

# 11 Individual-based Models

GEIR HUSE, JARL GISKE AND  
ANNE GRO VEA SALVANES

## 11.1 INTRODUCTION

Variability in states and traits is pronounced at all life stages of fish populations. This is mainly caused by spatial and temporal fluctuations in the environment, which in turn result in variation in feeding, growth history and adaptation among individuals in a population (Magurran 1986; Salvanes and Hart 2000). This individual variability often has consequences for population abundance, spatial distribution and fecundity. Traditional ecological models, such as the Lotka–Volterra competition models (Pauly and Christensen, Chapter 10, this volume) or the Ricker model for stock recruitment (Myers, Chapter 6, Volume 1), do not take into account variability among individuals. Rather, these models use population abundance as a single characteristic that defines the population dynamics and it is assumed that individuals are identical. Consequently, features such as size structure, known to be important in fish population dynamics, are left out from the model specifications.

The traditional models have been developed into structured population models where the population is divided according to age, stage or some physiological criterion (Metz and Diekman 1986; Sparre and Hart, Chapter 13, this volume). Such structured models have proven successful for many applications in ecology and fisheries science, and the use of differential equations or matrix models allows analytical solutions (Huston et

al. 1988; Caswell and John 1992). Even though the structured models do partition a population, it is difficult to incorporate features such as spatial detail into these models, because it is rarely reasonable to assume that all individuals of a certain state occupy the same position in space. Structured models also generally divide the population by one variable, but real individuals may differ with regard to many variables.

These features can be implemented in individual-based models (IBM), which keep track of each individual in a population (DeAngelis et al. 1979; Łomnicki 1988; Huston et al. 1988). In these models individuals can be characterized by state variables such as weight, age and length, and they also allow behavioural strategies to be implemented in a spatial context. This allows the properties of a population to be described by the properties of its constituent individuals. Model validations against data can be done at the individual level, which is an appealing property because observations often are performed on single individuals. Also, models based on individuals benefit from having the same basic unit as natural selection (Darwin 1859; Williams 1966). These issues make individual-based modelling an appealing tool in ecology. The approach is not new per se, but rather it is analogous to the old reductionism that has been very successful in empirical sciences (Łomnicki 1988).

The early work of DeAngelis et al. (1979) and Beyer and Laurence (1980) on modelling growth

and survival of largemouth bass (*Micropterus salmoides*) and winter flounder (*Pseudopleuronectes americanus*) respectively, set the scene for extensive later use of IBMs in early life history studies. The major motivation for individual-based modelling of these early life stages has been to explore causes of recruitment variability to commercial fish stocks, an issue that has prevailed and been studied empirically in fishery science since the work of Hjort (1914; see also Myers, Chapter 6, Volume 1 and Smith, Chapter 4, this volume). In order to simulate the survival and spatial distribution of early life stages of fish cohorts, it is important to take account of individual variability, since the eventual survivors tend to differ from average individuals at earlier stages (Crowder et al. 1992). Studies of early life history in fish have consequently been one of the topics where IBMs have been applied most extensively (Grimm 1999). Although the individual-based modelling 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. Still it has not been established whether or not IBMs give fundamentally different answers from the classical ecological models because very few paradigmatic studies have challenged the classic models (Grimm 1999). Nevertheless, IBMs provide a flexible tool for simulating individuals and populations.

In contrast to earlier reviews of IBMs (Huston et al. 1988; DeAngelis and Gross 1992; Grimm 1999), this chapter focuses on the use of individual-based modelling in fish ecology and fisheries science. Rather than providing a balanced review of what has been done using IBMs, we will present topics that modellers of fish populations might need to deal with and then provide some relevant examples for the particular fields. As a result of this we will not cover many replicate studies dealing with similar issues, but instead present a wider range of applications taking advantage of the individual-based approach. We start out with a presentation of the IBM concept, including development and evaluation, and provide some recipes for making different kinds of IBMs. Then we move on to a review of existing literature on IBMs.

## 11.2 SPECIFYING INDIVIDUALS IN IBMs

### 11.2.1 The attribute vector

Here we refer to IBMs as models that treat individuals as explicit entities, the so-called *i*-state configuration models (Caswell and John 1992). We will focus mostly on these models, but we will also discuss structured models that sometimes have been classified as IBMs (Caswell and John 1992). The *i*-state refers to individual features such as body weight, energy reserves and sex, while corresponding *p*-states represent the whole population such as population abundance and average *i*-states of the population. It can be fruitful to illustrate the concept of IBMs by using an attribute vector  $\mathbf{A}_i$  (Chambers 1993), which contains all the states  $\alpha m_i$  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*:

$$\mathbf{A}_i = (\alpha 1_i, \alpha 2_i, \alpha 3_i, \dots, \alpha m_i, x_i, y_i, z_i, t). \quad (11.1)$$

The greater the attribute vector, the more differences between individuals can be specified within the model.

In structured models (Metz and Diekman 1986; Tuljapurkar and Caswell 1997), populations are divided into stages based on some key variable, for example age, which is commonly applied in, for example, the virtual population analysis of quantitative fisheries science. Using the attribute vector concept, one may describe structured models as:

$$\mathbf{A}_j = (s_j, n_j), \quad (11.2)$$

where  $s_j$  is stage *j* and  $n_j$  is the number of individuals of the population in stage *j*. The changes in  $\mathbf{A}_j$  can then be projected using models such as Leslie matrix models or partial differential equations, which can be called *i*-state distribution models (Caswell and John 1992). In IBMs, each individual is specified independently, which means that the number term  $n_j$  of equation (11.2) is 1, and essentially removed from the attribute vector. However, even though the individual-based structure is appealing, it is virtually impossible to simulate

even small fish stocks on a truly individual basis because of the great abundances involved. To allow the advantages of the individual-based approach and still be able to simulate large populations such as fish stocks, the super-individual approach was introduced (Scheffer et al. 1995). A super-individual represents many identical individuals and in this case the number of such identical siblings ( $n_s$ ) thus becomes an attribute of the super-individual:

$$\mathbf{A}_s = (\alpha 1_s, \alpha 2_s, \alpha 3_s, \dots, \alpha m_s, x_s, y_s, z_s, n_s, t). \quad (11.3)$$

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). This is an efficient way of maintaining the individual-based structure, and still be able to simulate the large population sizes that occur in natural populations. When the  $n_s$  gets below a threshold value, the way the mortality rate operates can be changed to probabilistic mortality using Monte Carlo techniques (see below) for the remaining siblings. Populations with high mortality, such as fish populations, can effectively be simulated by replacing a dead super-individual through random resampling from the live portion of the population (Rose et al. 1993). The internal number  $n_s$  of the donor individual is then divided in two and the dead super-individual inherits the attributes of the donor. Thus one may keep the number of super-individuals constant while changing the number of individuals that actually are represented by each super-individual.

The aggregation in super-individuals has some obvious similarities with the structured models (Metz and Diekmann 1986; Tuljapurkar and Caswell 1997). However, the structured population models are based on partial differential equations or Leslie matrices, while the super-individual approach still maintains the same structure and representation of processes as in the IBMs discussed above. In structured models all stages are usually assumed to experience the same environment and therefore to respond similarly (Caswell 1996). The super-individual approach

is more flexible than the structured models (DeAngelis and Rose 1992), and allows a simple way of scaling IBMs to realistic fish stock abundances. Structured models and configuration models may differ in their applicability depending on the topic in question, but in cases where both approaches can be applied they tend to give similar predictions (DeAngelis et al. 1993).

### 11.2.2 The strategy vector

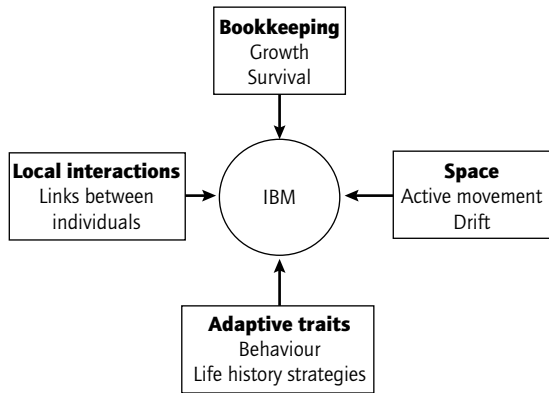
In addition to possessing states, real individuals have adaptive traits, such as life history and behavioural strategies that specify how they should live their life. The previous lack of IBM studies involving life-history strategies and behaviour of individuals could be due in part to a lack of appropriate techniques for implementing these features. However, adaptive traits can be modelled by introducing a strategy vector  $\mathbf{S}_i$  that specifies the adaptive traits, such as life-history traits or behaviour, of an individual:

$$\mathbf{S}_i = (b1_i, b2_i, b3_i, \dots, bm_i), \quad (11.4)$$

where  $bm_i$  is the adaptive trait  $m$  of individual  $i$ . The strategy vector may be considered as analogous to a biological chromosome as in the genetic algorithm (Holland 1975), but  $\mathbf{S}_i$  may also be updated during the individual's life as a way to simulate learning. For example, this can be done using reinforcement learning (e.g. Ackley and Littman 1992) by allowing rewards for advantageous behaviours and punishments for unprofitable ones. This process allows the individual to produce increasingly more favourable behaviours as it learns about its environment. The combination of attribute vectors and strategy vectors thus enables most relevant characteristics of individuals to be implemented in IBMs.

