

Modelling spatial dynamics of fish

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Abstract

Our ability to model spatial distributions of fish populations is reviewed by describing the available modelling tools. Ultimate models of the individual's motivation for behavioural decisions are derived from evolutionary ecology. Mechanistic models for how fish sense and may respond to their surroundings are presented for vision, olfaction, hearing, the

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lateral line and other sensory organs. Models for learning and memory are presented, based both upon evolutionary optimization premises and upon neurological information processing and decision making. Functional tools for modelling behaviour and life histories can be categorized as belonging to an optimization or an adaptation approach. Among optimization tools, optimal foraging theory, life history theory, ideal free distribution, game theory and stochastic dynamic programming are presented. Among adaptation tools, genetic algorithms and the combination with artificial neural networks are described. The review advocates the combination of evolutionary and neurological approaches to modelling spatial dynamics of fish.

Keywords: adaptation, artificial neural networks, fish, fitness, game theory, genetic algorithms, hearing, ideal free distribution, learning, life history theory, memory, migration, olfaction, optimal foraging theory, optimization, sensory organs, spatial modelling, stochastic dynamic programming, vision

Introduction

The oceans, as well as lakes and ponds, offer their inhabitants environments that are variable in time and space. Moving about, either vertically or horizontally, imposes gradients in growth and survival through the effects of temperature, food concentration, sensory capabilities, predator density and detection risk. All large and commercially important marine fish stocks undertake seasonal horizontal migrations, and freshwater fishes have ontogenetic and seasonal patterns in habitat use. The extent of these migrations varies with age, size and environmental conditions. Understanding the forces that create spatial distributions is a major challenge to ecology (Kareiva, 1994), but also has clear economic benefits to humans, by allowing more precise assessments of managed stocks. And while field studies may reveal patterns at a given time and place and laboratory investigations may isolate effects of single causes, models may combine several forces in continuous space and time.

Spatial models of aquatic organisms have deep roots. Models of nutrient and phytoplankton dynamics go back to Fleming (1939), Sverdrup *et al.* (1942) and Riley (1946), while spatial models of zooplankton and fish are more recent (reviewed by Franz *et al.*, 1991, and by Tyler and Rose, 1994). Spatial modelling of fish with individual behaviour was initiated by Balchen's group (Slagstad *et al.*, 1975; Balchen, 1976; Reed and Balchen, 1982). Individual-based models (IBMs) are founded on the recognition that individuals differ in their characteristics and abilities (Hamilton, 1964; Dawkins, 1976), and that such differences may be important in ecology and population dynamics (Metz and Diekman, 1986; Huston *et al.*, 1988; Lomnicki, 1988; DeAngelis and Gross, 1992). Perhaps the most interesting feature of IBMs with regard to spatial distributions has been the recent development of spatially explicit models (Tyler and Rose, 1994), which incorporate spatial heterogeneity, individual variability and individual movement. One of the problems with IBMs is that they are little more than a way of accounting for individuals in a population. If IBMs are to become an important tool for explaining the behaviour of individuals and populations, models that describe *why* individuals are motivated for actions are needed. This means that individual actions should be viewed in the light of what evolution has found favourable.

Three types of information may be relevant to maximize the reproductive rate: (1) the very general genetic information on how to build a body, allocate energy and

reproduce; (2) current information through sense organs to correct and update the genetic view of life; and (3) stored information from past experiences that will be relevant for improving behaviour in the future. After describing fitness maximization, we will therefore also show how sensory capabilities may be modelled for the different sensory organs of fish, and how memory and learning can increase the efficiency of the individual. Thus, our review covers both ultimate (evolutionary) and proximate (mechanistic) aspects of life, and throughout we emphasize the need for integration of these two approaches in models of spatial dynamics of fish.

Finally, our ability to model organs, individuals, populations and ecosystems depends on the available modelling techniques and computing power. We will therefore explore some of the recent methods in use. In particular, we describe the differences in attitude to modelling among neurobiologists and evolutionary ecologists. And as behavioural ecology benefited from the fusion of life history theory and optimal foraging theory in the 1980s, we believe that there is now a huge gain to be had by combining evolutionary and neurobiological approaches to understand the individual. This process is yet in its early stages.

Rate maximization

Imagine a planet with two species of objects able to reproduce, differing only with respect to their commitment to reproduction. Dissimilar commitments give dissimilar fecundities. With no mortality before reproduction, the numbers in each species will increase exponentially (Euler, 1760). The genetic codes for devoting less than maximum into offspring production will, over time, be rarer and rarer and the relative frequency of the more devoted species will approach 1 after a sufficiently long time. This simple reasoning would be the same for differences in the capacity to reproduce as for differential commitment. Hence, over evolutionary time, genetic codes that tend to produce fewer offspring than others will become rarer and rarer. The core of natural selection is that only those genomes that code for maximal investment into reproduction, will survive. Reproducers exist for reproduction, which probably makes them the only kinds of object in the universe that exist *for* something. No wonder then, that the first sentence God spoke to Man was '*Be fruitful and multiply, fill the Earth and subdue it*' (Genesis 1:28).

In a stable environment, the maximum reproductive rate ρ of an individual may be found from the Euler–Lotka equation (Euler, 1760; Lotka, 1907), which accounts for expected survival and fecundity at each age (Fig. 1). The Euler–Lotka model assumes that each generation will experience the same conditions for survival and reproduction. This is not the case on planet Earth, where the expected reproductive rate of a strategy is variable in time and space. The growth rate of a strategy (e.g. a genetic code) over a long time horizon is therefore better described by the product of the growth rates over each generation (Table 1; reviews: Yoshimura and Clark, 1993; Tuljapurkar and Caswell, 1997). However, as the environment is variable, the value of this geometric mean will depend on the time horizon. This is more a problem for modellers than for nature, and an individual (and a strategy) can do no better than to behave and allocate resources in a way that maximizes the expected reproductive rate in the environment in which it lives.

Individuals able to assess the current state of their environment and to respond adequately to this information, will potentially have higher reproductive rates than passive individuals or those expecting the average. Therefore, sensory abilities and phenotypic plasticities (Fig. 1) have developed through all kingdoms of life. Further, if

Table 1. Fitness measures

Fitness measure	Symbol	Major assumption	Review references
Energy efficiency maximization	e/t	Fitness proportional to feeding rate; predation risk not influenced by behaviour	Schoener (1987)
Gilliam's rule	minimize M/g	Juveniles with unconstrained age at maturity; generation time inversely proportional to somatic growth rate; current conditions will prevail	Werner and Gilliam (1984), McNamara and Houston (1994)
Net reproduction ratio	R_0	Stable population size	Roff (1992), Stearns (1992)
Deterministic reproductive rate	$\rho = r$	Deterministic (constant or regular) environment from generation to generation	Roff (1992), Stearns (1992)
Stochastic reproductive rate	$\rho = a$	Variable (stochastic) environment in time and space	Yoshimura and Clark (1993), Yoshimura and Jansen (1996)

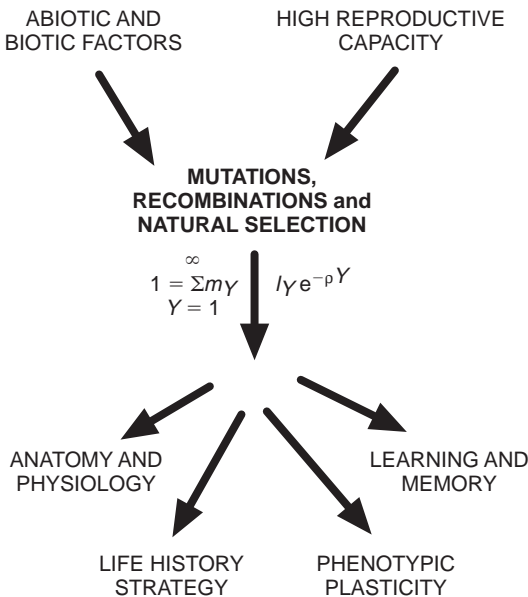


Fig. 1. Evolution by rate maximization: all aspects of life are optimized in order to maximize reproductive rate ρ , here given by the Euler–Lotka equation. The challenge to modelling is to find the optimal decision set (e.g. spatial behaviour, life history, growth allocations) given the constraints imposed by the environment.

the variation is not chaotic, so that conditions for life in the near future are related to conditions in the near past, it may pay to develop learning abilities and memory (Anderson, 1995). Hence, we should expect individuals to act in a way that takes note of the past, of current and anticipated future states of the environment (León, 1993; Zhivotovsky *et al.*, 1996), of their own physiological state and rank (Houston *et al.*, 1988; Mangel and Clark, 1988) and of the behaviour of their conspecifics (Fretwell and Lucas, 1970; Mylius and Diekmann, 1995).

