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Utilizing Different Levels of Adaptation in Individual-Based Modeling

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CONTENTS

33.1 Introduction

The most obvious trait of any biological organism is its functionality. It is so universal that its presence was almost unnoticed until the early 19th century. Charles Darwin's (1859) fundamental contribution to biology was to propose natural selection and adaptation as the explanation for the great variety of seemingly intelligent design in Nature. In biology, the most common use of the word *adaptation* is the modification of a trait by natural selection during evolution. For example the white camouflage color of hares in winter and their gray-brown fur in summer can be referred to as adaptations. Here we refer to adaptation in a wider sense: as any process that allows adjustments to the environment. The high importance of adaptation for biological units can be seen from the fact that there are three separate ways

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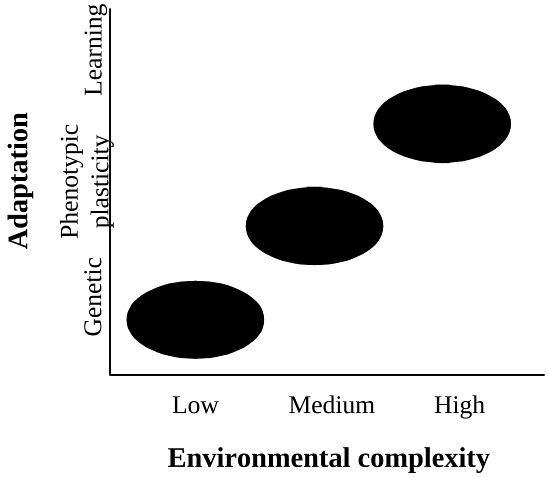

FIGURE 33.1 Different levels of adaptation related to environmental complexity.

that adaptation takes place in biology (Figure 33.1). All three types of adaptation may partly determine individual behavior; whichever is dominant may depend on the current circumstances. We refer to them as different levels of adaptation, which reflects the different timescales that they work on. Although most models of populations and organisms do not specify any process of adaptation, or assume the dominance of a particular kind of adaptation, the idea of adaptation underlies most, if not all, theories and models in ecology. If not for genetic adaptation, one could not assume that a parameter value measured for some individuals also would apply to other members of the population. If not for phenotypic plasticity, one could not assume life history adjustment resulting from climate changes. And if not for learning and memory, one could not assume group dynamics and territoriality.

Although an unconscious use of the power of adaptation in biological theory and in individual-based modeling often is sufficient for many purposes, it is also obvious that conscious attention to the effect of adaptations would improve our ability to mimic natural organisms and their responses to environmental variation (Railsback, 2001). The purpose of this chapter is to illustrate how different levels of adaptation, from fixed strategies to phenotypic plasticity and learning, can be utilized in individual-based modeling of life history and behavioral strategies, to improve models of aquatic populations.

33.2 Individual-Based Modeling

It is not evident from the name, but individual-based modeling is a tool for studying group and population processes. For young practitioners of individual-based models (IBMs), it can be useful to recall that before IBMs there were population-based models. This tradition goes back to Lotka and Volterra, and has roots in Euler (1760) and beyond. Before computers became standard equipment, there was a huge need to simplify problems. Thus populations were modeled as consisting of N identical individuals. Alfred Lotka (1925) and Vito Volterra (1926) developed the Lotka–Volterra equations, which enabled simulations of the dynamics of two (or more) interacting populations. These approaches thus described the dynamics of the population by the average members, and dynamics usually occurred only in the temporal dimension. The population approach is still a useful exercise, and the methods developed by Lotka, Volterra, and others have led to the development of structured population models where the population is divided according to age, stage, or a physiological criterion (Fisher, 1930; Metz and Diekman, 1986; Tuljapurkar and Caswell, 1997). Such structured models have proved successful for many applications in ecology and fisheries science. Their advantage, in addition to being more flexible than population models, is that the use of differential equations or matrix models allows analytical solutions (Huston et al., 1988; Caswell and John, 1992).

