem modelling. *Complexity International* 7: 1–19.
- Railsback, S. F. 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological Modelling* 139:47–62.
- Rasmussen, O. I., and J. Giske. 1994. Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. *Marine Biology (Berlin)* 120: 649–664.
- Roff, D. A. 1992. *The evolution of life histories*. Chapman & Hall, New York.
- Rosenblatt, F. 1958. The perception: a probabilistic model for information storage and organisation in the brain. *Psychological Review* 65:386–408.
- Rosland, R., and J. Giske. 1994. A dynamic optimisation model of the diel vertical distribution of a pelagic planktivorous fish. *Progress in Oceanography* 34:1–43.
- . 1997. A dynamic model for the life history of *Maurolicus muelleri*, a pelagic planktivorous fish. *Fisheries Oceanography* 6:19–34.
- Rummelhart, D. E., G. E. Hinton, and R. J. Williams. 1986. Learning representations by back propagation errors. *Nature (London)* 323:533–536.
- Salvanes, A. G. V., and B. M. Stockley. 1996. Spatial variation of growth and gonadal developments of *Maurolicus muelleri* in the Norwegian Sea and in a Norwegian fjord. *Marine Biology (Berlin)* 126:321–332.
- Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. *American Naturalist* 108: 783–790.
- Schmidt-Nielsen, K. 1983. *Animal physiology: adaptation and environment*. 3d ed. Cambridge University Press, Cambridge.
- Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? Pages 182–211 in P. H. Harvey and L. Partridge, eds. *Oxford survey in evolutionary biology* 4. Oxford University Press, Oxford.
- Sigmund, K. 1993. *Games of life: explorations in ecology, evolution, and behaviour*. Oxford University Press, Oxford.
- Skagseth, B. 1999. Feeding and gonad development of *Maurolicus muelleri* (Gmelin) in Herdlefjorden during spring. Cand. scient. thesis. University of Bergen, Bergen, Norway.
- Southwood, T. R. E., R. M. May, M. P. Hassell, and G. R. Conway. 1974. Ecological strategies and population parameters. *American Naturalist* 108:791–804.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3–47.
- . 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, N.J.

- Sumida, B. H., A. I. Houston, J. M. McNamara, and W. D. Hamilton. 1990. Genetic algorithms and evolution. *Journal of Theoretical Biology* 147:59–84.
- Tinbergen, N. 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20:410–433.
- Toquenaga, Y., and M. J. Wade. 1996. Sewall Wright meets artificial life: the origin and maintenance of evolutionary novelty. *Trends in Ecology & Evolution* 11:478–482.
- Uchmanski, J., and V. Grimm. 1996. Individual-based modelling in ecology: what makes the difference? *Trends in Ecology & Evolution* 11:437–441.
- van Rooij, A. J. F., L. C. Jain, and R. P. Johnson. 1996. Neural network training using genetic algorithms: series in machine perception and artificial intelligence. Vol. 26. World Scientific, Singapore.
- Yoshimura, J., and C. W. Clark, eds. 1993. Adaptation in stochastic environments. *Lecture Notes in Biomathematics* 98. Springer, Berlin.

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