In optimality models, fitness is described in terms of future expectations. But as with modellers, the organisms do not understand the world they live in and cannot react to what will happen in the future. The strategies that individuals undertake are not necessarily those that will maximize their expected reproductive rate, but rather those that have evolved and have been maintained in the population through aeons of natural selection. Through phenotypic plasticity, an individual assessment of the near future is possible and may be optimal. But the long-term assessment of optimality is taken care of by natural selection on past generations. In a stable but seasonal and heterogeneous world, as described by the Euler–Lotka equation, it is possible to find optimal solutions to life history decisions and behaviour. In a partly stochastic world, as described by the mean geometric growth rate model, optimal solutions do not exist. Yet evolution occurs, and the survivors become steadily adapted to the new twists of chance and change (Monod, 1971). All current survivors, including us, are evolutionary winners! And we have won because our ancestors have been ‘adaptation executors’, not ‘fitness maximisers’ (Wright, 1994). This distinction between optimization and adaptation has also been utilized in modelling. Adaptive modelling methods will search for improvements of current solutions, while optimization modelling derives the optimum from a fitness measure.

Just because natural selection has shaped all species to live as *for* the maximization of the reproductive rate, it is possible to construct predictive models for the behaviour of individuals and populations. In the final section we will describe several fitness-based modelling approaches, based on either optimization or adaptive algorithms, concentrating on methods for understanding spatial distributions of aquatic organisms. But first, we will discuss how fish sense and may respond to their surroundings.

Mechanistic understanding of spatial dynamics

ENCOUNTER RATES AND FEEDING

The average encounter rate between a cruising predator and a stationary prey is frequently described by the cylinder model, where encounter rate (e) is proportional to prey concentration (N), predator swimming speed (v) and the square of the reaction distance of the predator (r):

$$e = \pi r^2 v N. \quad (1)$$

In the following sections we shall describe the spatial variability of the reaction distance of several sensory systems. Gerritsen and Strickler (1977) showed that the velocity component of contact rates can be described from swimming speeds of both predators and prey, and Rothschild and Osborn (1988) showed that turbulence may increase the contact rates considerably, especially for slow-moving predators. Sundby (1997) predicted

that encounter rates between first-feeding cod (*Gadus morhua*, Gadidae) larvae and their *Calanus* nauplii prey increase by a factor of 7 when wind speed increases from 2 to 10 m s⁻¹. He found that wind-driven turbulence was especially effective for slow larvae feeding on small prey at high concentrations. Turbulence could increase feeding of juveniles up to 2 months old. (See Dower *et al.*, 1997, for a recent review.)

For the case of planktivores and most actively searching piscivores, predator swimming speed is generally an order of magnitude higher than turbulent velocity and prey swimming speed, and these variables can be ignored. Aksnes and Giske (1993) then showed that the maximum ingestion rate of the predator could be expressed by the Holling (1959) disc equation:

$$f = \frac{h^{-1}}{(h e)^{-1} + 1}. \quad (2)$$

This function is asymptotically limited to the inverse of handling time (h) at sufficient reaction distances and prey concentrations. The Holling model implies that feeding is limited by prey availability or handling time. This need not be the case, and a visual planktivore feeding in surface waters will encounter more prey than can be digested (Rosland and Giske, 1994; Giske and Salvanes, 1995). For this situation, maximum feeding rate must be calculated from stomach or gut evacuation rate (whichever is the smallest) (Henson and Hallam, 1995; Salvanes *et al.*, 1995; Stephens, 1996).

Many tactile predators are assumed to yield a linear functional response curve over a large spectrum of prey abundances (Allredge, 1984) because the handling time of individual prey is negligible. Hence, the maximum feeding rate is identical to the prey encounter rate.

RANGES OF SENSORY SYSTEMS

All variables in the encounter rate model can be rather easily obtained by field or laboratory investigations, except for the maximum detection range (r). This sensory range will be very variable, depending both upon which sensory organ is most efficient and upon the environmental conditions. As an empirical approach to its estimation would require a huge number of experiments, an attempt to describe each system by mechanistic models is the only realistic approach.

Aquatic organisms have a wide variety of sensory organs (Atema *et al.*, 1988; Bleckmann, 1993; Guthrie and Muntz, 1993; Hara, 1993; Hawkins, 1993) and are able to respond to current phenomena, in the near field by lateral line and vision and far away by hearing and chemical sensing, as well as to signals from their own body. Their reactions may also depend on past experiences by learning (Hart, 1993) and on expectations of the future, influenced by their memory and current perceptions. In this paper we will focus on how the sensory organs determine the encounter rate between a fish and its prey, mates and predators. The lateral line system, vision, olfaction and hearing can be used to detect information from different distances, as these systems operate at different spatial scales (Table 2). In addition to the sense organs themselves, each of them requires brain capacity to analyse and respond to the signals, as well as memory of past information. Within a given brain size of an individual, the sensory systems compete for space, and a huge brain will also impose hydrodynamical disadvantages for a swimming fish as well as increased detection risk. Hence, as for

Table 2. Models of reaction distances (r) for sensory systems

Sensory system	Detection range, r	Predator characteristics	Prey characteristics	Environmental characteristics	References
Hearing	$r = \frac{\rho ck^2 d^2}{-2P} U \cos \theta$	Pressure threshold for sound detection (P)	Prey radius (d), wavenumber (k), amplitude of source velocity (U), angle of radiation (θ)	Density of water (ρ), speed of sound (c), time (t)	Modified from Kalmijn (1988a), Bleckmann (1993)
Vision	$r^2 e^{cr+kz} = C_0 A E \frac{E_b}{K_e + E_b}$	Visual capacity (E), eye saturation parameter (K_e)	Prey contrast (C_0), prey area (A)	Background irradiance (E_b), depth (z), diffuse attenuation coefficient (k), beam attenuation coefficient (c)	Aksnes and Giske (1993), Aksnes and Utne (1997)
Olfaction	$r = Pt \left(-kt + \ln \frac{M/h}{C2\pi P^2 t^2} \right)$	Threshold concentration for odour detection (C)	Chemical decay rate (k), mass released (M), vertical dimension of release (h)	Diffusion velocity (P), time (t)	Jumper and Baird (1991)

other 'replicators' (Dawkins, 1995), an optimal fish does not have the best the market can bring of all components (cf. Schellart, 1992). Further, the nervous system must detect and analyse the status of the individual itself, e.g. its stomach fullness, blood sugar, and reproductive status. In this section we only consider detection of external stimuli, while input from internal sources will be mentioned in the section on the 'Neurological approach' (page 000). Further reviews are by Ketterson and Nolan (1992) and Legac *et al.* (1993), who deal with interactions of hormones and life history theory.

Sound and pressure perception

Models of sensors for sound and pressure are reviewed by Kalmijn (1988a,b) and by Rogers and Cox (1988). Most of these sensors are found in the inner ear and in the lateral line system. The reviews cited above, and others in Atema *et al.* (1988) and Coombs *et al.* (1989), explain the physics and biology in detail. Basically, sound has two components of importance for sensing: the sound pressure and the particle velocity. The acoustic pressure from a body can be expressed by models representing the propagating wave and the near-field pressure (Kalmijn, 1988a; Bleckmann, 1993).

Fish may determine the angle to a target (food source or whatever) by time and/or phase differences of the waves, while the distance to the object is primarily determined by the curvature, the amplitude spectrum and the local frequency and the frequency modulation of the wave train (Bleckmann *et al.*, 1989). As the lateral line system is most sensitive to the very near field, it is important for maintaining position and acquiring information whilst schooling (Bleckmann, 1993; Montgomery *et al.*, 1995), and may also aid in the detection of small prey (Montgomery, 1989). Particularly for the smallest fish larvae, near-field sensing may be crucial for start-feeding and survival. The startle response in fish larvae becomes more directional with the development of the lateral line (Blaxter and Batty, 1985). Probably owing to the very local range and the multitude of sensors on the body surface, the lateral line system has not been used much in spatial modelling. As the effect of the near-field pressure falls with the square of the distance travelled, this term can be neglected for all but the smallest distances. This makes modelling of the auditory detection of distances much simpler (Table 2). Directional hearing thresholds do not vary much with angle (Lu *et al.*, 1996) but are both frequency dependent and species specific (Popper, 1996).

Vision

All fish species, except those living in almost total darkness, have well-developed eyes. Due to the fast and directional travel of light beams, the visual perception of images gives very precise information over short distances. Individuals may see prey, predators, competitors, mates, school members as well as physical objects in their habitat. However, images decay quite rapidly underwater, either due to collision with particles or water molecules (scattering and absorption) or because of scattering of other light beams onto the image. Therefore, information from distant objects must be sensed by other receptors. Aksnes and Giske (1993) and Aksnes and Utne (1997) have developed a model for the detection range of fish (Table 2). The search volume of a cruising predator is further restricted by the visual search angle (Luecke and O'Brien, 1981; Dunbrack and Dill, 1984). Aksnes and Giske (1993) have predicted that the feeding rate of a pelagic visual predator will generally be far more sensitive to changes in visual range than to prey concentrations. Eiane *et al.* (1997) studied the potential exploitation competition between

tactile and visual predators. They concluded that light intensity, water clarity, small-scale turbulence and prey density were the major factors determining the relative success of these predators. They speculated that heavy eutrophication could lead to dominance of jellyfish through reduced water clarity and visual range of planktivorous fishes, and not through changes in species structure in the plankton communities.