One of the first applications of the individual-based approach was to explore causes of recruitment variability to commercial fish stocks (DeAngelis et al., 1979; Beyer and Laurence, 1980). This issue has prevailed and been studied empirically in fishery science since Hjort (1914). By IBMs it is possible to simulate the individual variability in survival and spatial distribution of early life stages of fish cohorts. This is important for population dynamics, because the survivors tend to differ from average individuals at earlier stages (Crowder et al., 1992). Studies of fish early life history have therefore become one of the major topics for IBM applications (Grimm, 1999). Although the individual-based modeling approach was initiated in the late 1970s, it is only since the influential review of Huston et al. (1988) that it has been applied extensively in ecology. The so far most valued ability of IBMs is clearly the disintegration of the population into individuals, and the reintegration of individual events into population processes. However, while the approach benefits from considering the population impact of local conditions on individual physiology, there has been little attention to the effect of adaptation to local conditions through differences in individual performance. On this matter IBMs have the advantage over population models in that they have the same basic unit as natural selection. This allows a fairly straightforward implementation of adaptation in IBMs. The individual-based modeling approach is not as formalized as the analytic life history models and the Lotka–Volterra models, and as the name implies it is an approach rather than a specific set of equations. Still, IBMs have some common structural elements, and below we provide a description of attribute and strategy vectors that are used for bookkeeping of individual characters and implementation of adaptation, respectively.

33.3 Methodology

33.3.1 The Attribute Vector

Individuals can be specified in IBMs by using an attribute vector $\mathbf{A_i}$ (Chambers, 1993), which contains all the states αm_i used to specify an individual i such as age, weight, sex, hormone levels, and spatial coordinates (x_i,y_i,z_i) at time t:

$$\mathbf{A_i} = (\alpha 1_i,\alpha 2_i,\alpha 3_i,\ldots,\alpha m_i,x_i,y_i,z_i,t) \qquad (33.1)$$

Even though the individual-based structure is appealing, it is often difficult to simulate populations on a truly individual basis due to the great abundances involved. This can be solved using the super-individual approach (Scheffer et al., 1995). A super-individual represents many identical individuals and the number of such identical siblings (n_s) thus becomes an attribute of the super-individual:

$$\mathbf{A_s} = (\alpha 1_s,\alpha 2_s,\alpha 3_s,\ldots,\alpha m_s,x_s,y_s,z_s,n_s,t) \qquad (33.2)$$

where $\mathbf{A_s}$ is the attribute vector of super-individual s. Mortality operates on the super-individual, and the number of siblings of each super individual is thus decreased in proportion to the mortality rate (Scheffer et al., 1995).

33.3.2 The Strategy Vector

In addition to possessing states, real individuals have adaptive traits, such as life history and behavioral strategies that specify how they should live their lives. The previous lack of IBM studies involving life history strategies and behavior of individuals is in part due to a lack of appropriate techniques for implementing these features. However, adaptive traits can be modeled by introducing a strategy vector $\mathbf{S_i}$ (Huse, 2001; Huse et al., 2002a) that specifies the adaptive traits, such as life history traits or behavior, of an individual:

$$\mathbf{S_i} = (\beta 1_i,\beta 2_i,\beta 3_i,\ldots,\beta m_i) \qquad (33.3)$$

where βm_i is the adaptive trait m of individual i. The strategy vector may be considered analogous to a biological chromosome as in the genetic algorithm (Holland, 1992), but may also be updated during the individual's life as a way to simulate learning. In both cases the trait values are modified iteratively in search of the best strategy vectors, and both these approaches for establishing trait values will be discussed below. The combination of attribute and strategy vectors thus enables most relevant characteristics of individuals to be implemented in IBMs. The classification based on attribute and strategy vectors can be used to describe IBMs verbally even though the actual programming implementation is not vector based, as, for example, in object-oriented programming (Maley and Caswell, 1993).

33.3.3 Criteria for Evaluating Adaptation

In nature, adaptation is evaluated by natural selection (Darwin, 1859). To allow analysis of behavioral and life history traits, criteria mimicking the process of natural selection have been constructed and implemented in models as Darwinian fitness measures. The argument behind the application of a fitness measure is that a particular feature or trait under investigation has become optimally adapted over evolutionary time under the given constraints (Stearns and Schmid-Hempel, 1987; Parker and Maynard Smith, 1990). Although there is an ongoing debate of what is the most appropriate definition of fitness (Stearns, 1992; Giske et al., 1993; Mylius and Diekmann, 1995; Roff, 2002), there seems to be a consensus about the importance of including aspects of survival and fecundity (growth) into the fitness definition. The common fitness measures based on this assumption are the instantaneous rate of increase r and the net reproductive rate R_0 (Roff, 1992). An alternative approach is to use endogenous fitness rather than an explicit fitness criterion (Mitchell and Forrest, 1995; Menczer and Belew, 1996; Huse, 1998; Strand et al., 2002). In endogenous systems, no fitness measure to maximize is provided, but rather fitness emerges by interactions between the organism and its environment. Individuals grow and die according to probability functions and Monte Carlo simulations (Judson, 1994). Criteria are set for reproduction and the fittest organisms will, by definition, be those that are able to reproduce more, relative to the other individuals under the set conditions. Such models operate similarly to the way in which evolution works: through “adaptation execution” rather than by “fitness maximization” (Wright, 1994).