## 11.3 FEATURES OF INDIVIDUAL-BASED MODELS

IBMs can be classified by the degree to which different factors such as bookkeeping (i.e. the



**Fig. 11.1** Schematic classification of various types of IBMs. Most IBMs keep track of growth and survival of individuals in a population. Implementation of space allows a wider range of studies to be undertaken. A further increase in the complexity and flexibility of models to incorporate adaptive traits such as behaviour and life history strategies may further promote our understanding of how individuals relate to each other. The simulation of local interactions involves a high resolution both in spatial detail and behavioural actions.

continuous update of the attribute vector), space, adaptive traits and local interactions are specified in the model (Fig. 11.1). Depending on the nature and scale of the problem of interest one may develop a simple bookkeeping model, or complex models taking into account more aspects of individuals. All IBMs contain a bookkeeping procedure, but they need not contain the other features listed in Fig. 11.1. Another common feature of IBMs is to represent ecological processes by mechanistic models.

### 11.3.1 Mechanistic models

As opposed to empirically fitted models, mechanistic models aim at representing the actual process that is taking place in more detail. Thus instead of simply fitting growth rate as an empirical relationship of, for example, size, a mechanistic model of growth will address the various processes involved. These include encounters with prey (Mittelbach, Chapter 11, Volume 1), the ingestion

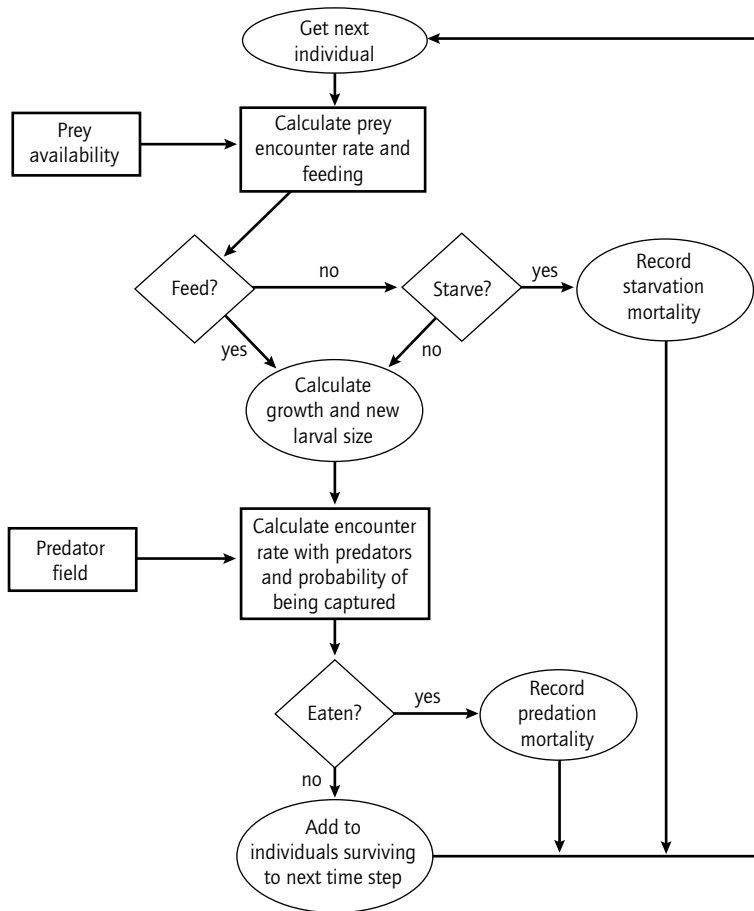
process (Juanes et al., Chapter 12, Volume 1), and bioenergetics (Jobling, Chapter 5, Volume 1). Mechanistic models are used extensively in IBMs to represent individual processes such as perception, predator and prey encounters, and bioenergetics. These are indicated by bold squares in Fig. 11.2, which shows a flow chart for events related to feeding, growth and predation of fish larvae. In addition to these individual processes, the environment is also often represented through mechanistic models of features such as light and ocean circulation. For a thorough discussion of mechanistic models in fish biology see Giske et al. (1998) and Carlotti et al. (2000).

### 11.3.2 Bookkeeping

A central aspect of IBMs is the bookkeeping of individuals. As shown above, this is facilitated using the attribute vector. The entire population is tracked using an attribute matrix with dimensions equal to the number of attributes times the number of individuals in the population. All events that may occur in a period of a time step will be addressed sequentially in the IBM, as if they appeared one by one, and it may be important to analyse the processes in a particular sequence. While an organism may be eaten after it has starved to death, it may not starve after having been eaten. The conceptual framework for bookkeeping illustrated in Fig. 11.2 is characteristic of most IBMs, which deal with growth and survival of fish. Monte Carlo simulations are continuously used to decide the outcome of feeding and mortality processes.

### 11.3.3 Monte Carlo simulations

Monte Carlo simulations are often applied in IBMs, but this approach is rarely well defined. In general, Monte Carlo techniques involve drawing random numbers from some probability distribution, in a way similar to gambling situations from which the name derives. The usual way to apply this concept in IBMs is to assume a probability for some event and then draw a number from a random-number generator to determine

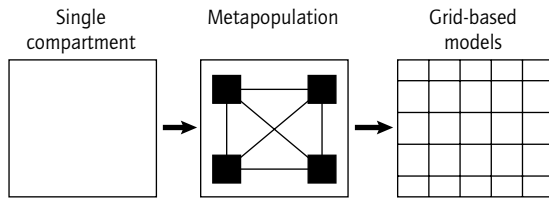


**Fig. 11.2** A conceptual model of a sequential representation of events related to growth and survival of fish larvae. The same sequence of events must be repeated for every individual in the population, before starting again with the first individual in the next time step. Bold squares indicate where mechanistic models are applied and ovals indicate where bookkeeping is performed. (Modified from Crowder et al. 1992.)

the outcome (Judson 1994). For example, one might imagine a certain probability that an individual dies during a time step. A random number is then drawn, and if the random number is smaller than the mortality risk, the individual dies. Given that the random numbers are uniformly distributed, the probability of drawing a number within an interval is equal to the size of the interval. If the mortality risk is 0.1, there is a 10% probability that the random number will be between 0 and 0.1, and a similar probability of dying. This can be carried out to determine whether an individual survives, eats food or obtains mating and so forth.

### 11.3.4 Spatial detail

Traditional ecological models specify space as a homogenous well-mixed compartment (Fig. 11.3). In metapopulation models, space is implemented as habitable patches surrounded by non-habitable areas (Levins 1969). Metapopulation models have been applied to some problems in fisheries science, for example to explain population structuring in herring stocks (McQuinn 1997). A still finer spatial resolution is to arrange space in two- or three-dimensional grids where essentially any spatial scale can be represented (Fig. 11.3). IBMs can be used in all these spatial arrangements.



**Fig. 11.3** Different ways of representing spatial detail in models. The complexity in spatial representation increases in the direction of the arrows.

The development of IBMs has made it possible to implement space in ecological models in a more realistic manner than structured models allow. Grid models have been extensively applied in fisheries science for studies of the distribution of eggs and larvae (Bartsch et al. 1989; Werner et al. 1996). An example of how such models are set up is provided below.

#### Recipe for simulating drift of larval fish

The flow chart in Fig. 11.2 does not contain any decisions made by the organism. This situation may be relevant for the planktonic larval stages. Spatial positioning of fish during this life stage is determined by their buoyancy, the turbulence of the environment and the advective transport of water. In lakes, however, the impact of advective forces is much smaller than in the sea and in rivers, where larval drift is an integrated part of the life cycle of many fishes. Although assuming a spatially homogenous compartment may be a reasonable simplification for some lakes, it is generally not so for ocean systems.

Models for marine fishes have therefore increasingly been developed to incorporate advective fields and temperature data from ocean circulation models (Bartsch et al. 1989; Werner et al. 1996). These models are grid based with a resolution typically of 1–20 km. Physical ocean circulation models provide current velocity vectors for each grid cell at each time step. These vectors are used to move individuals (or ‘particles’, representing drifting biological organisms) about (e.g.