Olfaction

Smells and odours spread in the water much more slowly than do light beams and pressure fields, but they also remain in an area much longer. Hence, odours may be tracked in time and space. Their spread and longevity depends on physical factors like molecular diffusion, turbulence and water currents, but also upon their chemical stability. The horizontal spread of a point source of a chemical component can be modelled as a combination of molecular diffusion and chemical instability by the Joseph and Sendner (1958) model, which was reformulated by Jumper and Baird (1991) to express detection range as a function of time since release. The chemical decay rate is important for long-distance detection of a target, but this factor may be neglected for search over shorter distances, such as food search in darkness or in turbid water.

In addition to the effect of molecular diffusion, the spread of a molecule will depend on turbulence and advection. These effects can be studied by models of 3D hydrodynamics (Parslow and Gabric, 1989; Baird *et al.*, 1996). Turbulence will act much like diffusion, only much stronger. Advection will act to change reaction distance along, transverse to or opposite to the current. Swimming against the current will allow the planktivore to smell its prey without being smelt. However, this will also apply to the piscivores following the planktivores. The impact of turbulence was modelled by Baird *et al.* (1996). Turbulence is much stronger in the upper mixed layer than in deep stratified waters. Baird *et al.* (1996) modelled vertical differences in detection distances of a pheromone and found a strong impact of the vertical gradients in turbulence. They also showed that there is a huge gain in detection distance by increased sensitivity. Baird and Jumper (1995) modelled the mate location problem of deep-living hatchetfish (*Sternoptyx diaphana*, Sternoptychidae) by analysing the sensory capabilities of the fish. They showed that with a sensory range of less than 2 m, mate location could take weeks in some populations. Increased perception distances, for example by using sound or by bioluminescence, as well as a high swimming speed of at least one of the sexes, are often required for mate location and reproduction.

Other sensory systems

In addition to the ability to locate prey and mates and to avoid predators and parasites, fish possess several other types of sensors which we will not describe here. Internal sensors for supervision of the physiological state are abundant and some can be modelled (Olsen, 1989; Legac *et al.*, 1993; Broekhuizen *et al.*, 1994). Further, it is common practice in optimality modelling to assume that the individual has abilities to acquire the necessary information, without specifying how this is done (e.g. Rosland and Giske, 1997). In the same way, we usually assume that the fish will register external changes in temperature gradients as they swim through them. The ability to navigate by geomagnetic fields is also documented for many species (Moore *et al.*, 1990; Kobayashi and Kirschvink, 1995; Walker *et al.*, 1997). An organ likely to be responsible for magnetic sense in rainbow trout (*Onchorhynchus mykiss*, Salmonidae) has recently been reported

(Walker *et al.*, 1997). Sharks are able to use weak electric fields, both in prey detection and in spatial orientation (Kalmijn, 1988b). To the best of our knowledge, this has not yet been used in modelling, although it is common to assume orientation using a magnetic sense when modelling large-scale migration (e.g. Huse and Giske, 1998).

PREDATION RISK

The models for sensory ranges and encounter rates can also be employed to model the spatial distribution of predation risk experienced by the prey. A model that is to be used to find the safest habitat for a prey, should not contain specific assumptions about predator location. If predation risk is assessed on the basis of predator distributions, the predators may afterwards redistribute themselves to match the new location of their prey. The only way to find gradients in risk is to search for environmental variation in the predator's ability to locate or catch prey.

The sense organs discussed here have different importances for detection by predators. This may be illustrated by the protection gained by schooling (Huth and Wissel, 1994; Vabø and Nøttestad, 1997). A dense school has a smaller surface than a loose school or the sum of single individuals, so that schooling tightly may reduce the ability of a visual predator to locate its prey. For olfaction, the amount released from a thin shoal and a dense school of N individuals is the same (M/h ; Table 2), and social behaviour has no obvious effect on detection risk. However, the concentration of the smell of a dense school is higher than that of a more dispersed shoal, although the total odour mass released is the same. But if the odour is transported with currents, then the initial concentration may determine from how far away the predator can track its prey. Turbulence may erase weak odour signals from single individuals, but may spread the news of a passing prey school. The fast vertical decay of light gives strong potential gradients in vision-based search efficiency, but sound and olfaction will eventually be dominant in less illuminated waters. We are not aware of models of detection or of risk caused by olfaction or hearing. Vertical gradients in predation risk for zooplankton were investigated by Giske *et al.* (1994) and Fiksen and Giske (1995), while Giske and Aksnes (1992) and Rosland and Giske (1994, 1997) have studied gradients in mortality risk for planktivores. Rosland (1997) investigated how small changes in the ecosystem could select for different kinds of planktivorous fishes and Eiane *et al.* (1997) have compared vertical gradients in the efficiencies of visual and tactile planktivory.

While there is no spatial escape from tactile predators, it is often possible to grow out of their reach. Most tactile predators, being jellyfish or large zooplankton, prey on small organisms. Size-dependent mortality risk has been described by an empirical relationship for pelagic organisms spanning 12 orders of magnitude (McGurk, 1986). By growing fast, the time during which an individual is susceptible to tactile predation is reduced. However, larger prey are also more easily detected by visual predators. The optimal growth pattern is therefore a complex trade-off involving several kinds of predators as well as the impact of size for age at maturation and for fecundity.

LEARNING AND MEMORY

The learning abilities of fish have been reviewed by Thorpe (1963), Gleitman and Rozin (1971) and Kieffer and Colgan (1992), with many good examples of learning in long-distance migrations, spatial orientation, foraging, detection of threats, recognition processes and social learning. Learning is modelled separately in two fields of biology.

The neurobiological approach studies *how* information is acquired and *where* in the brain it is stored, while the evolutionary ecologist studies *why* animals learn and *what* they should learn or forget. There are obvious benefits in combining these approaches.

Ecological approach

Fish utilize memory of past experiences in finding food and avoiding predators. Past experience is often modelled as a memory array. If recent information is more likely still to apply than older observations, a short-term memory is desirable. If conditions apply for longer periods, a long-term memory will do better. Fish will usually have both sorts, and use them simultaneously (Harley, 1981). McNamara and Houston (1985) modelled optimal patch choice (according to the marginal value theorem – Charnov, 1976) as a result of learning, where the individual did not know beforehand the return rate of any patch or the average return rate. For a changing environment, McNamara and Houston (1985) gave exponentially declining weight to older information. In their model individuals do not keep records of the quality of each feeding patch, and the important information is whether the current patch is better than the experienced average. Then the individuals need only keep the memory of the estimate of the average patch quality from the last patch. This model allows the individual to learn the maximum feeding rate in its habitat and then to live according to the marginal value theorem.

Resident animals must recognize the spatial structure of the habitat so as to orientate. Benhamou *et al.* (1995) have developed a place navigation model, based on the recognition of distance and angle to all landmarks. Central in their model is the ‘location’, which is the place of interest, such as a point in the territory, and the individual learns the ‘panorama’ determined by the angular sizes and relative bearings of all landmarks seen from the location. By comparing and relating panoramas, the animal may orientate in a complex two-dimensional landscape, as shown for a planktivorous reef fish by Noda *et al.* (1994).

The quality of a food type can be learned by the general learning rule (Bush and Mosteller, 1955; Turner and Speed, 1996). Learning is modelled here as change in the probability of attacking a food type during an encounter, depending on the learning rate and the learning asymptote for attack probabilities. Turner and Speed (1996) give several learning rules for these two factors. The model may apply with some modifications also to handling times, palatabilities, encounters with predators, the assessment of habitat quality and to prey encounters.