33.4 Three Levels of Adaptation

33.4.1 Fixed Genetic Strategies

Traditionally, evolutionary adaptations have been implemented in IBMs in two ways. First, all parameter values that are results of experiments on the modeled organism, such as physiological and morphological parameters, reflect the results of natural selection. In such cases modelers may not always be conscious about their application of adaptation, but application of measured parameters is a shortcut to the adapted state without performing the selection process over again. Second, rules of behavior implemented in IBMs are often derived from evolutionary considerations. The major source of such rules is life history theory, and we take the much-used “Gilliam’s rule” as an example. This rule states that juvenile fish should seek the habitat where the mortality risk per growth rate (μ/g) is minimal. Werner and Gilliam (1984) showed that for a specific life history pattern of fish, a given growth and mortality regime, and under the assumption that fitness could be modeled by the net reproductive rate (R_0), this was the optimal policy for pre-reproductive organisms. This rule has been applied in many studies of fish spatial distribution, but also in studies of many kinds of organisms for which it was not developed. Aksnes and Giske (1990) developed other life history–based rules for other aquatic life histories.

Although Gilliam’s rule and other rules for optimal behavior yield both analytical and intuitive understanding of the major trade-offs for individuals in a given environment, they cannot be said to be truly individual, but rather population rules. The rule is derived from typical aspects of the life cycles, not from individual characteristics. Also, when using such life history–based rules, all individuals tend to make the same decisions. An alternative approach to deriving rules from some theory could therefore be to evolve them. The genetic algorithm (GA) developed by Holland (1992) is a technique that applies evolution by natural selection in computer programs to find optimal solutions to a problem by representing solutions in “genetic code.” It involves: a numeric genetic code, selection of the best combination of numbers in consecutive generations using a fitness criterion, and mutations and recombinations to produce

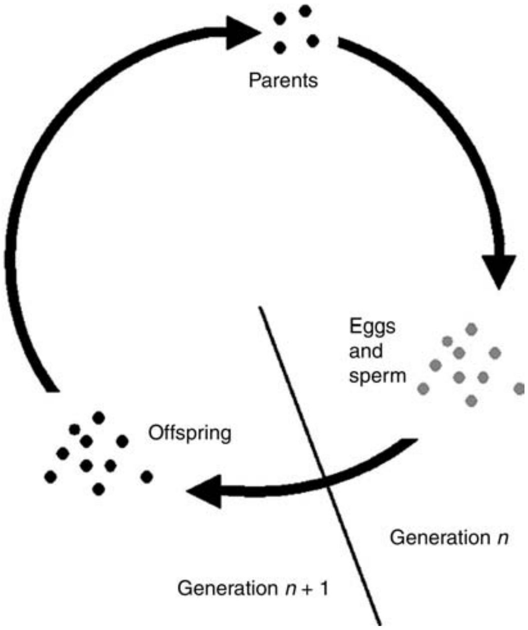

FIGURE 33.2 The genetic algorithm. Of a large initial population of newborn offspring, a smaller number will survive and become the parents for next generation. These survivors produce sexual products in proportion to their accumulated reserves. These sexual products form the eggs for next generation, possibly after recombinations and mutations of the parent strategy vectors. This process is repeated in an individual-based model over a number of generations. In each generation, strategy vectors that make the offspring more likely to become parents will increase in abundance, and hence the individual genomes and the whole gene pool of the offspring population will become better adapted to the local conditions.

new variation (Figure 33.2). The GA has successfully been applied to problems within a large number of fields, such as engineering, physics, economics, medicine, artificial life, and biology (Goldberg, 1989; Mitchell, 1996). For recipes on applications of GAs in IBMs, see Huse et al. (2002a).

The simplest application of GAs to evolve adaptations in an IBM is through life history switch genes. In classical models of zooplankton dynamics, the seasonal dynamics of the population was taken care of by programming codes, such as

$$\text{IF (JulianDay = 280) THEN descend to overwintering depth} \tag{33.4}$$

The programmer knew that zooplankton in spring and summer fed in surface waters, and overwintered at greater depths during the winter season. Hence, the programmer used the first level of adaptation by driving the model through observations and fixed preset values. Alternatively, the GA could be used to search for the optimal date for seasonal migration, and the pseudocode could have been as

$$\text{IF (JulianDay = character } \beta m\text{) THEN descend to overwintering depth} \tag{33.5}$$

where now character βm (Equation 33.3) is the character value of character number m in the strategy vector of an individual. Individuals with the same character values at character m would then descend to overwintering depths the same day. After some generations of adaptation, the gene pool of the population would consist of one single character value of character m, or a series of values that on average gave their bearers the same fitness. Another modeling technique related to the GA is genetic programming (Koza, 1992), where computer code rather than allele values are evolved. GP can be used instead of the GA for most of the cases discussed in this chapter.