**Table 11.1** Pseudo-code for implementing spatial detail in studies of larval fish.

- 1 Create current vector from a hydrodynamic model.
- 2 Add component of active individual movement.
- 3 Integrate velocity vector over the duration of the time step to produce individual trajectories.
- 4 Find temperature, food concentration, light intensity, predator density, etc. along trajectory.
- 5 Estimate food encounter rate, predation risk, bioenergetics etc.
- 6 Find state (spatial position, physiological state, alive/starved/eaten) of organism at the end of time step.

Werner et al. 1996; Lynch et al. 1998; Asplin et al. 1999). The drift path may also be impacted by swimming of the larvae, which is then added to the physical vector (Bartsch et al. 1989; Bartsch and Knust 1994). Once the drift path of a larva is found, the temperature, food, light intensity etc. along this path can also be estimated (Table 11.1). A more thorough description of this coupling is given by Carlotti et al. (2000).

### 11.3.5 Adaptive traits

As mentioned above, the strategy vector  $S_i$  can be used to specify the adaptive traits of an individual. In some studies IBMs are simply tailored to match the life history of target species (e.g. van Winkle et al. 1993), in which case behaviour is not specified explicitly in the model, but the consequences of certain behavioural strategies for growth and mortality may still be simulated. In other cases, finding the best behavioural trait is part of the modelling exercise itself. We mainly discuss behaviour below, but life-history strategies can often be implemented in the same manner. In general three approaches prevail for specifying behaviour in IBMs: rule-based approaches, optimization, and adaptation.

#### Rule-based approaches

Even though rules may be chosen based on their evolutionary profitability, the essential part of the rule-based approach is that the rules are



provided by the modeller and that behaviour results directly from the specified rule. One example of a behavioural rule is random walk, which simply is to move individuals about in a random fashion with equal probability of going in each direction at each time step. Such a simple behavioural procedure resembles a natural situation in many cases of local searching in animals (Berg 1993). Other rule-based concepts specified in models are the use of taxis and kinesis, which specify reactions to stimuli by orientating relative to stimuli position or responding in proportion to stimuli intensity respectively (Tyler and Rose 1994).

### Optimization

The second approach to modelling behaviour is generally referred to as the 'optimization approach' (Parker and Maynard Smith 1990). This approach underlies many of the discussions of fish behaviour in Volume 1, as exemplified by Mittelbach's discussions of foraging theory in Chapter 11, Volume 1. The optimization approach in behavioural ecology is ultimate, based directly on the survival value of behavioural traits. Stochastic dynamic programming (SDP) (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000), where the entire solution space is sought and the best solution is chosen, is an example of the optimization approach. SDP relates to states rather than individuals and the optimal strategy is calculated for each state (for example, weight or energy level) at each time step in a backward iteration. This allows state variability and state-specific behaviour to emerge. Once the backward iteration procedure is complete, an IBM can be used to simulate individual trajectories from the start to the horizon of the model. SDP models may use Monte Carlo simulations for determining growth and reproduction, which makes this approach individual-based (Clark and Mangel 2000). Traditionally, population growth rates such as the instantaneous rate of increase  $r$  or the lifetime reproductive success  $R_0$  have been applied as fitness measures in optimization models (Roff 1992; Hutchings, Chapter 7, Volume 1). These measures

are well suited for situations where the entire lifespan of the animal is considered. However, it is more difficult to assess the profitability of behaviours at an instant. Solutions to this problem can be achieved using 'rules of thumb' that are generated as predictions from evolutionary ecology, such as the ideal free distribution (Fretwell and Lucas 1970), the marginal value theorem (Charnov 1976) and Gilliam's rule (Werner and Gilliam 1984). These concepts are applied to foraging and to habitat choice by Mittelbach (Chapter 11, Volume 1). Given the assumptions, these approaches will provide optimal solutions to the respective behavioural problems.

### Adaptation

Adaptive models find 'good' behavioural strategies by using gradual improvements in behaviour through simulated evolution or learning. When simulating evolution, the behavioural strategies are coded numerically on the strategy vector (equation 11.4) and passed on from parents to offspring. This technique is known as the genetic algorithm (GA) (Holland 1975). In the GA a specific measure of fitness such as  $R_0$  can be used to determine which strategy vectors and hence which individuals are the best, and these become parents for the new generation. Variability in the new strategy vectors are provided through recombinations among parents, and mutations (Holland 1975). As mentioned above, reinforcement learning can be used to update behaviours within the lifetime of the individual (Ackley and Littman 1992). This approach can also be used in combination with evolved strategies (Ackley and Littman 1992). When the environment changes markedly on a short time-scale, for example within generations, it can be profitable to allow adaptation through learning. In an artificial neural network (ANN) model this would mean that the weights are changed within the life of individuals, and not only between different generations. Artificial neural networks (ANNs) apply neurobiological principles of synaptic brain activity to perform systematic output by differential weighting of input variables (Rummelhart et al. 1986).

**Table 11.2** Recipe for incorporating behaviour and spatial detail in an IBM of a planktivorous fish. The pseudo-code illustrates how the model is executed in a sequential manner, using a programming language such as FORTRAN.

---

1	Initiate attribute and strategy vectors for each individual
2	Year loop
	Create physical environment for the entire year: light, temperature, currents
	Initiate food and predator distribution
3	Day loop
	Update distribution and abundance of food, competitors and predators
4	Individual loop
	Perform behavioural actions
	Determine growth and mortality
	Update abundance of food items after feeding
	Reproduce if criteria are fulfilled

---

An alternative approach for evolving behaviour in models is to use so-called emergent (endogenous) fitness, which means that individuals with strategy vectors live and reproduce in an evolving population (Strand et al. in press). Thus rather than maximizing a specific fitness measure, those individuals who manage to pass on their own strategies by reproducing with other individuals in the population will be the most fit. However, the degree to which this reflects a natural system depends upon the way the environment is specified in the particular model system. For applications of adaptive models in ecology see below and Huse and Giske (1998), Huse et al. (1999), and Strand et al. (in press).

#### Recipe for adaptive models with a strategy vector

IBMs containing both spatial detail and behaviour are generally very complex, since they often involve a range of mechanistic models for specifying temperature, drift, feeding and behaviour. The following recipe describes the conceptual flow of a model containing both attribute and strategy vectors and spatial detail. It is based on the model of Huse (1998) and Huse and Giske (1998), where fish behaviour and life history strategies for a plankti-

vorous fish are adapted over many consecutive generations (Table 11.2).

**1** The attribute and strategy vectors are initialized for each individual in the population. While the attribute vectors are set to 'common' values, the strategy vectors are initiated randomly within certain intervals. The attribute vector is specified as:  $A_i$  (age, weight, energy level, position), and the corresponding strategy vector is:  $S_i$  (timing of spawning, spawning location, energy allocation rule, size at maturity, movement). Movement behaviour is determined using an ANN and its weights are implemented in the strategy vector.

**2** At the start of the year the environment for the coming year is established. As in the previous recipe, temperature and current fields are produced by an ocean circulation model. The predator abundance is assumed to increase linearly with increasing temperature. The food distribution is initiated and is consistently updated below.

**3** The day loop runs over each day of the year, and, most importantly, the food distribution is updated according to the production and import from advective transport provided by the physical model.

**4** In the individual loop most of the biological features of the IBM are implemented. The first task is to infer mortality. Since the model uses the super-individual approach, a proportion of the number of clones is removed according to the predation risk at the present location. In the same fashion one may include removal of fish caused by fishing mortality. Food intake is determined from local encounters with food, and growth is then calculated using the bioenergetic model of Hewett and Johnson (1992). For adults, surplus energy is divided among growth and reproduction according to the individual allocation strategy. Juveniles, on the other hand, are assumed to put all their energy into growth. At an individually specified spawning time and location, individuals may reproduce given that certain criteria are fulfilled. The new individuals inherit behavioural and life history strategies from their parents by recombination with a probability for mutations, to mimic biological reproduction. These are essential parts of the genetic algorithm. At the end of the individual loop, movement is determined using the ocean



drift for the planktonic larvae (see recipe above) or the ANN for fish above a certain size. The ANN calculates movement from information about the local abundance of predators, growth, temperature and position.

These points make up the basic structure of a spatial life-history model of fish. The model is run for a large number of years (300–500) and generates life-history and migration strategies that resemble observed migration patterns (Huse 1998). Although the example is for capelin migrations in the Barents Sea, the model approach is general and can be applied to virtually any fish stock. It has also been applied successfully for simulating vertical migration in mesopelagic fish (Huse et al. 1999; Strand et al. in press).

