Evolutionary models for fisheries management

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ABSTRACT

The potential use of functional evolutionary models and mechanistic ecological models as predictive tools in fisheries ecology is discussed. Evolution by natural selection is a force that leads to ecological adaptations of the individuals in the populations. By mechanistic modelling of the sense organs, we may model how individuals perceive their environment, and by life history theory we may predict optimal responses to environmental variation. Modelling tools such as dynamic programming and individual-based modelling are discussed, and the coupling to physical models of the sea allows analyses that hindcast with explanatory power. Currently, our ability to forecast is limited by weather models. However, the quasi-periodic oscillations of the hemisphere-level ocean–atmosphere interactions bring hope for increased ability to make predictions in the future.

28.1   INTRODUCTION

In the first five years of the 20th century, the Norwegian Vöringen expedition investigated the physical and biological conditions of the Norwegian Sea, an area that was almost unknown beforehand. Helland-Hansen and Nansen discovered that the Barents Sea was fed by irregular transport of warmer Atlantic water along the coast of Norway. As there

was a two-year delay in the pulse of water from western Norway to the Barents Sea, they anticipated that ocean temperatures might be monitored and predicted. Large-scale biological events such as invasions of beluga whales and Greenland seals to Norwegian coastal waters, as well as poor growth and low condition of Atlantic cod, *Gadus morhua*, indicated food shortage in these waters at the time, and Helland-Hansen and Nansen linked this to water transport: 'We think that these discoveries give us the right to hope that by continued investigations it will be possible to predict the character of climate, fisheries, and harvests, months or even years in advance' (Helland-Hansen and Nansen, 1909, pp. iv–v).

While Helland-Hansen and Nansen cruised the unknown Norwegian Sea, the Wright Brothers were constructing the first motorized aeroplane. As this chapter is written, the Hubble telescope seeks out distant stars and planets. There has been tremendous scientific achievement in the 20th century, but the hopes of the early oceanographers have not been fulfilled. Will we ever be able to predict the future of fish stocks?

During the past 30 years, fisheries assessment has been based on catch-at-age analyses of various sorts, including virtual population analysis (VPA) and elaborations of it (Sampson, 1988). By measures of recruitment and assessment of fishing mortality, the year class strengths may be calculated. Hence, the number and biomass of fish aged $n + 1$ in year $y + 1$ may be predicted from numbers of fish aged n in year y. This method works well, in many cases. However, there are two cases where this is not a good tool: for short-lived fish and for variable environments.

Short-lived fish exist, but the stable ecosystem does not. Because the classical mathematical assessment tools assume stability, new methods are needed. In a world with stable ecosystems from which high-quality empirical relationships exist, theoretical approaches are of only academic interest. However, such models are valuable for management in fluctuating environments, i.e. where it is hardest to make predictions. And even if future events could not be predicted with much certainty, adaptive management would benefit from revealing causal relationships, as this understanding is needed to evaluate possible effects of a proposed management.

28.2   EVOLUTION AS A FORCE

The theory of evolution by natural selection gives a frame for understanding the processes of development, allocation patterns, life cycles and habitat choice. Individuals with a genetic composition that makes them more successful in reproduction, leave on average more offspring than other members of the population. By this process, the gene pool of the population is under continuous selection for alleles that are suited for

coping with the physical and biological environment. After 3.5 billion years of mutations, recombinations and natural selection, we are left with the evolutionary winners (Dawkins, 1976, 1996). This implies both: (1) that all species on Earth are reasonably well adapted to the environment in which their ancestors lived; and (2) that individuals are likely to have a genome that allows them to live almost optimally in order to spread their genes.

Therefore, there exists a predictive evolutionary force that operates on units exposed to natural selection: the behaviour of individuals will be aimed at maximizing their potential reproductive rate (Sibly, 1989, McNamara and Houston, 1996). This force can be utilized in environmental modelling to yield predictions of individual behaviour and growth patterns as well as life cycles and population dynamics (Fiksen *et al.*, 1995; Rosland and Giske, 1997; Giske *et al.*, 1998a). The objective for predictive ecological and fisheries modelling is to provide functional models, relating the activities of the individuals to fitness (and thereby to understand their ultimate motivations for behaviour), and mechanistic models relating the potentials for feeding, growth, reproduction and survival to the state of the environment. The mechanistic models will estimate the immediate gains and losses associated with, for example, a series of habitats, while the functional models will trade off these forces so that the action taken is the one that is most likely to maximize fitness. Mechanistic models will focus on sensory systems and physical, chemical and bioenergetical laws, while functional models must address which traits will spread in a population under natural selection.