33.4.2 Phenotypic Plasticity

Above we discussed how to adapt fixed strategies for maximizing survival, growth, and reproduction using the GA. When the environment varies in a fairly predictable fashion such as the seasonal changes

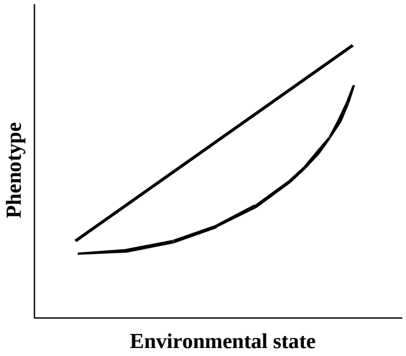

FIGURE 33.3 Reaction norms emerge as different phenotypes are expressed under different environmental states. The relationship between phenotype and environment is shown for two different genotypes.

in day length or interannual climatic variation, fixed strategies (Equation 33.5) tend to yield for flexible strategies that are dependent on the state of the environment. We now come to the second level of adaptation in biology: phenotypic plasticity.

Phenotypic plasticity is defined as "a change in the average phenotype expressed by a genotype in different macro environments" (Via, 1987). Thus one genotype adapts by expressing different phenotypes under different environmental states. This does not imply that an individual is equally well adapted to all environmental states, but rather that the individual resources are allocated to give the best attainable life history for the particular environment (Lessells, 1991). The relationship emerging between the expressed phenotype for an environmental state and the environmental state is referred to as the reaction norm. This concept is illustrated in Figure 33.3.

To implement phenotypic plasticity in models it is necessary to include environment state (E) as a variable in the model. To model, for example, the linear reaction norm seen in Figure 33.3, one needs intercept and slope characters embedded on the strategy vector. In this case the phenotype is $\beta_1 E + \beta_2$. To allow more complex reaction norms the complexity of the equation needs to be increased, along with the number of adapted variables. The variables are estimated using the GA as discussed above. In some cases several environmental features affect a trait. One way to model this would simply be to add more terms to the reaction norm. A different approach would be to use an artificial neural network (ANN), as discussed below.

State dependency is a phenomenon similar to phenotypic plasticity. From the perspective of the organism, phenotypic plasticity is the genes' changes in strategy under a variable external environment, whereas state dependency is the genes' changes in strategy under a variable internal environment. But from the perspective of a gene, the nearest external environment is the rest of the genome and the organism. The organism is the survival tool for its genes (Dawkins, 1982; Keller, 1999). State-dependent behavior or life history decisions appear because the genes code for flexible strategies. State-dependent decisions are usually modeled by stochastic dynamic programming (Houston and McNamara, 1999; Clark and Mangel, 2000). This method, however, is backward running, and therefore not always easy to combine with other individual-based methods. An alternative would then be to use ANN and a GA, which also can solve state-dependent problems (Huse et al., 1999). ANN is explained in the next section.

33.4.3 Individual Learning

The final and perhaps most refined level of adaptation is learning. Learning can be defined as "any process in an animal in which behavior becomes consistently modified as a result of experience" (Lawrence, 1989). As opposed to the other two kinds of adaptation discussed previously, learning is not passed on to offspring. Instead, learning is an independent process for each individual, although it may be facilitated by parents. Still the capacity for learning is evolved. Learning is particularly efficient in complex or unpredictable environments where changes take place at a small timescale. Learning requires a higher mental capacity than the other means of adaptation, and in general it is more important for

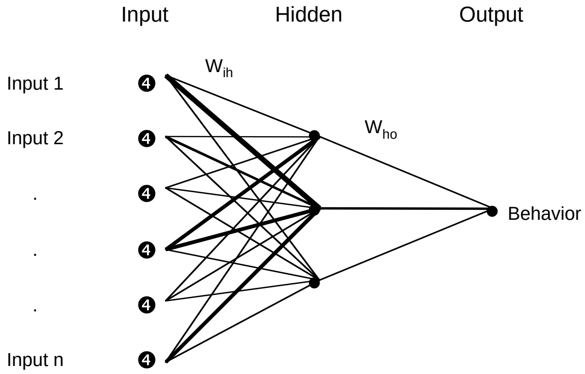

FIGURE 33.4 A schematic outline of an ANN. The connection points of the lines are referred to as nodes.

marine mammals (Rendell and Whitehead, 2001) than for fish, and rather restricted in invertebrates. The evolutionary role of learning is very obvious in mammals, where parents usually teach their offspring to find food and to avoid predators. For good introductions to learning and modeling learning, respectively, see Schmajuk (1997) and Ballard (1997).