#### **What is the best modelling approach?**

What type of model is ‘best’ for implementing adaptive traits, or which one of these techniques should one use? The answer is, as often – ‘it depends’. For a full discussion of individual-based techniques see Tyler and Rose (1994) and Giske et al. (1998). Some general recommendations emerge from the discussion above. In terms of specification of adaptive traits in IBMs, the strategy vector and the adaptation concept is appealing in many ways. The advantage of this concept is its generality because it can encompass most ecological processes including density dependence, state dependence and stochastic environments (Huse et al. 1999; Strand et al. in press). Furthermore, when using ANNs it is possible to simulate behaviour from stimuli, thereby allowing the use of conventional behavioural terminology and perspective. The downside of the adaptive approach is that it is impossible to know whether the optimal solution is found unless this is calculated by other means. This is, however, ensured using optimality models such as SDP, which is one of the great advantages of that approach. Another advantage of SDP is the ability of this technique to include individual state and time constraints in the optimization criterion. A conclusion can therefore be that if the biological question involves state dependence or making sure that the optimal strategy is found, then SDP should be used. On the other hand, if the study

involves problems that have high dimensionality and/or include stochasticity or density dependencies, then the adaptive models will be the best approach. If one is interested in how large-scale patterns and/or complex phenomena emerge from individual behaviour, it can be productive to apply simple behavioural rules.

### **11.3.6 Local interactions**

In some cases, for example in fish schooling (Reynolds 1987; Vabø and Nøttestad 1997; Stöcker 1999), behaviour is dependent mainly upon what conspecifics and predators in the vicinity are doing. A simple modelling approach that takes local interactions into account is cellular automata (for review see Phipps 1992). Under this approach, the modeller defines strict rules that are similar for each individual cell in a lattice. The rules then specify how the automata change state according to the state of their surrounding cells. The emerging pattern of the lattice then results from the local interactions among the automata.

## **11.4 FORMULATING AND TESTING IBMS**

### **11.4.1 Model formulation**

Since IBMs typically are built from an extensive set of submodels, there are many things that can go wrong during model formulation. It is therefore important to develop a common framework for putting together IBMs. Railsback (2001) provides six points that should be considered when formulating an IBM: (1) Emergence: what processes should be imposed by empirical relations and what should emerge from mechanistic representations? (2) Adaptive traits: what kind of adaptive processes should be included in the model? This point has to be related to the spatial scale and the major questions being addressed. (3) Fitness measure: what is the appropriate fitness measure for the adaptive traits of the model? (4) State-based dynamics: how should decision processes depend on individual state? (5) Prediction: what are realistic assumptions about how animals predict the consequences

of decisions? (6) Computer implementation: what user interface is necessary for implementing, validating and testing IBMs? In addition to these points it is important to provide results that can be tested against observations. Although testing against real data is not always necessary, since models may provide valuable insight through sensitivity analyses, it is most often an advantage in model development. The points shown above are important to keep in mind when constructing an IBM, and we shall return to some of these as we go along. Other things to keep in mind when formulating a model are that the choice of complexity and model structure should be based on the level of understanding of the environmental and biological processes operating. Lastly a model is at best a highly simplified but biased representation of nature, and uncertainty can be reduced by attacking the problem with several models that differ in assumptions and structure (see also Sparre and Hart, Chapter 13, this volume).

### 11.4.2 Evaluation of IBMs

Model evaluation is an important part of model development, and for full descriptions of this process see Jørgensen (1988) and Bart (1995). The evaluation process can be divided into verification and validation (Jørgensen 1988). Verification is the process of checking that the internal logic of the computer model is correct and that the model actually does what it is intended to do. This process is performed continuously as a model is developed. Validation, on the other hand, aims at determining the ability of the model in describing observed phenomena. This process can be divided further into checking the validity of: parameter values, and secondary and primary model predictions (Bart 1995). The validity of parameter values is traditionally tested through a sensitivity analysis. Sensitivity analyses involve varying parameter values and studying the effect on model output. For IBMs, which usually have a great number of parameters, it is simply not feasible to test the sensitivity of all these. Rather some 'key' parameters should be chosen for testing. Since IBMs tend to be composed of submodels, many features of an IBM can be tested. This is what is referred to as sec-

ondary model predictions. With regard to a fish model this can be, for example, testing the performance of a bioenergetic model used, even though the primary aim of the model is to provide population dynamics of a target species. The primary and secondary model predictions can then be tested independently of each other. A consequence of model evaluation is either to accept the model's performance or, alternatively, to try to revise parts of the model that produce erroneous predictions. One should, however, be careful not to make the model fit observations by changing parameter values or submodels uncritically. This is especially important for IBMs, which typically simulate processes in a mechanistic manner using a large number of parameter values.

When it comes to software implementation, any kind of programming language can be used, but object-orientated languages such as C++ are especially well suited for constructing IBMs (Maley and Caswell 1992). In addition to providing a nice structured programming with individuals as the basic units, these languages generally also provide good visualization opportunities. For example, the object-orientated Swarm package (Langton et al. 1999) is tailored for individual-based simulations and provides a number of features for visualization of results and bookkeeping of individuals and processes. Using Swarm, several aspects of the model may be monitored during development and evaluation. Swarm, which is a shareware product, is currently available for the Objective C and Java languages. Another software package especially developed for individual-based simulations is ECOSIM (Lorek and Sonnenschein 1998). This is not the same as the Ecosim discussed by Pauly and Christensen (Chapter 10, this volume).

## 11.5 REVIEW OF INDIVIDUAL-BASED MODELS IN FISHERIES BIOLOGY

The ontogenetic development in fishes from eggs to maturity typically involves manyfold increases in body size associated with discrete changes in morphology and increased behavioural repertoires. The way individuals vary therefore changes

**Table 11.3** Features characterizing different aspects of the early life history of fish.

What characterizes . . .	Variables	References
the survivors?	egg quality birth date birth position egg size development prey encounter bioenergetics	Kjesbu et al. (1991) Schultz (1993) Berntsen et al. (1994); Slotte and Fiksen (2000) Knutsen and Tilseth (1985) Blaxter (1986) Fiksen and Folkvord (1999) Crowder et al. (1992); Fiksen and Folkvord (1999)
the environment?	food concentration small-scale turbulence water transportation ocean climate light turbidity temperature predators	Cushing (1990); (1996) Sundby and Fossum (1990); MacKenzie et al. (1994) Bartsch et al. (1989); Berntsen et al. (1994); Hermann et al. (1996) Cushing (1996); Anderson and Piatt (1999) Miner and Stein (1993); Fiksen et al. (1998) Chesney (1989); Fortier et al. (1996) Houde (1989); (1997) McGurk (1986); Bailey and Houde (1989); Cowan et al. (1996)

through the life cycle. This suggests that modeling should focus on different aspects of life at different times of the life cycle, and that each ontogenetic stage might be specified differently. For example, in the period of change from intrinsic to extrinsic energy uptake, each prey caught by a larval fish is very important, which makes food gathering a vital process to simulate in models. During overwintering or spawning, on the other hand, feeding will be a virtually unimportant activity. In the following we will review studies using IBMs in fish biology by using the structure of Fig. 11.1. Hence we initially discuss relatively simple models, and then add features to the IBMs as we go along. The first paragraph therefore focuses on growth and survival in early life-history studies, whereas the later paragraphs discuss studies of greater relevance to older life stages.

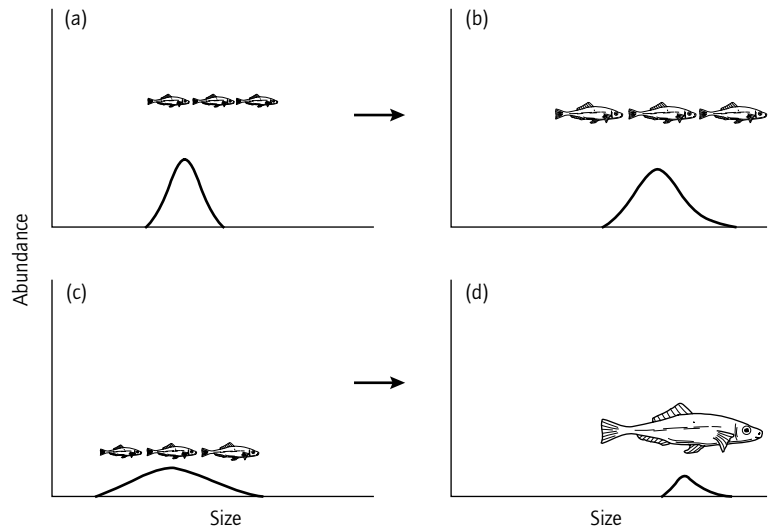
### 11.5.1 Models of growth and survival

For most, if not all, fish species, mortality at the egg and early larval stages is enormous compared to later in life. Therefore, as early as 1914, Hjort

considered recruitment variation as a major research area in fisheries science (Myers, Chapter 6, Volume 1). Recruitment variation may be caused by factors related to the state of the organism, its environment or its parents (Table 11.3; see Myers, Chapter 6, Volume 1). IBMs allow a mechanistic representation of ecological processes, and consequently such models have been applied extensively in studying growth and survival of young-of-the-year fish (see review by van Winkle et al. 1993). Beyer and Laurence (1980) recognized the importance of initial chance events in feeding of larval winter flounder. Since prey ingestion can be described as a Poisson process, some individuals will initially have success and capture prey while others have poor fate. Given that the ability to obtain food is size dependent (Juanes et al., Chapter 12, Volume 1), there will be a positive feedback so that initially successful individuals will grow faster than the others and thus have a higher survival probability. Such scenarios are well represented in IBMs (Beyer and Laurence 1980).