Neurological approach

A different approach to model learning is to apply techniques inspired by how the brain works. The artificial neural network (ANN, Hopfield, 1982; Kohonen, 1984) is such a computer technique that uses neurobiological principles of brain activity to learn tasks. The ANN started as an outgrowth of artificial intelligence, and has since been applied to solve a variety of problems within different fields. The ANN consists of layers of nodes that are linked together by weights (Fig. 2), simulating the way in which brain synapses work. By gradually adjusting the weights according to a training method, the desired output (actions, Fig. 2) can be achieved. It is common to classify ANN learning as supervised or unsupervised (Anderson, 1995), where in the former situation the correct output is known but not in the latter. In supervised learning the weights of the ANN are often adjusted using back propagation (Rummelhart *et al.*, 1986). Learning can also be

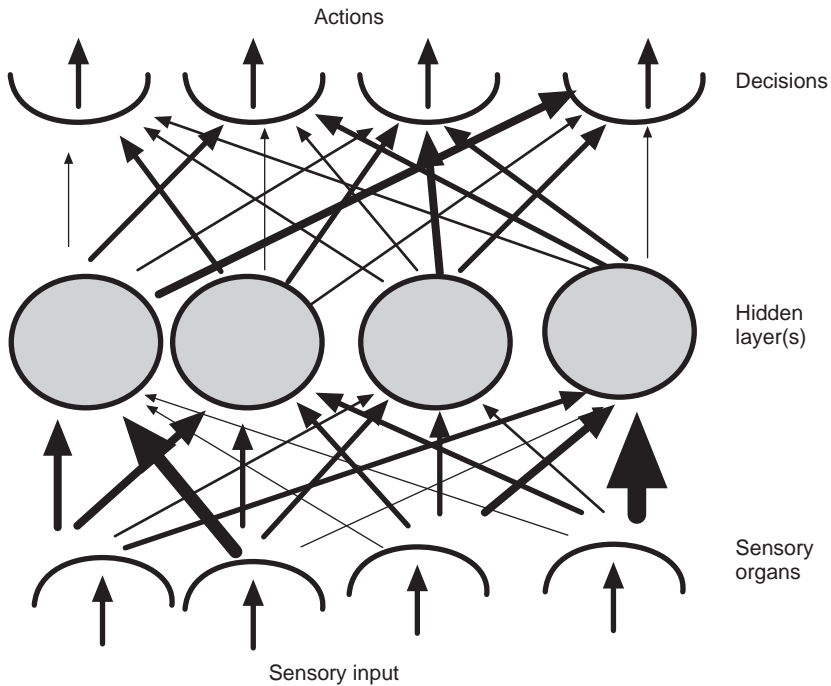


Fig. 2. Artificial neural networks: a schematic drawing. Information from external and/or internal sources is retrieved at 'input neurons' (here termed sensory organs). If the numerical value of the input is above a threshold value, the neuron will transmit the message through a synapse to one or more neurons. In the simplest case, sensory input is sent directly to an output layer, where decisions are made. More complex neural networks will contain one or several 'hidden layers'. Each neuron in a hidden layer will receive information from many or all neurons in the level below, and send a new signal to the layer above if the sum of the input values is above the threshold. The threshold values are usually set, but the strength of each synapse must be learned so as to adjust to this level. Synapse strength is indicated by line thickness. The learning may occur as a training if the correct response to all types of input is known, or as a gradual evolution of improved solutions by genetic algorithms, if the optimal structure is unknown.

achieved through gradual adaptation of weights using a genetic algorithm (GA) (Montana and Davis, 1989) through indirect evaluation of the ANN. The GA method of 'synapse' training (van Rooij *et al.*, 1996) will be discussed later.

As an example of a mechanistic neurological model of animal behaviour we refer to the model of Hallam *et al.* (1994). The central unit in the model is a neuroconnector net, which connects sensory input data with behavioural actions. Information from the sensory neurons is passed by adjustable 'synapses' to a series of releaser 'neurons'. Between these and a corresponding repetition of 'behaviour' neurons there is a series of weighted synapses. Finally, there are inhibition synapses between behaviour neurons. A neuron will 'fire' a signal through a synapse if the inputs are above an 'input threshold'. In the first series of adjustable synapses, the neuroconnector set may learn to find the appropriate weights of the signal as well as the optimal thresholds for each

input register. The neural basis for movement in the lamprey (Petromyzonidae) has been intensively studied and several ANN models have been published. This detailed mechanistic approach has been reviewed by Ekeberg *et al.* (1995).

Modelling learning by ANNs has been applied extensively in artificial life studies (Hinton and Nowlan, 1987; Parisi *et al.*, 1990; Ackley and Littman, 1992; Menczer and Belew, 1996). Although ANNs have rarely been applied to model learning in fish, they have the potential to become important in this field as well (Reeke and Sporns, 1993; Nolfi *et al.*, 1994).

Functional tools for behaviour and life history

OPTIMIZATION APPROACH

Optimal foraging theory

In 1966, two papers appeared back-to-back in *The American Naturalist* (MacArthur and Pianka, 1966; Emlen, 1966). These papers were directly influenced by economic reasoning, and formed the start of optimal foraging theory (OFT). Emlen (1966, p. 611) formulated the evolutionary premise for OFT: 'Let us assume that natural selection will favor the development ... of feeding preferences that will ... maximise the net caloric intake ... per unit time' (Table 1). Hence, OFT relied on a link with the Darwinian force of evolution, which gave OFT a foundation for generating predictive biological hypotheses open for testing (Calow and Townsend, 1981). The theoretical work in the OFT era was to express optimal behaviour with the energy efficiency assumption in mind (Schoener, 1987). However, there is no direct deduction of this optimality assumption from maximization of the reproductive rate. It is implicitly assumed that increased feeding rate may enhance survival probability, or enhance fecundity without also enhancing predation risk or other variable fitness costs. Hence, the theoretical results from OFT will be invalid for situations where the behavioural action may greatly affect predation risk (Table 3). But there is an extensive experimental backup of predictions from OFT where animals have been offered choices in relatively simple experimental situations (Stephens and Krebs, 1986; Schoener, 1987).

The classical OFT has been reviewed by Schoener (1987), who included optimal diet theory, optimal patch choice and optimal patch residence time and departure. More recent OFT approaches have included risk-prone and risk-averse behaviour when confronted with environmental variability in expected feeding rate (Caraco, 1980; Stephens, 1981). Clark and Mangel (1986) modelled stable school sizes for fish. They constructed several models for food intake rate as a function of school size and environment, and investigated the feeding gain of schooling under common search and exploitation in relation to prey variables such as patchy versus regular distributions, ephemeral food patches, and under despotic exploitation.

Life history theory (LHT)

After Darwin and Wallace, the focus of evolutionary biology centred on the morphology of organisms, and Lotka (1925) may have been the first to consider the 'elastic behaviour schedule' (p. 350) or 'the free-choice schedule' (p. 351) as a way to maximize rate of increase. Also Fisher (1930) saw life history traits as an integrated part of the phenotype that could be analysed on an adaptive demographic basis. The first spatial model of distribution of aquatic organisms based upon adaptive values of habitat profitability was

Table 3. A comparison of tools for functional modelling

Desired property	Optimality approach				Adaptation approach	
	OFT	LHT (Euler–Lotka)	IFD	Game theory		
Individually variable motivation	Feeding state	Age dependent (‘static’ motivation) No	In despotic IFD	No	Age, time and state dependent	Age, time and state dependent
Density-dependent growth and survival	Only through feeding		Yes	Yes, and frequency dependent	Possible only for very simple scenarios	Yes
State-dependent growth and survival	Only through feeding	No	Very computer intensive	No	This is what SDP is best at	Yes
Morphological and physiological plasticity	No, OFT covers shorter intervals	No	No	No	Phenotype characterized by states	Probably possible, not yet done
Individual behaviour at several trophic levels	No	Static	Dynamic games	Find optimal strategies	Only as dynamic game	Probably possible, not yet done
Dynamic behaviour and life history strategy	Does not cover the whole life, concentrates on feeding situations	Only in stochastic LHT	Density-dependent solutions	Frequency-dependent solutions	Of one actor in a specified environment	Will evolve according to environment
Find optimal strategies	To simple problems without predation risk	Yes	Equilibrium analysis	Equilibrium analysis	Will find global optimum	May get stuck at local optima
Learning	Yes	No	No	No	Yes	Yes

Ecosystem modelling	No	The environment is described implicitly in the l_x and m_x vectors	Predator–prey equilibrium	Can search for equilibrium	Scenario modelling or dynamic games	Not granted that global optimum or stability will be found
Heterogeneous and temporally variable environment	Only through feeding	Euler–Lotka demands that conditions are equal for each generation, genetic foresightedness	Computer intensive	Equilibrium analysis	Unrealistic adaptation owing to perfect foresightedness	Variation at all scales possible, genetic foresightedness
Fitness measure	Partial: feeding rate and growth	Analytical, rate maximization (or a derivative)	Usually partial (feeding or growth)	Any, but frequency dependent	Full or partial, derived from analytical	Endogenous (implicit) fitness function
References*	2, 3, 16, 22, 28	5, 18, 21, 24, 27, 28, 30	6, 7, 9, 26	9, 11, 15	8, 12, 13, 14, 17, 18, 23, 28	1, 4, 10, 19, 20, 25, 29

*References: 1, Ackley and Littman (1992); 2, Charnov (1976); 3, Clark and Mangel (1986); 4, Dagorn *et al.*, (1995); 5, Fisher (1930); 6, Fretwell and Lucas (1970); 7, Giske *et al.* (1997); 8, Houston *et al.* (1988); 9, Hugie and Dill (1994); 10, Huse and Giske (1998); 11, Iwasa (1982); 12, Katz (1974); 13, Mangel and Clark (1986); 14, Mangel and Clark (1988); 15, Maynard Smith (1982); 16, McNamara and Houston (1985); 17, McNamara and Houston (1986); 18, McNamara and Houston (1996); 19, Menczer and Belew (1996); 20, Nolfi *et al.* (1994); 21, Roff (1992); 22, Schoener (1987); 23, Sibly and McFarland (1976); 24, Stearns (1992); 25, Terzopoulos *et al.* (1995); 26, Tregenza (1995); 27, Tuljapurkar and Caswell (1997); 28, Tyler and Rose (1994); 29, van Rooij *et al.* (1996); 30, Werner and Gilliam (1984).

presented by McLaren (1963). He discussed how increased water temperature reduced fecundity and shortened egg development time for zooplankton, and described optimal temperatures with respect to maximizing the reproductive rate. He also found that an individual in most cases could increase its fitness by diel vertical migration. McLaren (1963) did not invoke predation risk as an environmental variable; this was not included in a model for another 20 years (Iwasa, 1982).