Learning can be implemented in models in different ways and below we address some basic methods for doing this. Simulation models of learning can be divided into supervised learning paradigms and reinforcement learning. Common to many of the models is that they are based on ANNs.

33.4.3.1 ***Artificial Neural Networks*** — The ANN is a computing method inspired by a conceptual model of how the human brain functions. Neurons in the brain are interconnected by synapses; similarly layers of nodes in an ANN are linked together and pass signals between each other (Figure 33.4). Thus, the ANN is made to mimic the decision process in a biological organism, with multiple sensory inputs, a complex and hidden brain, a decision and a muscle output. This paradigm was initiated by McCulloch and Pitts (1943) and their theoretical outline of the two-state neuron. Since then, there has been considerable development in ANNs, and today a wide variety of ANN architectures are available (Rosenblatt, 1958; Rummelhart et al., 1986; Montana and Davis, 1989). In Figure 33.4 a three-layer feedforward ANN is illustrated.

The connection between a series of stimuli and the decision in an ANN goes from the input layer through one or several layers of hidden nodes. Each hidden node adds and weighs the input from a series of input nodes:

$$N_h = \sum_{i=1}^{m} W_{ih} \cdot I_i \tag{33.6}$$

where I_i is input data i, W_{ih} is the connection weight between input data i and hidden node h (i.e., the relative influence of input data i for hidden node h), N_h is the sum of the weighted input data of hidden node h, and m is the number of input nodes connected to hidden node h. At the hidden node, values are transformed to the [0,1] range using the standard sigmoid transformation:

$$TN_h = \frac{1}{(1+e^{-(N_h+B_h)})} \tag{33.7}$$

where TN_h is the transformed node value and B_h is the bias (van Rooij et al., 1996) of hidden node h. The bias B_h is similar to an intercept value in a regression model. The transformation in the ANN introduces nonlinearity, which allows the network to solve complex problems. The output O is calculated by adding together the sums of the transformed hidden node values multiplied by the output weights (W_{ho}):

$$O = \sum_{h=1}^{n} W_{ho} \cdot TN_h \tag{33.8}$$

where n is the number of hidden nodes. Finally the output is transformed using an equation similar to Equation 33.7. The ANN is adapted by defining all connection weights and biases as separate characters on the strategy vector select for the best ANNs using the GA or learning techniques. With an initial random set of connection weights in each modeled individual in the first generation, there is a potential risk that no phenotype will be able to perform sensible decisions. This can be overcome by introducing the first few generations in the GA to a simpler and friendlier environment, where the pressure to perform is weaker than for later generations.

33.4.3.2 Supervised Learning —

Supervised learning is a method where a training set of known input–response pairings is used to produce generalizing capabilities in an ANN. This corresponds to having an omniscient teacher, hence the name. In supervised learning, the output produced by the ANN is compared to the correct response and the weights are modified according to the discrepancy in an iterative procedure. This procedure is repeated for the entire training set. The trained network can then be used to generate predictions for cases outside of the training set. One of the simplest ANNs is the so-called perceptron (Rosenblatt, 1958). This network consists of an input and an output layer and can be trained using the Widrow-Hoff or delta learning rule (Ballard, 1997). In this case the output is the sum of the input to the network multiplied by the weights (W) between the input and the output node, and the weights are then changed by

$$W = W_{old} + d \cdot L \cdot I \tag{33.9}$$

where L is the learning rate, I is the input, and d is then defined as $O_{\text{target}} - O$. Thus, the discrepancy between the observed and predicted output is used to modify the weights. This procedure is a simple way to implement associative learning into models, for example, classical conditioning. In classical conditioning, a conditioned response toward a conditioned stimulus, which does not elicit response, is learned as the conditioned stimulus is presented in conjunction with an unconditioned stimulus that elicits response (Schmajuk, 1997). In the classic case of Pavlov’s dog, the bell ringing before the food is presented is the conditioned stimulus and the food is the unconditioned stimulus. After several pairings of the two stimuli, the conditioned stimulus is able to produce a conditioned response similar to an unconditioned response. This is referred to as stimulus substitution (Schmajuk, 1997). Classical conditioning can be simulated by presenting the stimuli as input to the ANN and then correcting the weights through iterations to reproduce conditioned responses similar to the observed (unconditioned) responses using Equation 33.9.