The important survival factors for eggs and larvae are prey and predator encounters, bioener-

**Fig. 11.4** The effect of initial variation in size distribution on the outcome of cannibalistic interactions. Low initial variance (a) produces a cohort with homogeneous individuals at a later stage (b), while with a high initial variance (c) the biggest individuals get cannibalistic (d). (From Huston et al. 1988; reproduced by permission of BioScience.)



genetics and organismal development. With so many factors interacting, modelling is essential in understanding how this affects individuals and populations (Houde 1997). And since egg and larval mortality are high, models of survival should be able to focus on the lucky or clever few. The important decision variables are mainly governed by parent behaviour through choice of spawning site and time, anatomical properties such as egg size and energy density, and by developmental 'programme' displayed through the sequence of organ development (Jobling, Chapter 5, Volume 1). A range of ecological conditions will bring stochasticity to all these variables (Table 11.3). The reliability of predictions from a complex recruitment model will depend on how well these processes are represented mechanistically (Fiksen and Folkvord 1999). In a classic study, DeAngelis et al. (1979) modelled the growth of young-of-the-year largemouth bass. They found that the initial variance in the cohort was important for its development and for whether cannibalism was possible or not. In the case of low initial variance, shown by an even size distribution (Fig. 11.4a), the fish remained homogeneous with none growing big enough to eat the others (Fig. 11.4b). With large initial variance (Fig. 11.4c), however, the individuals that had largest

initial size were able to become cannibalistic and eat the smaller fish, which the model run predicted to lead to survival of few but large individuals (Fig. 11.4d). It was demonstrated that the individual variability is clearly important for cohort development even though the initial average weight was the same in the two cases. The model presented by Fiksen and Folkvord (1999) provides a state-of-the-art mechanistic description of the feeding process taking into account environmental features such as small-scale turbulence, light, turbidity, temperature, prey density and size structure. Alongside the model development there has been experimental work used for generating parameter values and testing of model predictions. The great detail of the mechanistic description enables this model to make more realistic predictions than models with simpler environmental description.

### 11.5.2 Models with adaptive traits

The simplest behavioural models are those without spatial detail. There have been some studies addressing how spawning strategies are affected by seasonal variation in temperature, growth and predation risk. Trebitz (1991) used an IBM to find the best timing and temperature for spawning with

and without density dependence. Initially the spawning temperature was given randomly, but subsequent spawning strategies (temperature) were given in proportion to the survival of the strategies (individuals) until age 1. The biomass of each temperature strategy at age 1 was therefore used as a measure of strategy performance. Density-independent and density-dependent model runs predicted different optimal spawning temperatures, with a broad peak at intermediate temperatures for the density-independent situation and an almost temperature-independent profitability for the density-dependent case. This model is in many ways similar to the genetic algorithm discussed above.

### **11.5.3 Simple spatial systems**

Natural systems are very complex. It may therefore be profitable to conduct simulation experiments, which is a computer analogy to laboratory or field experiments, in which focus can be put on a specific research topic without necessarily defining a particular natural system. A simulation experiment is especially fruitful early in theoretical developments or if the problem is general rather than linked to a specific population or environment. Tyler and Rose (1997) studied cohort consequences of different habitat choice rules in a simple spatial system using life-history-based criteria such as Gilliam's rule. Their results suggest that habitat choice rules have strong effects on cohort survivorship and that no single departure rule can be an evolutionarily stable strategy. They therefore concluded that the use of static life-history rules is not an appropriate way to model behaviour in a dynamic environment, as confirmed elsewhere (Railsback et al. 1999). Tyler and Rose (1997) also found that density-dependent effects on juvenile survival can be much greater in spatially explicit models with fitness-based habitat choice than in spatially homogeneous models. SeaLab (LePage and Cury 1997) is a spatial simulator that can be used to test hypotheses about fish reproduction and space use. This model divides space into hexagonal structures, and individuals may choose in which

cell to stay and/or reproduce. LePage and Cury (1997) used SeaLab to simulate how reproductive strategies depended on the degree of variation in variable environments. An obstinate strategy, where spawning is performed under the same conditions as the individual is born, and an opportunistic strategy where individuals spawn under novel environmental conditions, were investigated. For extreme environmental variation, only populations with both the opportunistic and obstinate strategies survived. The authors discuss the results with regard to straying in natural populations. A similar artificial environment was applied by Anneville et al. (1998), who explored the effect of density-dependent recruitment relationships using rule-based movement in an hexagonal lattice. Their main conclusion was that local density dependence was often not detectable at large spatial scales, which stresses the importance of being explicit about scale when analysing ecological processes (Levin 1992).

### **11.5.4 Models of fish distribution**

Spatially explicit IBMs incorporate spatial heterogeneity, individual variability and individual movement (Tyler and Rose 1994). Although such models are complicated and necessarily consist of many modules, they provide the potential for highly realistic simulations of fish populations. Many fishes undertake extensive horizontal migrations between feeding, spawning and overwintering areas (Metcalfe et al., Chapter 8, Volume 1). Such migrations involve complex interactions between individuals and the environment that are generally not well understood. Tagging experiments have provided first-hand information about the distribution of migratory fish stocks, and lately telemetric tags have enabled real-time observations of fish movements in the sea (Metcalfe and Arnold 1997; Metcalfe et al., Chapter 8, Volume 1). However, it is difficult to understand the mechanisms controlling the movement of fish just from observations, and model simulations are therefore an important part of exploring the proximate and ultimate processes involved in fish migrations.

Although there is likely to be some common features among fish stocks in how they move horizontally, local adaptation will be important, and it may not be trivial to transfer knowledge about the migration of one stock to other stocks. In the case of vertical migration, however, there may be more common features due to the pronounced vertical gradients and diurnal changes in light that strongly influence visual feeding and predation risk.

Larval drift was among the first topics where spatially explicit IBMs were applied. Werner et al. (1996) considered trophodynamics and ocean circulation in a study of cod larvae on Georges Bank by providing drift and growth trajectories of individuals. They concluded that the region of highest retention coincided with the region of highest growth, illustrating the complementary interaction between trophodynamics and circulation processes. In a similar model of walleye pollock (*Theragra chalcogramma*), Hinckley et al. (1996) found that the inclusion of mechanisms that determine the depth positioning of the drifting larvae are important for determining the direction of horizontal advection.

Through a combination of simple decision rules and a library of surface currents, Walter et al. (1997) modelled sockeye salmon (*Onchorhynchus nerka*) movement in the Northeast Pacific Ocean. Movement was simulated based on random walk, with directed swimming at certain times of the year. Their simple rules for compass bearing predict migration patterns that challenge prevailing complex models of sockeye migration. The most striking result was that inter-annual variation in the surface current led to great changes in the distribution of the salmon given that the same movement rules apply each year. The rule-based approach used by Walter et al. (1997) does not take into account that individual differences in state can cause differences in behaviour. State-dependent habitat choice was considered by Fiksen et al. (1995), who used a stochastic dynamic programming (SDP) to simulate the horizontal distribution of the Barents Sea capelin (*Mallotus villosus*). The model was based on prior simulation results, which specify the physical environment of