28.3   THE STATUS OF COMBINING MECHANISTIC AND FUNCTIONAL MODELS

For a long period, mechanistic models of aerodynamics and hydrodynamics have been used to predict water movements, salinities, and temperatures in the sea. More recently, dynamics of nutrients and primary production have also been modelled mechanistically and have been coupled to the physical models (Aksnes, 1993; Aksnes *et al.*, 1995; Giske *et al.*, 1998b).

Far fewer models are available for the higher trophic levels: zooplankton, fish and sea mammals. The new challenge at these levels is that the organisms are (relative to phytoplankton and bacteria) long lived with complex life histories. They have, through evolution, been selected for performing different tasks through their lives, and they are to a high degree able to sense both their internal state and the external environment and behave optimally using evolved responses. Hence, modelling these higher

trophic levels may require different, but perhaps not more complex, mechanistic models. Modelling populations of animals that are able to relocate requires functional models that properly describe the fitness values of the multiple choices these individuals continuously perform (Tyler and Rose, 1994; Giske *et al.*, 1998a). The meagre success in modelling higher trophic levels in classical bottom-up biogeochemical models is probably related to the lack of proper behavioural control that only fitness-maximization imposes.

Theories that combine optimal behaviour with optimal life cycles first appeared in the 1980s (Mangel and Clark, 1986; Aksnes and Giske, 1990). Models of the sensory fields of fish (Jumper and Baird, 1991; Schellart, 1992; Bleckmann, 1993; Aksnes and Utne, 1997), bioenergetics (Kitchell *et al.*, 1977, Hewett and Johnson, 1992; Salvanes *et al.*, 1995) and of the environmental impact on growth and survival (Clark and Mangel, 1986; Giske *et al.*, 1994) are available, although only developed for a limited number of species and situations. The relatively homogeneous and transparent pelagic environment should give the best opportunities for linking ecological variables like depth and diet selection, group size, and swimming speed to growth and survival, as required by managers.

Predictive models are in need of biological theories but also of numerical methods to find solutions. Over the past decade, a series of techniques have become available. Optimizations based directly on life history theory (by the Euler–Lotka equation or a derivative) are often called static optimization (Leonardsson, 1991), as the state of the individual is not included and motivation is not allowed to change over short time intervals. Static optimizations are therefore best suited for principal analyses or large-scale phenomena, and can often yield analytical solutions. Examples are the growth–mortality trade-off for juvenile fish (Werner and Gilliam, 1984), habitat choice as a function of life history (Aksnes and Giske, 1990), age-dependent difference in acceptance of mortality risk (Giske and Aksnes, 1992), optimal timing for settling of codlings (Salvanes *et al.*, 1994), diet versus depth selection (Giske and Salvanes, 1995) and density-dependent habitat profitability (Giske *et al.*, 1997). There now also exists an extensive theoretical treatment of demography (Tuljapurkar, 1990) and adaptations in stochastic environments (Yoshimura and Clark, 1993).

Optimizations are called dynamic if the outcome will depend on changes in state of the individual. The state may be internal factors such as stomach fullness, fat reserves, body mass, or external factors such as group size or the spatial position within the habitat, and the optimal policy of the individual will change over time according to these variables and their fitness values. The most widely used dynamic optimization technique is stochastic dynamic programming (SDP, Houston *et al.*, 1988; Mangel and Clark, 1988). This method has been used to study vertical distributions of

fish populations (Clark and Levy, 1988; Rosland and Giske, 1994, 1997) as well as large-scale horizontal distributions (Fiksen *et al.*, 1995).

The use of individual-based modelling (IBM), whereby the population is represented by a large number of artificial individuals, has recently provided interesting results on how fish population processes are governed by the success of the few, rather than by the average success rate (Crowder *et al.*, 1992; DeAngelis and Rose, 1992; Rose *et al.*, 1993; Brandt and Hartman, 1993, and references therein). While SDP models are used to study individual variation in motivation for behavioural decisions, IBMs are good at resolving population consequences of variability in performance owing to stochastic processes and at interactive processes including density dependencies or trophic couplings. This approach has recently been much used in studying the ecology of fish larvae and in recruitment studies (Hinckley *et al.*, 1996; Letcher *et al.*, 1996; Werner *et al.*, 1996) and on growth rate estimates (Mason *et al.*, 1995; Mason and Brandt, 1996). The potential uses of IBMs in resource management have been discussed by Barnthouse (1992), Hansen *et al.* (1993) and Bart (1995).