There are some limitations to what problems the perceptron can solve, and for more complex problems, backpropagation is a better technique (Rummelhart et al., 1986). Implicit in this approach is the use of a hidden layer, as seen in Figure 33.4, in addition to the input and output layers of the perceptron. This along with a sigmoid transfer function and a generalized delta rule that is propagated backward into the ANN allows solution of complex problems (Ballard, 1997). Thus errors are computed for each unit in the hidden and output layers and the weights are modified correspondingly.

33.4.3.3 Reinforcement Learning —

While the supervised learning paradigm assumes the presence of an omniscient supervisor able to tell the network the correct response, one often does not know the correct answer. Instead, it may be possible to evaluate actions in a less rigorous manner. Such situations are suited for reinforcement learning where actions are associated with rewards and punishment for “good” and “bad” behaviors, respectively (Ackley and Littman, 1992). Thus as opposed to supervised learning where the correct output is known during training, the ANN has to discover the desired output. This process allows individuals to produce increasingly more favorable behaviors as they explore and learn about their environment. A behavior network can be updated by calculating a reinforcement signal based on the fitness consequence of the previous action, so-called delayed rewards. The weights of the ANN are then modified according to a reinforcement learning procedure that resembles backpropagation, to produce increasingly “better” behavior. Recipes for applying reinforcement learning can be found in Ballard (1997), and for an application of reinforcement learning to simulation of movement behavior in a spatial lattice, see Ackley and Littman (1992).

33.5 Case Studies

The discussion above has focused on presenting and categorizing adaptation and adaptive modeling techniques. Below some cases are provided where we discuss the different levels of adaptation and model implementation. The cases focus on diapause in zooplankton, vertical migration in salmonids, and antipredator responses.

33.5.1 Overwintering Diapause in Daphnids

In autumn, many life-forms shift focus from growth to overwintering survival. This applies to boreal trees as well as to boreal bears. We illustrate this with two examples, starting with hibernation decision in a freshwater herbivorous zooplankter. *Daphnia* enters diapause in fall in temperate lakes by producing two resting eggs, which overwinter in the lake sediments. Next spring the resting eggs hatch and grow into adult females that commence asexual reproduction at maturity. The timing of the onset of diapause is important because the alternative is to produce several female offspring that reach maturity and can reproduce themselves again. On the other hand *Daphnia* strains that remain in the water column through winter risk extinction due to the long generation time, low fecundity, a potentially high predation pressure, as well as environmental hazards.

The simplest modeling strategy for this phenomenon would be to obtain the most probable date for hibernation from a field study. In many cases this would also be the most appropriate method, as this date reflects the actual adaptation that has taken place in this or a similar lake, and as it allows the modeler to concentrate on other dynamic aspects of the model. But if one were to model the timing, the first approach would be to assume a Julian day for descent and code this on the strategy vector. However, if interannual variation in the environment is great, this fixed strategy might be inferior to a more flexible strategy taking the state of the environment into account. By assuming that temperature is a key variable in this respect, the decision variable (D) could be expressed, for example, as a power function of the temperature T at some early stage:

$$D = \beta_1 T^{\beta_2} \tag{33.10}$$

The corresponding strategy vector is $\mathbf{S_i} = (\beta_1,\beta_2)$. A similar approach has been used in a model of the life cycle of the boreal marine copepod *Calanus finmarchicus* (Fiksen, 2000). Fiksen equipped each individual in the population with three evolvable characters: (1) the day of the year (i.e., the day length) at which a resting stage V copepodid should wake from overwintering diapause, (2) the day of year when it should shift allocation pattern from somatic growth to production of fat reserves for overwintering, and (3) the fat/somatic tissue ratio required to initialize overwintering diapause. Thus, he used two static characters and one state-dependent character.

If in addition to the interannual variation in temperature, additional factors such as the predation pressure or density of conspecifics, or both, are important, the problem of the *Daphnia* becomes a lot more complex. To model this, one could build on Equation 33.5, and include more factors in a similar fashion. This kind of model would soon become rather complicated, especially if the different factors interfere with each other in affecting the survival of *Daphnia*. An alternative way of doing this would be to use a formalized structure such as the ANN. For example, the problem could be solved sequentially so that each day the *Daphnia* would be presented with the relevant information and perform the decision whether to enter diapause or continue producing regular offspring. This example illustrates how increasing environmental complexity needs to be approached with increasing model complexity in order to solve the important trade-offs.