the Barents Sea, and assumed distributions of predators and prey. By using a time step of one month, the optimal habitat for each state (body weight) was calculated using the SDP equations with lifetime reproductive success as a fitness criterion. The model results compared favourably with the observed distribution of the Barents Sea capelin. In contrast to Walter et al. (1997), Fiksen et al. (1995) assumed that the individual capelin actively made habitat choices to maximize their Darwinian fitness. Huse and Giske (1998) and Huse (1998) used a similar environmental description as Fiksen et al. (1995) to simulate movement of the Barents Sea capelin using an adaptive model with a strategy vector (equation 11.4) containing the weights of an artificial neural network and several life-history traits. Similarly to Fiksen et al. (1995), they assumed that the capelin is adapted to the environment of the Barents Sea. However, rather than assuming optimal habitat choices, an adaptive process over many hundreds of generations was simulated using emergent fitness (see above). The model was applied to study evolution of spawning areas, and it predicted, in accordance with field observations, capelin spawning to occur along the coast of Northern Norway. ANN-based models may rely on proximate sensor information, and at the same time the weights of the ANN are adapted using ultimate forces. In this way ANN models provide a link between proximate and ultimate factors in behavioural ecology. ANNs have also been applied to study tropical tuna (*Katsuwonus pelamis* and *Thunnus albacares*) migrations between the Mozambique Channel and the Seychelles using temperature data gathered by remote sensing (Dagorn et al. 1997). In this case the tuna was assumed to search for areas of low temperature, which are often associated with food-rich frontal zones. The ANN was used to determine which movement action the artificial tuna should make based on information about the temperature map within the daily search radius. The fitness criterion used in the GA for training the ANN was to minimize the distance to the observed arrival point near the Seychelles. As a result of the adaptive process, the simulated tuna eventu-



ally managed to get from the starting point in the Mozambique Channel to the Seychelles. In this model the tuna is assumed only to consider foraging potential when making habitat choices and not to consider predation, as in the two studies on capelin mentioned above. Nevertheless, because adult tuna are large they tend to have a low risk of predation compared with smaller fish, and foraging is therefore the key aspect of tuna migrations outside the spawning season.

### 11.5.5 *Local interactions: schooling*

Schooling consists of behaviours where coordination between individuals is important. As different from more loosely organized shoals, schools are defined as compact, coordinated and polarized collections of fish (Pitcher and Parrish 1993; Krause et al., Chapter 13, Volume 1). Schooling is a characteristic phenomenon of many fishes, explained mainly as a behavioural feature for predatory defence, but it also acts as a collective mechanism for coordinating migration and reproduction (Pitcher and Parrish 1993). Even though the ultimate causes of schooling are well known, the sensory and behavioural mechanisms involved in coordination and control of schooling remain largely unresolved. Schooling relies on the coordinated movement of individuals, and school models are usually based on the assumption that individuals follow similar behavioural rules, as opposed to most IBMs which allow individual variability. Reynolds (1987) simulated general flocking behaviour, which includes schooling, in a seminal paper on collective behaviour. He showed that by using three simple individual rules, including matching of the movement vector of neighbours, staying close to others, and avoiding contact with other individuals and obstacles, flocking behaviour that resembles observations of birds could be recreated. Vabø and Nøttestad (1997) used a similar rule-based IBM to simulate the behaviour of herring schools (*Clupea harengus*) when attacked by a killer whale (*Orcinus orca*). The model was able to recreate most of the avoidance manoeuvres seen in herring, and the results thus suggest that herring may use simple rules

to coordinate their behaviour during predator attacks.

Stöcker (1999) used cellular automata to study energetic aspects of schooling. The results were discussed with regard to tuna, for which saving energy is believed to be an important motivation for school formation. The model predicts school break-ups due to oxygen depletion, and can thus be used to estimate maximum school sizes for tuna. Both Vabø and Nøttestad (1997) and Stöcker (1999) assumed identical rules for each individual. Romey (1996), on the other hand, in another schooling model showed that individuals with biased behaviour compared with the remaining group had a large influence on school behaviour. The degree to which individual differences in behaviour impacts school dynamics may be a function of school size, with a greater impact of individual variability in small schools. The cellular automata technique is well suited for simulating the dynamics of schools with similar individual behaviour, but the IBM models developed by Reynolds (1987) and Vabø and Nøttestad (1997) are more applicable than cellular automata if individual differences in behaviour are believed to be important. For a general discussion of predictions made by cellular automata and a conventional IBM respectively see Lett et al. (1999).

### 11.5.6 *Responsive environments and natural stock sizes*

Most of the models above describe individuals in non-responsive environments. This means that individuals are not assumed to impact on their environment, which is unrealistic when density dependence is important. Huse and Giske (1998) applied the super-individual approach to model long-distance migration of the Barents Sea capelin. The number of super-individuals was limited to a maximum of 15 000, and at birth each super-individual represented one million identical siblings. Depletion of zooplankton from feeding and consequent relocation is important for understanding capelin distribution dynamics (Hassel et al. 1991), and by using this approach it was possi-

ble to simulate realistic stock sizes of capelin while incorporating trophic feedback. The model predicts that fish should be more dispersed in model runs with trophic feedback compared to those where food was not removed as a result of feeding by the fish, and hence illustrates the importance of including trophic feedback even at large spatial scales.

### **11.5.7 Applications of IBMs in fisheries assessment**

While structured models, such as the virtual population analysis and related approaches, are common in fisheries assessment, IBMs have not been used for this purpose to any degree. Most applications of IBMs have focused on ecological questions of general interest with the aim of exploring how individual variability in state and strategies influence the dynamics at the population level. Improved understanding of the causes of temporal and spatial variation in mortality, growth and recruitment, but also of migration and distribution patterns, has been achieved. Along with the ongoing increase in computing power, new possibilities for individual-based approaches to management problems of fish populations can be possible. In order for IBMs to be used for management purposes it will be essential that the IBMs are robust and reliable with regard to structural assumptions, parameter values, primary and secondary model predictions (Bart 1995). These factors reflect the general recommendations for formulating and evaluating IBMs as discussed above. IBMs have been applied to some degree in combination with bioenergetics models for management purposes (Hansen et al. 1993). IBMs can also be fruitful for management purposes in at least four other areas: (1) in predicting stock recruitment, (2) predicting the response of different exploitation patterns on the stock, (3) by facilitating the abundance estimation process and (4) through estimating stock prognoses in spatially explicit models.

Detailed IBMs (e.g. Fiksen and Folkvord 1999) can be used to elucidate which processes control recruitment to a target stock. For example, it may

be profitable to use models that simulate both the dynamics of the parents as well as those of the recruiting larvae. Such models potentially may yield early forecasts of stock recruitment, which is part of the management process.

Since different age and size groups of fish often exhibit different behaviours, spatial dynamics and reproductive capabilities, they impact the stock dynamics in different ways. How fishing effort is distributed over the different size groups and spatial areas may thus affect the population response to harvest (Sparre and Hart, Chapter 13, this volume). IBMs are well suited to simulate the effects that management decisions can have both on population dynamics in the short run and on evolutionary dynamics in the longer run (Martinez-Garmendia 1998).

IBMs can also be used in fisheries assessment to facilitate the abundance estimation process, often performed by acoustics, sampling, or a combination of these. One potential application of IBMs is to predict distribution patterns of fish populations in the ocean given a certain environmental regime, which can allow improved temporal and spatial survey coverage. IBMs can also be applied to take into account the behavioural response of fish to survey vessels and sampling equipment. Diving behaviour and changes in tilt of fish can strongly impact on its echo-reflecting properties from the swim bladder of the fish (Huse and Ona 1996; Brix, Chapter 4, Volume 1), and hence impact on the acoustic estimate obtained. If such behaviours can be predicted and corrected for, the quality of acoustic estimates may be improved. This can be approached using ANNs, where observations of fish behaviour can be used to train the network. By presenting many sets of observed behaviours and relation to the vessel such as angle, depth and distance, the network can be trained using these observations to generalize responses of fish to vessel presence. The response to trawls and other sampling equipment can be simulated in a similar fashion.

IBMs can also be used to predict population dynamics of stocks through spatially explicit models covering the entire target stock. Such models have not made an impact on stock assessment. How-

ever, it can be a potential future application area of IBMs, and the modelling approaches of Fiksen et al. (1995) and Huse and Giske (1998) are attempts to move in this direction.

## 11.6 CONCLUSIONS

Even though IBMs are yet to have made an impact on fisheries management, the modelling technique has become especially popular among fish biologists (Grimm 1999). The reason for this popularity is partly historical, as some of the first applications of IBMs (DeAngelis et al. 1979; Beyer and Laurence 1980), were in fish biology. But as important is the great interest in explaining the observed recruitment variability seen in most fish species (Grimm 1999). IBMs are particularly useful for studying recruitment variability, but in addition the approach allows features such as behaviour and life histories to be studied as discussed above. IBM predictions are generally easy to compare with individual observations, which is another advantage of the approach. The use of super-individuals (Scheffer et al. 1995) allows simulation of realistic fish stock abundances while maintaining an individual-based modelling structure. IBMs are often very complex and composed by many submodels. Model evaluation is therefore very important, and preferably both primary and secondary model predictions should be validated (Bart 1995). Whether or not IBMs really give different answers to ecological problems than do the traditional state-variable models remains to be seen, but nevertheless, IBMs provide modellers with a highly flexible tool for studying individuals and populations.