Although McLaren (1963) described vertical migration of copepods as a means of maximizing reproductive rate, the study of life history strategies had its breakthrough three years later, in the same volume of *The American Naturalist* in which OFT was published. Murdoch (1966) discussed individual flexibility as a strategy for coping with environmental variability and Williams (1966a) introduced the concept of the residual reproductive value and the fitness consequence of a behavioural action. In his book, Williams (1966b) showed that the individual (rather than the group or the species) was the unit of selection. Suddenly, ecologists had two sets of optimality theories at hand, and both theories expanded vastly during the next two decades. In retrospect it is strange to observe that the central papers in OFT and LHT were published in the same journals, by scientists at the same or very similar departments, with a very low rate of theoretical cross-over. OFT assumed that feeding rate defined as energetic gain per time unit was proportional to fitness, without including into their models other components of fitness such as predation risk. LHT was used to find optimal strategies, but not at the time scale of behavioural decisions. Both theories relied on the optimality assumption, but even 30 years later there is still a debate over what is to be maximized.

Life history theory has traditionally been concerned with the strategic trade-off decisions that organisms make about their schedules of fecundity and survival with age. A shift from age-dependent to state-dependent life history theory has lately been advocated as a more realistic frame for further progress. The proponents of this change prefer to view age as only one of a number of states relevant to the adaptive life history, and one of the least important, as it is difficult to find examples where vital rates are shaped by age *per se*, rather than by the apparent effects correlated with age (Ebenman and Persson, 1988; Clark, 1993; McNamara and Houston, 1996). The age-based approach cannot incorporate many relevant trade-offs, such as maternal effects, the offspring number/quality decision, or the allocation patterns between reproduction, growth or storage unless the vital rates are correlated only with age. The tradition of age-based life history theory probably relates to the more tractable mathematics and the applicability of analytical methods stemming from this assumption, while the recent use of computers, even among biologists, now makes the state-based approach more attractive (Table 3).

The core of LHT is the maximization of reproductive rate. By using fitness-maximization as a target function, it has been possible to analyse optimal lifetime reproductive patterns, energy allocation rules, phenology and willingness to take risk (Fig. 1; reviews: Roff, 1992 or Stearns, 1992). As has been shown earlier, it is not straightforward to employ a proper fitness measure, as evolution is a continuous and historical process (Table 1). For simplicity, most of LHT has been worked out for stable environments, where the Euler–Lotka equation (Fig. 1) may be used. When the population size is stable, $\rho = 0$. It may be seen from the Euler–Lotka equation that to maximize ρ at steady state is equivalent to maximize R_0 , the net reproductive ratio (Table 1). As R_0 is much easier to calculate, this measure has been used in several

studies of optimal life histories and behaviour. This must be done with caution, as the steady-state assumption will generally be invalid in evolution and ecology (Giske *et al.*, 1993; Kozłowski, 1993; Fiksen, 1997) because (1) although population size is stable, individual performance may vary; and (2) the steady state will not be permanent. For both these cases, strategies that seek to maximize ρ may never leave fewer offspring to later generations than do R_0 -maximizers.

Werner and Gilliam (1984) predicted that if generation time is a function of the growth rate (g) of juvenile fish, and fitness is maximized by R_0 , the profitability of a habitat is determined by the mortality risk: growth rate ratio (M/g). This should be minimized (Table 1). Further, if growth is proportional to feeding rate (f), individuals should seek to minimize (M/f). Aksnes and Giske (1990) and Giske and Aksnes (1992) predicted that for adult fish or for other organisms with an environmentally determined reproductive pattern where feeding acts to increase body size and thereafter fecundity, but does not decrease generation time, the fitness value of feeding is much reduced. Such individuals should choose the habitat that minimizes ($M/\ln f$). However, if generation time is dependent on environmental temperature, as is common for many aquatic organisms, the habitat profitability function will also change. Aksnes and Giske (1990) predicted that temperature should be the major environmental signal for the continuously reproducing copepod *Paracalanus parvus*, while light intensity, which affects survival from visual predators, is of highest importance for the annually reproducing *Calanus finmarchicus*. However, the optimal trade-off between feeding and predator avoidance depends on future expectations. This has been shown by McNamara and Houston (1992, 1994). We will discuss their result in the section on state-dependent behaviour.

Gilliam (1990) provided a link from OFT to LHT. He studied the classical optimal foraging scenarios for the case in which the individual is at risk while feeding. The average feeding rate of a foraging individual followed the prey choice model (Schoener, 1971). Gilliam then assumed that the forager suffers one mortality rate while searching for prey and is killed with a duration-dependent probability while handling prey. Finally, this individual has a lower mortality risk when hiding in a refuge. Its risk then depends on prey type when feeding, and on the environment when searching. Gilliam (1990) investigated how this risk while feeding changed optimal diet breadth and optimal patch residence time, and the effect of the energetic state of the predator on the optimal diet selection and activity level.

Although classical life history theory emerged from a static demography where fecundity and survivorship were deterministic functions of age (cf. the Euler–Lotka equation), it need not be so. McNamara and Houston (1992) developed a state-dependent version of the Euler–Lotka equation where individuals optimize their behaviour given their current state in order to maximize reproductive rate. The framework for this and similar models (Mangel and Clark, 1986; Clark, 1993; McNamara, 1991, 1993; McNamara and Houston, 1996) is stochastic dynamic programming (SDP), which we will discuss later.

Ideal free distribution

The classical OFT and LHT models consider the optimal behaviour of an individual as a function of its environment, and as a result all individuals are supposed to end with the same optimal solution. However, it is not always optimal to do the same as all the others.

The ideal free distribution (IFD) is one of a set of theoretical spatial distribution rules investigated by Fretwell and Lucas (1970). The original IFD is based on five assumptions: (1) competitors are equal; (2) resources are patchily distributed; (3) the competitors incur no cost to move; (4) each individual will go to the patch with highest gain; and (5) competition between individuals is 'scramble', without any contest or combat. IFD was developed in the era of OFT, and although Fretwell and Lucas (1970) stated that food was but one component of fitness, the examples they provided assumed a direct relationship between feeding rate ('gain') and fitness (but see Oksanen *et al.*, 1992). Under this basic version of IFD, the total number of individuals distribute among the patches so that the gains by all individuals are equal in all patches, which are utilized in such a way that gain cannot be increased by relocation. The number of individuals in a utilized patch will be proportional to the resources available (which in a stability analysis, as IFD is, means the resource input rate). Later IFD models have been developed for despotism (Fretwell, 1972), unequal competitors (Parker, 1982), interference feeding (Sutherland, 1983), resource wastage (Sutherland and Parker, 1992), perceptual constraints (Abrahams, 1986), travel costs (Beauchamp *et al.*, 1997), residence costs (Tyler and Gilliam, 1995), and combined food reward and predation risk in habitat profitability (McNamara and Houston, 1990). A recent review of the IFD family is given by Tregenza (1995).

MacCall (1990) used the IFD concept in creating the 'basin model' of the spatial distribution of fish stocks. He envisioned the geographical fitness landscape of a fish stock as a basin, where the bottom topography of the basin was formed by habitat profitability (deeper is better). The population size determined the sea level in the basin, so that a small stock would reside in the deepest pool of the fitness basin whereas a large stock would occupy most of the available area and with higher densities all over. By this graphical theory, MacCall explained interannual variation in the horizontal distribution of fish stocks as a combined effect of habitat profitability and intraspecific competition.

Tyler and Gilliam (1995) developed several IFD models for stream fish which experience increased energetic costs of maintaining position and reduced capture success of drifting prey as current speed increases. The model was designed for two 'patches', differing with respect to supply rate of food and cost of maintaining position. They compared the predictions of these models and the classical IFD models in a laboratory investigation of minnows and found that the behaviour of the fish was best described by these extended models. This is a good example of a situation where more complexity enhances the predictive power of a model.