33.5.2 Diel Vertical Migration in a Salmonid

Vertical migration is a classic theme in ecology occurring in a wide range of aquatic organisms. Diel vertical migration (DVM) comes about as an adaptation to the daily light cycle and usually moves organisms between deep waters during the day and shallower waters at night (Figure 33.5). This behavior

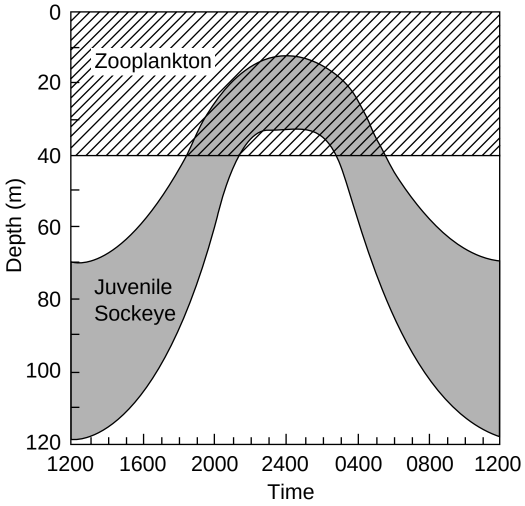

FIGURE 33.5 The diel vertical distribution of salmonids in a lake. (From Clark, C.W. and Levy, D.A., *Am. Nat.*, 131:271–290, 1988. With permission.)

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is driven by the trade-off between feeding and predation risk. Below we develop a model for vertical migration in a small freshwater fish, for example, a small salmonid (Clark and Levy, 1988). The fish feed on zooplankton and are eaten by visually foraging fish.

The surface light level goes through tremendous changes during the diel cycle, peaking at midday and going to virtually zero at night, except for regions with a midnight sun. A simple way of performing DVM would thus be to adapt to a constant light level and adopt this throughout the day. Thus the fish would always stay at or move toward the depth corresponding to this light level, and the best isolume will be estimated iteratively using the GA. Movement would be constrained by the surface and the bottom, and at night the fish would tend to occupy the surface layer.

The isolume strategy is simple, but also rather inflexible, and might leave the fish more exposed to predation than optimal, for example, when it is satiated. A state-dependent strategy involving stomach fullness (SF) would therefore improve the flexibility of the model:

$$D = \beta_1 + \beta_2 \cdot \mathrm{SF}^{\beta 3} \tag{33.11}$$

where D is the decision variable (depth), and β_1 is the isolume level, and β_2 and β_3 represent the depth dependence on stomach fullness. The strategy vector would then be $\mathbf{S_i} = (\beta_1, \beta_2, \beta_3)$. In addition to the state dependence, there could be other factors influencing depth selection, such as the distribution of food resources, conspecifics, or the temperature. Again it can be profitable to use ANNs if several factors are to be taken into account. See Strand et al. (2002) for an application of ANNs and GAs in an IBM of vertical migration in the mesopelagic fish *Maurolicus muelleri*.

33.5.3 Antipredator Responses

A number of aquatic species are able to learn antipredator responses. Even flatworms with a very simple nervous system are able to learn avoidance of predators by associating it with odors of injured conspecifics (Wisenden and Millard, 2001). This is a case of classical conditioning where the response to chemical cues released by injured conspecifics is evolved. Once this smell is associated with a strange odor, the strange odor is responded to as the presence of a predator. In this case the predator odor becomes the conditioned stimulus, and the smell of injured conspecifics is the unconditioned stimulus. Similarly, young stages of daphnids can alter their morphology on detection of chemicals associated with digestive processes of their predator, the phantom midge *Chaoborus* sp. (Krueger and Dodson, 1981; Larsson and Dodson, 1993). The alteration reduces the likelihood of *Daphnia* being ingested by the predator. Because the morphological alteration is irreversible and costs energy, it can be fruitful to study at what predator densities or *Daphnia* densities or time of year it should be induced. Alterations in morphology can be predicted using an ANN with the factors mentioned above as input data along with equations for the costs and benefits associated with the alterations. So here we see examples of adaptation by phenotypic plasticity toward a specific and evolutionary well-known predator, and through learning toward any new predator. This is seen in fish species as well. For example, gobies in western Norway do not have inherited aversion against cod, their main predator, but rather learn to be averse through combined visual-olfactory associations (Utne-Palm, 2001). Mathis et al. (1996) further showed that such predator aversions could be transferred culturally from experienced to naive individuals, also across species barriers.