## ACKNOWLEDGEMENTS

We thank Steve Railsback and David Kirby for fruitful comments on an earlier draft of this chapter. Anne Gro Veia Salvanes and Geir Huse were supported by the Research Council of Norway.

## REFERENCES

- Ackley, D. and Littman, M. (1992) Interactions between learning and evolution. In: C. Langton, C. Taylor, J. Farmer and S. Rasmussen (eds) *Artificial Life III*. Reading, MA: Addison-Wesley, pp. 487–509.
- Anderson, P.J. and Piatt, J.F. (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* **189**, 117–23.
- Anneville, O., Cury, P., LePage, C. and Treuil, J.P. (1998) Modelling fish spatial dynamics and local density-dependence relationships: detection of patterns at a global scale. *Aquatic Living Resources* **11**, 305–14.
- Asplin, L., Salvanes, A.G.V. and Kristoffersen, J.B. (1999) Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. *Fisheries Oceanography* **8**, 255–63.
- Bailey, K.M. and Houde, E.D. (1989) Predation on the eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* **25**, 1–83.
- Bart, J. (1995) Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications* **5**, 411–20.
- Bartsch, J. and Knust, R. (1994) Simulating the dispersion of vertically migrating sprat larvae (*Sprattus sprattus* L.) in the German Bight with a circulation and transport model system. *Fisheries Oceanography* **3**, 92–105.
- Bartsch, J., Brander, K., Heath, M., Munk, P., Richardson, K. and Svendsen, E. (1989) Modelling the advection of herring larvae in the North Sea. *Nature* **340**, 632–6.
- Berg, H.C. (1993) *Random Walks in Biology*. Princeton, NJ: Princeton University Press.
- Berntsen, J., Skagen, D.W. and Svendsen, E. (1994) Modeling the drift of particles in the North Sea with reference to sandeel larvae. *Fisheries Oceanography* **3**, 81–91.
- Beyer, J.E. and Laurence, G.C. (1980) A stochastic model of larval fish growth. *Ecological Modelling* **8**, 109–32.
- Blaxter, J.H.S. (1986) Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society* **115**, 98–114.
- Carlotti, F., Giske, J. and Werner, F. (2000) Modeling zooplankton dynamics. In: R. Harris, P. Wiebe, J. Lenz, H.R. Skjoldal and M. Huntley (eds) *ICES Zooplankton Methodology Manual*. London: Academic Press, pp. 571–667.
- Caswell, H. and John, A.M. (1992) From the individual to population in demographic models. In: D.L. DeAngelis and L.J. Gross (eds) *Individual-based Models and Approaches in Ecology*. New York: Chapman & Hall, pp. 36–66.

- Caswell, H. (1996) Matrix methods for population analysis. In: S. Tuljapurkar and H. Caswell (eds) *Structured Population Models in Marine, Terrestrial, and Freshwater Systems*. New York: Chapman & Hall.
- Chambers, R.C. (1993) Phenotypic variability in fish populations and its representation in individual-based models. *Transactions of the American Fisheries Society* **122**, 404–14.
- Charnov, E.L. (1976) Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**, 129–36.
- Chesney, E.J. (1989) Estimating the food requirements of striped bass larvae *Morone saxatilis*: effects of light, turbidity and turbulence. *Marine Ecology Progress Series* **53**, 193–200.
- Clark, C.W. and Mangel, M. (2000) *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford: Oxford University Press.
- Cowan, J.H., Houde, E.D. and Rose, K.A. (1996) Size-dependent vulnerability of marine fish larvae to predation: An individual-based numerical experiment. *ICES Journal of Marine Science* **53**, 23–37.
- Crowder, L.B., Rice, J.A., Miller, T.J. and Marschall, E.A. (1992) Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. In: D.L. DeAngelis and L.J. Gross (eds) *Individual-based Models and Approaches in Ecology*. New York: Chapman & Hall, pp. 237–55.
- Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* **26**, 249–93.
- Cushing, D.H. (1996) Towards a science of recruitment in fish populations. In: O. Kinne (ed.) *Excellence in Ecology*, vol. 7. Oldendorf/Luhe: Ecology Institute.
- Dagorn, L., Petit, M. and Stretta, J.M. (1997) Simulation of large-scale tropical tuna movements in relation with daily remote sensing data: the artificial life approach. *Biosystems* **44**, 167–80.
- Darwin, C. (1859) *The Origin of Species*. [1968], New York: Penguin Books.
- DeAngelis, D.L. and Gross, L.J. (eds) (1992) *Individual-based Models and Approaches in Ecology*. New York: Chapman & Hall.
- DeAngelis, D.L. and Rose, K.A. (1992) Which individual-based approach is most appropriate for a given problem? In: D.L. DeAngelis and L.J. Gross (eds) *Individual-based Models and Approaches in Ecology*. New York: Chapman & Hall, pp. 67–87.
- DeAngelis, D.L., Cox, D.C. and Coutant, C.C. (1979) Cannibalism and size dispersal in young-of-the-year largemouth bass: experiments and model. *Ecological Modelling* **8**, 133–48.
- DeAngelis, D.L., Rose, K.A., Crowder, L.B., Marshall, E.A. and Lika, D. (1993) Fish cohort dynamics – application of complementary modelling approaches. *The American Naturalist* **142**, 604–22.
- Fiksen, Ø. and Folkvord, A. (1999) Modelling growth and ingestion processes in herring *Clupea harengus* larvae. *Marine Ecology Progress Series* **184**, 273–89.
- Fiksen, Ø., Giske, J. and Slagstad, D. (1995) A spatially explicit fitness-based model of capelin migrations the Barents Sea. *Fisheries Oceanography* **4**, 193–208.
- Fiksen, Ø., Utne, A.C.W., Aksnes, D.L., Eiane, K., Helvik, J.V. and Sundby, S. (1998) Modeling the influence of light, turbulence and development on foraging in larval cod and herring. *Fisheries Oceanography* **7**, 355–63.
- Fortier, L., Gilbert, M., Ponton, D., Ingram, R.G., Robineau, B. and Legendre, L. (1996) Impact of fresh water on a subarctic coastal ecosystem under seasonal ice (southeastern Hudson Bay, Canada): III. Feeding success of marine fish larvae. *Journal of Marine Systems* **7**, 251–65.
- Fretwell, S.D. and Lucas Jr, H.J. (1970) On territorial behavior and other factors influencing habitat distributions in birds: 1. Theoretical development. *Acta Biotheoretica* **19**, 16–36.
- Giske, J., Huse, G. and Fiksen, Ø. (1998) Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries* **8**, 51–91.
- 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**, 129–48.
- Hansen, M.J., Boisclair, D., Brandt, S.B., Hewett, S.W., Kitchell, J.F., Lucas, M.C. and Ney, J.J. (1993) Applications of bioenergetics models to fish ecology and management – where do we go from here? *Transactions of the American Fisheries Society* **122**, 1019–30.
- Hassel, A., Skjoldal, H.R., Gjøsæter, H., Loeng, H. and Omli, L. (1991) Impact of grazing from capelin (*Mallotus villosus*) on zooplankton: a case study in the northern Barents Sea in August 1985. *Polar Research* **10**, 443–60.
- Hermann, A.J., Hinckley, S., Megrey, B.A. and Stabeno, P.J. (1996) Interannual variability of the early life history of walleye pollock near Shelikof Strait as inferred from a spatially explicit, individual-based model. *Fisheries Oceanography* **5**, 39–57.
- Hewett, S.W. and Johnson, B.J. (1992) *An Upgrade of a Generalized Bioenergetics Model of Fish Growth for Microcomputers*. University of Wisconsin, Wisconsin Sea Grant College Program, Sea Grant Technical Report, WIS-SG-92-250, Madison.