Giske *et al.* (1997) developed a complex model for the density-dependent habitat profitability of copepods, where the habitat (pelagic vertical axis) was characterized by its food concentration, the sensory range of predators, temperature and concentration of conspecifics. All copepods were assumed equal, so the functional model resembled "equal competitors under predation hazard" (Gilliam and Fraser, 1988). Giske *et al.* (1997) studied a scenario where fitness was measured by Gilliam's criterion (maximize growth rate per mortality risk). Because habitat profitability is influenced by both risk dilution and feeding interference, the density-dependent profitability curve was dome-shaped at many depths, with maximum potential reproductive rate at intermediate copepod concentrations. More competition may be better, and it may be more profitable to concentrate at a few depths than to spread out to match resources. As an IFD model

with peaked profitability curves may yield a very high number of possible population distribution patterns, Giske *et al.* (1997) investigated the validity of several simplifying methods to find the optimal solution faster.

In all these IFD models, individuals do not differ in their energetic state. The impact of individual energetic state on spatial distribution of a population was analysed by McNamara and Houston (1990) by dynamic programming (SDP, see below). They studied habitat use when animals experience different risks of starvation or predation among two patches. Studying IFD by SDP can only be done as an analysis of optimal behaviour, and cannot be done as part of a simulation model. However, when the optimal state-dependent habitat selection is found by SDP, a forward-running IFD model could be able to look up the optimal policies from the SDP model and find the spatial distribution and population dynamics. But this is probably not a practical way of modelling spatial distributions, mainly because the IFD assumption of equal fitness demands huge computational powers for even moderately complex scenarios (Giske *et al.*, 1997). IFD will probably remain as a tool for scenario modelling for problems of low complexity, where the assumptions are more valid (Table 3).

Game theory

Game theory, like optimality theory in OFT, was introduced to ecology from economics (Maynard Smith, 1982; Parker, 1984). Commonly, the goal of a game is to find a strategy (pure or mixed) that can persist in a population (Table 3), and the evolutionarily stable strategy (ESS) is a well-known example (Maynard Smith and Price, 1973; Maynard Smith, 1974). A strategy is an ESS if, once established in the population, a new mutant or immigrant cannot invade the population. However, a mixed ESS, or an evolutionarily stable polymorphism, can be established if the pay-offs of the two (or more) strategies are the same at some frequency of occurrence and when a change in frequency of occurrence from this balance leads to reduced fitness of the strategy. (IFD is an ESS in this sense, but Giske *et al.*, 1997, found situations when the IFD would not be stable.)

Iwasa (1982) modelled the vertical distribution of zooplankton and fish day and night in two vertical layers, assuming that the fitness of the fish was dependent on zooplankton catchability and density. He further assumed fitness of zooplankton to depend on feeding gain and visual predation risk. Iwasa then found that the equilibrium concentrations occurred when all zooplankton and fish concentrated in the upper phytoplankton-rich layer at night, with some fraction of both the zooplankton and fish populations remaining in the deeper layer during the day. This fraction depended on the efficiency of the visual predator and on the impact of phytoplankton in the surface water on zooplankton fitness. The model of Iwasa (1982) was an important reminder of the work of McLaren (1963, 1974), that zooplankton vertical migration is a balance between several selective agents. A weakness of Iwasa's model was that neither zooplankton nor fish had negative influence on their conspecifics. This was included in the zooplankton model of Gabriel and Thomas (1988a,b). They also allowed zooplankton to distribute in the surface and deeper water and modelled the frequencies of two strategies: (a) migratory: stay at the surface at night and go deep during the day, and (b) stationary: always stay near the surface. The strategies were explored under different environmental conditions. Visual predation and food concentration was highest in the surface habitat, but feeding gain was reduced by increased competition. They found many scenarios where the two strategies would coexist, and some where only one

could be maintained. Hence, they gave a theoretical argument for the coexistence of genetically and ecologically different clones that have pay-offs that vary with time, but have the same annual success. Yet, one should keep in mind that Gabriel and Thomas (1988a,b) compared two fixed strategies against each other, not against a behaviourally flexible strategy.

Hugie and Dill (1994) constructed a game-theoretical IFD model of habitat selection by fish and their prey. As did Giske *et al.* (1997), they used R_0 as the fitness measure and demanded that all habitats occupied should yield the same density-dependent profitability. While Giske *et al.* (1997) only modelled prey distribution in response to the inherent riskiness of a habitat due to the reaction distances of visual and tactile predators, Hugie and Dill (1994) modelled the stable solution to the game between these two trophic levels. In their basic model, which had no interference between predators, Hugie and Dill found that equilibrium prey densities should be proportional to the inherent riskiness of the habitat caused by the predator's search abilities. Predator distributions were influenced by both their efficiencies and the productivity of their prey. These analytical results, particularly with respect to prey distributions, differ strikingly from the assumptions of the 'continuous input' versions of IFD, where distribution of optimal consumers match the input of their prey (Milinski, 1979). The model of Hugie and Dill (1994) thus shows that optimality solutions derived from a partial perspective of fitness, as with growth maximization in the standard IFD, may yield erroneous conclusions. According to the Hugie and Dill (1994) dynamic game model, all habitats will be utilized by the prey. In the IFD model of copepod distribution by Giske *et al.* (1997), prey will concentrate in the best habitats at low overall abundances, and will only exploit all depths at very high population sizes. These different predictions could be tested experimentally.

Stochastic dynamic programming

For many years now it has been clear that feeding behaviour of fish is best understood as a trade-off between food intake and risk of predation (review: Milinski, 1993). Lately, virtually every aspect of behavioural ecology and life-history theory has become centred on this dichotomy: to reproduce or survive. This development seems to have been driven by observations rather than by theory, as foraging theory in the late 1970s (OFT) was concentrated on single components of fitness (Pyke *et al.*, 1977) and lacked the mathematical tools to treat risk of mortality and food simultaneously within the frame of Darwinian fitness. The tool appropriate for such analysis was pioneered by McFarland and others (e.g. Sibly and McFarland, 1976; McFarland, 1977, but see also Katz, 1974; Craig *et al.*, 1979) in the late 1970s, and involved state-dependent optimal control theory.

Since then, Mangel and Clark (1986, 1988), McNamara and Houston (1986) and Houston *et al.* (1988) have promoted the use of stochastic dynamic programming (SDP) to study how optimal individuals should trade off different components of fitness. The book by Mangel and Clark (1988) made the computational and mathematical skills needed to build dynamic optimization models available to biologists. SDP is a handy device to merge life history theory and short-time behaviour in ecological models based on sound evolutionary theory (Fig. 3; Table 3) by the unification of several components of fitness in one currency (Mangel and Clark, 1986; McNamara and Houston, 1986).

In general, SDP assumes the decision maker to be perfectly adapted to its environment. In SDP models, behaviour or life history will change immediately when