33.6 Discussion

33.6.1 Pros and Cons of the Different Levels of Adaptation

There has been no thorough account of the relative profitability of the different levels of adaptation (Frank, 1996), although some preliminary efforts have been attempted (Boyd and Richerson, 1985; Holland, 1992). The lack of a lucid theory for understanding the profitability of the different levels of adaptation makes it difficult to provide recommendations for when to use the different approaches in IBMs. However, there is a general tendency for the level of adaptation to increase with the complexity of the environment (Figure 33.1). Thus in constant environment a fixed strategy is favorable as no time or energy is wasted on failed explorations (Frank, 1996). In a seasonally variable environment or if the environment varies between rather predictable states, phenotypic plasticity would be the adaptive level of choice. For short-term variation caused, for example, by the tidal cycle, learning might be the most profitable way of exploiting the environment. In general, it is useful to consider the kind of adaptation exerted in nature and the capabilities of the target species when deciding on what level of adaptation to use in a model. Each level of adaptation has its pros and cons. Genetic adaptation, through fixed or flexible phenotypes, is slow, inflexible, and irreversible in the organism. Mental adaptation, through learning, is quick and reversible, but requires individual association and explorations by trial and error. Hence, very dangerous or very rare events are not open to learning. Learning is costly to the organism in several ways. It costs time, lost opportunities, and sometimes enhanced mortality risk to make the observations and associations that can be learned. It also costs energy to transfer them into storage, and keep them stored in the neural system. The storage capacity itself is also under adaptive evolution, competing for resources with all other anatomical structures (Fisher, 1930). The capacity for learning is therefore strongly dependent on the evolutionary lineage, and learning ability is, for example, much greater in mammals than in fish. Finally, with a limited storage capacity, different elements of learning compete for available memory. This explains also why organisms should be quick to forget as soon as the learned association is not of high fitness value any more (Healy, 1992).

Social learning is widespread in primates and other mammals. Similar cultural exchange between age groups is seen in herring where young individuals seem to learn features of their migration pattern from schooling with older ones (McQuinn, 1997; Fernö et al., 1998). However, the collective dynamics of the herring schools are important for the information exchange among herring cohorts, and in years when the recruiting year class is especially abundant, the information exchange seems to be interrupted (Huse et al., 2002b). This shows that social learning can be vulnerable to interference at large population sizes.

33.6.2 The Baldwin Effect

James Mark Baldwin (1896) proposed a mechanistic connection between individual learning and genetic evolution. In a variable environment, the genome can improve its survival by including genes that code for alternative phenotypes. Hence, phenotypic plasticity is a genomic bet-hedging strategy in variable environments. But in a complex fitness landscape, where events seldom repeat, the organisms cannot possess a genetic preparedness for all possible circumstances. It is therefore in the interest of genes in a genome to include new members that code for mental structures facilitating learning. Hence, individual learning is adaptive if learners reproduce their genetic codes more frequent than nonlearners. This is the standard explanation for all types of phenotypic adaptation. However, Baldwin suggested an additional mechanism: in variable environments, new external factors can appear, impacting genetic fitness of the organism. Individuals with genomes that contain genes coding for a capacity to learn how to handle new situations can more easily survive and reproduce their genome. One can say that learning smooths the peaks and valleys in the fitness landscape, allowing the genes in the learner to be fit in more environments. And while the genes are kept alive through individual learning, any mutation in the genome leading toward genetic adaptation toward the changed environment will be facilitated. So although random favorable mutations are equally likely in learners and nonlearners, learners are more likely to remain alive and reproducing until the favorable mutation has occurred. As a result, Baldwin said, adaptive genetic evolution is more likely in learners, and hence the genetic trait of learning is maintained and spread.

The Baldwin effect moves the evolutionary level of selection upward from single genes and genomes to organisms and groups. The effect of the third level of adaptation is that social information transfer on the level of groups, as well as nonsocial individual learning, affects both the behavior of the organism and the survival of its genes. In fish, this is clearly seen in the potential strength of imitation-learning in fish feeding (Baird et al., 1991), in predator avoidance (Mathis et al., 1996; Krause et al., 2000), and mating behavior (Dugatkin and Godin, 1993), but is also likely to affect long-range migrations (McQuinn, 1997; Fernö et al., 1998). Hence, to study population processes in fish and other Baldwinian creatures, consideration of all three levels of adaptation may be warranted.

33.7 Conclusions

Above we have presented an approach for thinking about adaptation as well as a conceptual framework for utilizing different levels of adaptation in IBMs. In behavioral ecology it has been commonplace to disregard the level of adaptation involved and simply assume that optimal behavior is achieved. Adaptation in aquatic animals spans from fixed genetic strategies via phenotypic plasticity, to individual and social learning, and IBMs can be used to address all these levels of adaptation. The cases discussed above illustrate the importance of including adaptation in IBMs, as well as being specific about the level of adaptation.

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