- Hinckley, S., Hermann, A.J. and Megrey, B.A. (1996) Development of a spatially explicit, individual-based model of marine fish early life history. *Marine Ecology Progress Series* **139**, 47–68.
- Hjort, J. (1914) Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **20**, 1–28.
- Holland, J.H. (1975) *Adaptation in Natural and Artificial Systems*. Ann Arbor: University of Michigan Press.
- Houde, E.D. (1989) Comparative growth, mortality and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin* **87**, 471–95.
- Houde, E.D. (1997) Patterns and consequences of selective processes in teleost early life histories. In: R.C. Chambers and E.A. Trippel (eds) *Early Life History and Recruitment in Fish Populations*, Fish and Fisheries Series 21. London: Chapman & Hall.
- Houston, A.I. and McNamara, J.M. (1999) *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.
- Huse, G. (1998) Life history strategies and spatial dynamics of the Barents Sea capelin (*Mallotus villosus*). PhD, thesis, University of Bergen.
- Huse, G., Strand, E. and Giske, J. (1999) Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* **13**, 469–83.
- Huse, G. and Giske, J. (1998) Ecology in Mare Pentium: an individual based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* **37**, 163–78.
- Huse, I. and Ona, E. (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES Journal of Marine Science* **53**, 863–73.
- Huston, M., DeAngelis, D.L. and Post, W. (1988) New computer models unify ecological theory. *BioScience* **38**, 682–91.
- Jørgensen, S.E. (1988) *Fundamentals of Ecological Modelling*. Amsterdam: Elsevier.
- Judson, O. (1994) The rise of individual-based models in ecology. *Trends in Ecology and Evolution* **9**, 9–14.
- Kjesbu, O.S., Klungsoyr, J., Kryvi, H., Witthames, P.R. and Walker, M.G. (1991) Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body-composition. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 2333–43.
- Knutson, G.M. and Tilseth, S. (1985) Growth, development and feeding success of Atlantic cod (*Gadus morhua*) larvae related to egg size. *Transactions of the American Fisheries Society* **114**, 507–11.
- Langton, C.G., Minar, N., Burkhart, R., Askenazi, M. and Ropella, G. (1999) *The Swarm simulation system*. Web-based documentation at <http://www.swarm.org>.
- Le Page, C. and Cury, P. (1997) Population viability and spatial fish reproductive strategies in constant and changing environments: an individual-based modelling approach. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 2235–46.
- Lett, C., Silber, C. and Barret, N. (1999) Comparison of cellular automata network and an individual-based model for the simulation of forest dynamics. *Ecological Modelling* **121**, 277–93.
- Levin, S.A. (1992) The role of space in ecology. *Ecology* **73**, 1943–67.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**, 237–40.
- Łomnicki, A. (1988) *Population Ecology of Individuals*. Princeton, NJ: Princeton University Press.
- Lorek, H. and Sonnenschein, M. (1998) Object oriented support for modelling and simulation of individual-oriented ecological models. *Ecological Modelling* **108**, 77–96.
- Lynch, D.R., Gentleman, W.C., McGillicuddy, D.J. and Davis, C.S. (1998) Biological/physical simulations of *Calanus finmarchicus* population dynamics in the Gulf of Maine. *Marine Ecology Progress Series* **169**, 189–210.
- MacKenzie, B.R., Iller, T.J., Cyr, S. and Leggett, W.C. (1994) Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. *Limnology and Oceanography* **39**, 1790–9.
- Magurran, A. (1986) Individual differences in fish behaviour. In: T.J. Pitcher (ed.) *The Behaviour of Teleost Fishes*. Baltimore, MD: The Johns Hopkins University Press, pp. 338–65.
- Maley, C.C. and Caswell, H. (1992) Implementing i-state configuration models for population dynamics – an individual based approach. *Ecological Modelling* **68**, 75–89.
- Mangel, M. and Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton, NJ: Princeton University Press.
- Martínez-Garmendia, I. (1998) Simulation analysis of evolutionary response of fish populations to size selective harvesting with the use of an individual based model. *Ecological Modelling* **111**, 37–60.
- McGurk, M.D. (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Marine Ecology Progress Series* **34**, 227–42.
- McQuinn, I.H. (1997) Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries* **7**, 297–329.



- Metcalfe, J.D. and Arnold, G.P. (1997) Tracking fish with electronic tags. *Nature* **387**, 665–6.
- Metz, J.A.J. and Diekmann, O. (1986) *The Dynamics of Physiologically Structured Populations*. Berlin: Springer-Verlag.
- Miner, J.G. and Stein, R.A. (1993) Interactive influence of turbidity and light on larval bluegill (*Lepomis macrochirus*) foraging. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 781–8.
- Parker, G.A. and Maynard Smith, J. (1990) Optimality models in evolutionary ecology. *Nature* **348**, 27–33.
- Phipps, M.J. (1992) From local to global: The lessons from cellular automata. In: D.L. DeAngelis and L.J. Gross (eds) *Individual-based Models and Approaches in Ecology*. New York: Chapman & Hall, pp. 165–87.
- Pitcher, T.J. and Parrish, J.K. (1993) Functions of schooling behaviour in teleosts. In: T.J. Pitcher (ed.) *The Behaviour of Teleost Fishes*, 2nd edn. London: Chapman & Hall, pp. 364–439.
- Railsback, S.F. (2001) Concepts from complex adaptive systems as a framework for individual based modelling. *Ecological Modelling* **139**, 47–62.
- Railsback, S.F., Lamberson, R.H., Harvey, B.C. and Duffy, W.E. (1999) Movement rules for individual-based models of stream fish. *Ecological Modelling* **123**, 73–89.
- Reynolds, C.W. (1987) Flocks, herds and schools: A distributed behavioural model. *Computer Graphics* **21**, 25–34.
- Roff, D.A. (1992) *The Evolution of Life Histories*. New York: Chapman & Hall.
- Romey, W.L. (1996) Individual differences make a difference in the trajectories of simulated fish schools. *Ecological Modelling* **92**, 65–77.
- Rose, K.A., Cowan, J.H., Clark, M.E. and Houde, E.D. (1999) An individual-based model of bay anchovy population dynamics in the mesohaline region of Chesapeake Bay. *Marine Ecology Progress Series* **185**, 113–32.
- Rose, K.A., Cristensen, S.W. and DeAngelis, D.L. (1993) Individual-based modelling of populations with high mortality: A new method based on following a fixed number of model individuals. *Ecological Modelling* **68**, 273–92.
- Rummelhart, D.E., Hinton, G.E. and Williams, R.J. (1986) Learning representations by back propagating errors. *Nature* **323**, 533–6.
- Saila, S.B. and Shappy, R.A. (1969) Random movement and orientation in salmon migration. *Journal du Conseil International pour l'Exploration de la Mer* **28**, 153–66.
- Salvanes, A.G.V. and Hart, P.J.B. (2000) Is individual variation in competitive ability in juvenile cod related to haemoglobin genotype? *Sarsia* **85**, 265–74.
- Scheffer, M., Baveco, J.M., DeAngelis, D.L., Rose, K.A. and van Nes, E.H. (1995) Super individuals: a simple solution for modelling large populations on an individual basis. *Ecological Modelling* **80**, 161–70.
- Schultz, E.T. (1993) The effect of birth data on fitness of female dwarf perch, *Micrometrus minimus*. *Evolution* **47**, 520–39.
- Slotte, A. and Fiksen, Ø. (2000) State-dependent spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology* **56**, 138–62.
- Stöcker, S. (1999) Models of tuna stock formation. *Mathematical Biosciences* **156**, 167–90.
- Strand, E., Huse, G. and Giske, J. (2002) Artificial evolution of life history strategies and behavior. *The American Naturalist* **159**(6).
- Sundby, S. and Fossum, P. (1990) Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild and Osborn theory on small-scale turbulence and plankton contact rates. *Journal of Plankton Research* **12**, 1153–62.
- Trebitz, A.S. (1991) Timing of spawning in largemouth bass: implications of an individual-based model. *Ecological Modelling* **59**, 203–27.
- Tuljapurkar, S. and Caswell, H. (eds) (1997) *Structured Population Models in Marine, Terrestrial and Freshwater Systems*. New York: Chapman & Hall.
- Tyler, J.A. and Rose, K.A. (1994) Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries* **4**, 91–123.
- Tyler, J.A. and Rose, K.A. (1997) Effects of individual habitat selection in a heterogeneous environment on fish cohort survivorship: a modelling analysis. *Journal of Animal Ecology* **66**, 122–36.
- Uchmański, J. and Grimm, V. (1996) Individual-based modelling in ecology: what makes the difference? *Trends in Ecology and Evolution* **11**, 437–40.
- Vabø, R. and Nøttestad, L. (1997) An individual based model of fish school reactions: predicting antipredator behaviour as observed in nature. *Fisheries Oceanography* **6**, 155–71.
- van Winkle, W., Rose, K.A., Winemiller, K.O., DeAngelis, D.L., Christensen, S.W., Otto, R.G. and Shuter, B.J. (1993) Linking life history theory, environmental setting and individual-based modelling to compare responses of different fish species to environmental change. *Transactions of the American Fisheries Society* **122**, 459–66.
- Walter, E.E., Scandol, J.P. and Healey, M.C. (1997) A reappraisal of the ocean migration patterns of Fraser River sockeye salmon (*Onchorhynchus nerka*) by individual-based modelling. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 847–58.
- Werner, E.E. and Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured popu-



- lations. *Annual Reviews in Ecology and Systematics* **15**, 393–425.
- Werner, F.E., Perry, R.I., Lough, R.G. and Naimie, C.E. (1996) Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep Sea Research II* **43**, 1793–822.
- Williams, G.C. (1966) *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.