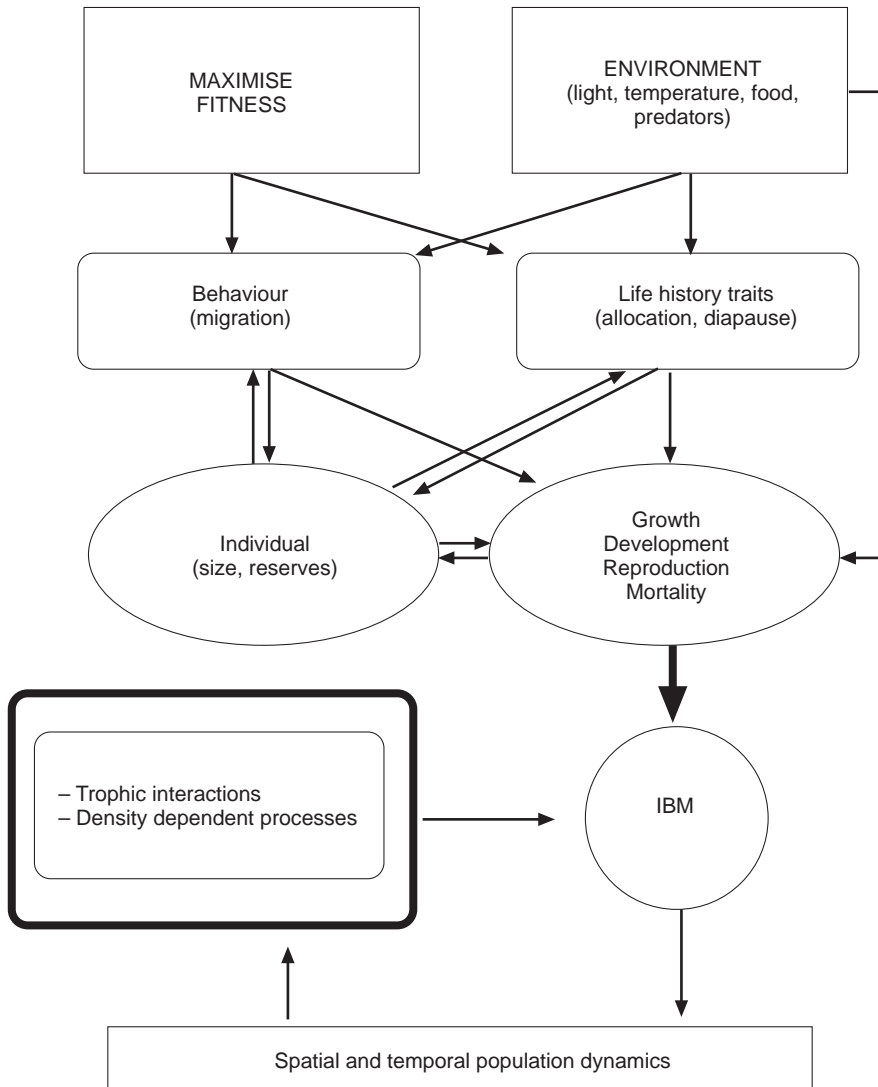


Fig. 3. Stochastic dynamic programming: a conceptual overview of how short-term behaviour and life history theory may be integrated by SDP. Fitness maximization and environmental forcing are both affecting behaviour (e.g. migration) and life history traits, which in turn are decisive for growth, mortality, reproduction, development and individual states. Mechanistic submodels are central in relating states and environment to processes such as growth and mortality. These processes are an essential forcing in individual-based models (IBM), and can be derived from the dynamic programming algorithm. Then, the basic predictions from the IBM are spatial and temporal population dynamics, optimal life history decisions and patterns of behaviour. Trophic interactions, frequency dependence and density dependence can be included in IBM models, but not in SDP. Thus it is possible to add density dependence through the IBM, while behaviour and life history remains constant except for the feedback on state: increased density may cause competition for food – reduced physiological condition – changed behaviour and life history – new distributions – new density dependence. The new behaviours will not be truly optimal, but fitness will increase. However, we do not know of any models exploring these possibilities.

growth or predation risk change. This is most realistic for situations of strong phenotypic plasticity, which is often the case for behaviours acting on short time intervals such as diel vertical migration (DVM), schooling, swarming, foraging or hiding decisions. Organisms are amenable to fluctuations in internal states such as stomach fullness, condition, fat reserves or body size. Also, a growing body of evidence suggests that prey often possess advanced sensory mechanisms to measure the presence and density of predators (Smith, 1992; Jachner, 1995a,b; Utne and Bacchi, 1997), and thus are able to respond in an adaptive manner to this information. A particularly convincing example of this is the variations in patterns of diel vertical migration in the water flea *Daphnia magna* when the concentration of fish smell increases or decreases (Loose and Dawidowicz, 1994). High concentrations of fish smell in the environment cause an instantaneous switch to more intense DVM and less exposure to light. This is a case where SDP modelling has been applied (Fiksen, 1997) and where the assumption of much environmental information seems to be fulfilled.

DVM is an example where SDP models have been very useful in the formulation of quantitative theories of the adaptive value of a behavioural phenomenon (Clark and Levy, 1988; Rosland and Giske, 1994, 1997; Fiksen and Giske, 1995; Fiksen, 1997; Fiksen and Carlotti, 1998). These models apply mechanistic submodels to study how the environment and physics influence the behavioural patterns, and some include both DVM and other traits as decision variables, such as allocation between growth and reproduction. State variables such as stomach content, fat reserves and body size are shown to modify optimal DVM for a range of organisms. SDP has also been used in a study of the seasonal horizontal migrations of capelin (*Mallotus villosus*, Osmeridae) in the Barents Sea (Fiksen *et al.*, 1995), in an attempt to view the migration pattern as a trade-off between growth in the south-western part and safety from predation by cod in the north-east. In that model the spatial grid position was included as a state variable.

The LHT-based habitat profitability models of Werner and Gilliam (1984) and Aksnes and Giske (1990) describe situations with spatial but not temporal variation in the environment. McNamara and Houston (1994) showed that 'Gilliam's criterion' is a proper fitness measure when future expectations will be the same as the current conditions (Table 1). If, on the other hand, current conditions do not persist, the value of a great feeding opportunity increases as does the cost of an increased risk. Moody *et al.* (1996) studied habitat selection forced by maximizing state-dependent reproductive value (McNamara and Houston, 1992) as a state-dependent ideal free distribution model of foragers under predation risk.

The output of an SDP model is the state- and time-dependent options which maximize fitness. To be used in the study of population dynamics, the optimal solutions can be applied in traditional state projection matrices and Monte Carlo simulations (IBM). Then the population consequences and sensitivity of deviations from the optimal policy can be investigated, or the adaptive change in strategy or behaviour that may be expected if the external forcing by the environment or by predation is altered. Probably, the road forward for SDP modelling is to utilize these possibilities by transferring the optimal solutions found by SDP into IBM ecosystem models and physical transportation models (Fig. 3).

Nature is inherently stochastic and only to a certain limit predictable. In some cases, such randomness has been included in SDP models (Yoshimura and Clark, 1991; McNamara, 1995; McNamara *et al.*, 1995), although to find the correct measure of

fitness becomes more complicated (McNamara and Houston, 1996). Another property of nature is that the future prospects of an individual may depend on the presence and actions of conspecifics and competitors, i.e. there is frequency- and density dependence. State variable models have been used to study evolutionary games (Clark and Ekman, 1995; McNamara, 1995), while density dependence can only be embedded by the assumption of stable populations such that juvenile growth or mortality must decline to compensate for larger population densities.

ADAPTATION APPROACH

Optimal control theory (e.g. SDP) ensures that optimal solutions to a specific problem are found by calculating all possible solutions and selecting the best (Schaffer, 1983). Computing power, however, puts severe restrictions on the size of solution spaces that can be studied using optimal control methods (Table 3). A range of ecological problems are too complex for all solutions to be calculated. Such complex optimization problems can instead be solved using heuristic techniques (Reeves, 1993). This is a group of computer techniques that search for optimal solutions to a problem by using an algorithm for moving about in solution space without keeping track of all possible solutions. A problem when using these techniques is that one is never certain that the global optimal solution to a problem is found unless this is verified by other means. Consequently it is possible to get stuck on local optima, although methods exist for decreasing the probability of this (Sumida *et al.*, 1990). The most common heuristic techniques are simulated annealing (Blarer and Doebeli, 1996), tabu search and genetic algorithms (Reeves, 1993; Saila, 1996). We will concentrate on the last, because this has been the most popular approach among ecologists.

Genetic algorithms

The genetic algorithm (GA) uses the principle of evolution by natural selection to evolve optimal solutions to a given problem (Holland, 1975). Although the GA was inspired by evolution, the method has had very few applications in ecology (Goldberg, 1989; Davis, 1991; Saila, 1996; Toquenaga and Wade, 1996). In addition to being an optimization tool, the GA has played a central role in the development of artificial life, a field that studies synthetic human-made life – life as it could be (Langton, 1989). We think that the GA may have some advantages over conventional methods in ecology, specifically in cases of a multi-dimensional state space, trophic couplings and density dependencies. To avoid confusion regarding mixing traditional genetic and GA genetic terminology, a ‘chromosome’ will be termed a string and a ‘gene’ will be termed a character (Goldberg, 1989). For an introduction to GAs see Goldberg (1989) or Mitchell (1996).

The GA may be considered as a wheel where each turn represents a generation, and some basic features are given below.

1. A major asset and potential difficulty in application of GAs is the representation of solutions to a problem as strings of bits (with values of 0 or 1), where the solutions are initiated randomly.
2. Each string is then passed through an evaluation routine where its fitness is calculated based on some fitness criterion. This procedure is the essence of relating the strings to the problem that needs to be solved. The string may be divided into several characters which together act to determine the fitness of the string.

3. When all the strings have been evaluated, they are ranked and selected in proportion to their fitness (Goldberg, 1989).
4. The selected strings may then be modified by recombinations and 'mutations'. Recombination is carried out by letting the pairs of strings exchange pieces of bits with each other. The length of such pieces can be chosen randomly, and from one to several 'crossing-over' points can be used. Furthermore, bit values may be changed by mutations from 0 to 1 or vice versa. More elaborate mutations such as inversions may be implemented if desirable. The modified 'new' strings are then ready to enter the next generation. This fulfils the GA, and this procedure will produce better and better solutions to the problem as the generations go by (Holland, 1975).

Evolving populations of motivated individuals

Most biological applications of GAs seem to be in molecular biology (Goldberg, 1989). The few applications in fish biology are, however, mostly related to spatial distributions. D'Angelo *et al.* (1995) used a GA to examine relationships between the physical characteristics and trout distribution in a stream. They found that the GA was a more efficient predictor of trout (*Oncorhynchus* sp.) distribution than was proportional trout distribution and multiple linear regression techniques. Dagorn *et al.* (1995, 1997) used a GA to study schooling and migratory behaviour in tropical tunas (Scombridae). In the latter paper (Dagorn *et al.*, 1997), a GA was applied to adjust the weights of an ANN (artificial neural network – p. 67) in a study of the spatial distribution of tuna in the Indian Ocean. The ANN was used to search for thermal fronts that are normally associated with high concentrations of food (Lehodey *et al.*, 1997). Two different models were applied to solve the problem, and the ANN model where the tuna were given learning abilities proved to be a much better predictor of tuna movement than the method using search without learning. Huse and Giske (1998) presented a modelling concept where a linked GA–ANN model is applied in an individual-based setting which they referred to as the ING (individual-based neural network genetic algorithm) model (Fig. 4). This model is used to explore the spatial distribution of a fish through its entire life span of two years with a daily resolution. Fish with favourable synaptic weights reproduce more because they are able to move about the heterogeneous and seasonal environment in a more productive manner than fish with poorer weights. From starting with randomly initiated synaptic weights, the populations of fish becomes increasingly better adapted to its environment by simulating the process of evolution by natural selection. As in real evolution, solutions to complex tasks such as homing behaviour and predator avoidance are best found by incremental evolution where the criterion for success changes in a stepwise way and gets progressively more narrow (Gomez and Miikkulainen, 1997). The behaviour of the fish (Huse and Giske, 1998) is determined by using reactive or predictive movement control. Reactive movement enables movement in environmental gradients whereas predictive movement relies on regular features of the environment, such as seasonal changes. In the model the fish applies these types of movement control for specific purposes: during feeding it uses reactive control whereas predictive control is more often applied during migration. This use of reactive and predictive control (Neill, 1979; Fernø *et al.*, 1998) is evolved in the model. After 300 years were simulated, the population achieved a migration pattern that was similar to that of the migrating fishes of boreal regions, such as the Barents Sea capelin.

Within the field of artificial life, several studies using GAs and ANNs have been

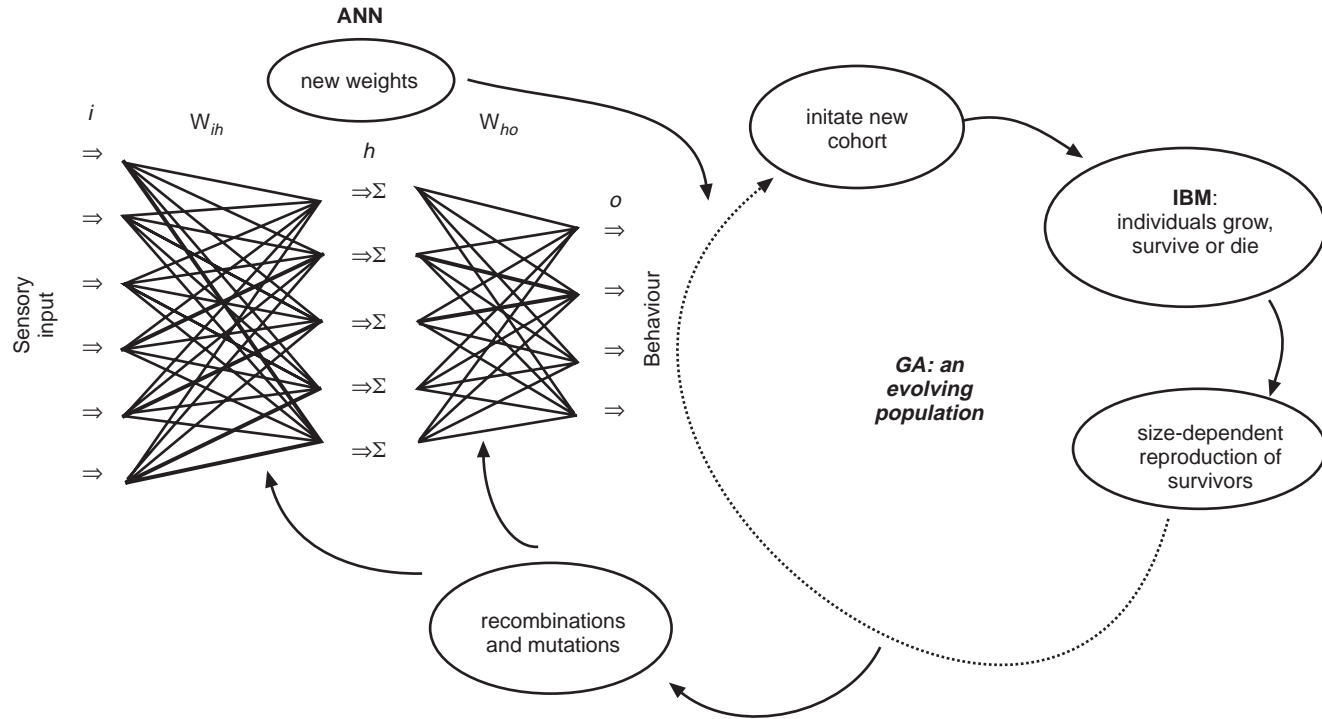


Fig. 4. The ING concept: one or more artificial neural networks (ANN) code for the decision process of individuals that are followed in an individual-based model (IBM). A cohort of individuals with randomly set strings coding for the weighting of the ANN are initiated in the first time step. The strings are then adapted using the genetic algorithm (GA) through the principle of evolution by natural selection. Differences between the strings are expressed through differences in weights of the ANN, which lead to behavioural differences. The i , h , and o refer to input, hidden, and output layers respectively (Fig. 2). The input layer consists of internal or environmental input. An output node fires if its value is above the threshold value. The lines indicate the relationship between the different layers. Each node in the i -layer is connected to all nodes in the h -layer, which again are connected to all nodes in the o -layer. W_{ih} and W_{ho} are the weight matrices of connection strengths between the nodes of the layers. Potential weight differences are indicated by the variation in line thickness of the connections. The GA will act to evolve the gene pool to contain the best possible response to the combinations of sensory input received throughout the lives of the individuals, as measured by the fecundity that results from the IBM given a particular ANN.

carried out and interested readers are referred to this literature (Langton, 1989, 1997; Ackley and Littman, 1992; Nolfi *et al.*, 1994; Menczer and Belew, 1996). A slightly different, but very interesting approach has been undertaken by Terzopoulos *et al.* (1995). They model artificial fishes with sensory abilities, learning, locomotion and behaviour. Their model is rooted in artificial life, and gives a candidate example of the benefit that ecological modellers would gain by paying attention to this literature.

Summary and conclusions

There exist mechanistic models for prey and predator location in aquatic environments, although the poor understanding of several sensory organs still limits their applicability in spatial modelling. We also have functional models of learning, motivation and decision making. Finally we have several different modelling tools for optimization and adaptation modelling. Evolutionary biology and rate maximization gives biological modelling a solid basis relative to other sciences. In economics, modern utility theory states that utility, the currency of welfare that is to be maximized, is neither measurable nor comparable between individuals (Quirk, 1987, p. 104). While ecologists are notoriously sceptical about optimality reasoning, this approach is mainstream within economics, despite the rather weak foundation of the objective function in utility maximization (Maynard Smith, 1996). This difference may be a result of history; while economists have thought in terms of optimality since Jeremy Bentham (1748–1832), optimization theory in ecology goes back only some 30 years, excepting the work by Lotka (1925) and Fisher (1930) which did not catch on at the time. The starting point of biology is more axiomatic than the utility maximization in economics. In biology there is variation generated by mutations and recombinations and adaptation shaped by natural selection over evolutionary history. Hence, biological optimization should be less susceptible to the criticism faced by economics, and should become equally important in due course. However, while physics remains with its rather restricted set of particles and forces, the numerous variables and processes in fish ecology may quickly become unmanageable. Any biological model must therefore be focused and parsimonious if process uncertainty and parameter uncertainty are not to ruin the credibility of the model (Håkansson, 1995).

Yet, we should accept that as a model can only incorporate a small subset of the universe, let alone the physiology of a fish larva, no single model or modelling technique should be regarded as *the* superior approach. Rather, any complex problem should be investigated by several models, which compete over predictability and explanatory power, and complement each other so that the scientist or manager may understand more (Hilborn and Mangel, 1997).

The functional models presented in this paper are concerned with how life history and behaviour should be so as to maximize the reproductive rate (fitness) of the individual. Such models are called ultimate, as they seek the most basic level of explanation. Yet, individuals are not aware that they are faithful obeyers of the rate maximization doctrine, so they need concrete external and internal stimuli to act upon. Models that explain behaviour in terms of these stimuli are called proximate. To date, optimality models are almost exclusively ultimate in design. There is therefore much work left to be done to establish the proper links between the ultimate forcings and the proximate triggers. It may seem that the artificial neural network combined with the genetic algorithm may develop into such a unifying approach. By this method of

evolving optimal solutions rather than by the analysis of them, the fitness function itself becomes invisible, as it does in the process of evolution. An understanding of ecology and evolution will still be needed to construct the most relevant ANNs, although the precise trade-offs will be found by the GA. This research programme may also overcome the problems we face today with combining state- and density-dependent forcings.

ING models are justified only for complex scenarios. The method will only yield numerical solutions and the mechanics of the evolved trade-offs are not made explicit. Although SDP is almost equally computer intensive, and cannot handle density dependency and strong trophic couplings, a clear benefit of SDP is that the optimal strategies become explicit. Both analytical (LHT and game theory) and less complex numerical tools (IFD) will also continue to be important research tools in spatial modelling of fish.

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