Biological models of oceanic populations must interact with physical models of ocean dynamics. The forcing functions for the most-used oceanographic models are meteorological fields, such as air temperatures, air pressures, wind field, precipitation, solar radiation and cloud cover. Historical data for these forcing variables are stored in open archives, enabling models to mimic quite precisely the physical conditions that forced a particular historical biological event. For example Aksnes *et al.* (1989) calculated the spread of the toxic flagellate *Chrysochromulina polylepis* (killing salmon in aquaculture) in the North Sea in 1988, Hinckley *et al.* (1996) used meteorological forces to simulate drift of eggs and larvae in the Gulf of Alaska, and Fiksen *et al.* (1995) utilized meteorological data to calculate sea temperatures and zooplankton advection (to calculate habitat profitability for capelin) in the Barents Sea in 1979–1981. But, while this method gives eminent opportunity to recapitulate history, it also disables predictions of future events, as the horizon is limited to the weather forecast. Therefore, these models are currently used in hindcast analyses of past events, not in predictions.

To predict, a different type of physical forcing of hydrodynamical and biological models is needed. There is a strong chaotic element in the current weather forecasting models, but weather itself is not chaotic: seasonality itself shows that strong deterministic forces are operating. Also, on longer time scales, oceanographic and meteorological phenomena indicate strong influence from ordering forces. Examples are the El Niño–Southern Oscillation (ENSO: Rogers, 1984; Ropelewski and Halpert, 1987; Halpert and Ropelewski, 1992) in the Pacific and the North Atlantic Oscillation (NOA: Walker and Bliss, 1932; Van Loon and Rogers, 1978;

Wallace and Gutzler, 1981). These and other huge weather systems exhibit quasi-periodic oscillations (WMO and UNEP, 1995). Understanding these oscillations and how they are forced (Ikeda, 1990), will put us in a different situation with regard to predicting biological change as a function of climate oscillations months or years in advance.

28.4   PERSPECTIVES

The use of predictive models on historical data has already revealed causal relationships from physics and phytoplankton to fish. Theoretical models have also given insight into how the different external and internal forces interact to produce life histories and behaviour. With the continuous increase in computer capacity, in numerical methods, and in quantitative biological theories, a variety of theoretical models and predictive simulation models may soon play an increasing role in marine management.

More recently, complex ecological models (Aksnes *et al.*, 1995; Fiksen *et al.*, 1995) also indicate that the biological basis is improving for the creation of models predicting the future state of biological resources and environmental variables. However, these efforts are at present limited by the physical forcing, which so far hinges on meteorology. A different set of forcing functions, e.g. based on statistical analyses of climate variability or forcing by Earth and astronomical events, or on measured upstream changes in physical factors (Helland-Hansen and Nansen, 1909), will be needed for this purpose. Still, the uncertainties associated with these predictions will be formidable.

Meanwhile, we can do no better than to forecast by scenario modelling. From the current state of the environment, it may be possible to select a limited number of similar past situations and through them simulate possible outcomes. For capelin in the Barents Sea, the present ice and temperature conditions could be compared with those in previous years, and the meteorological conditions for similar situations could then be used to simulate some scenarios for the further development of temperatures and currents. In these physical scenarios, the biological models could be run, to simulate the probable development of the capelin stock. This may seem unsatisfactory, but nature is inherently stochastic, and the future in particular.

Scenario modelling is also a means of both quantifying and reducing the inherent uncertainties of nature as well as in process representations, parameter values and field data (Moxnes, 1996; Hagen *et al.*, 1998). The precautionary principle is already in use in the management of sea mammals (Gambell, 1993), and may also be adopted for fisheries (Garcia, 1994). By developing more advanced quantitative tools for understanding

nature, and by using them in models accounting for the potential variabilities in the forcing functions, we may be able to narrow the security measures needed for the protection of stocks and the environment (Mangel *et al.*, 1996), so allowing a sound utilization of the resources.

As the different theoretical approaches and numerical methods are only capable of handling bits of the total complexity, managers should be trained at using a variety of tools. By comparing results from very different models, managers will be more able to assess possible outcomes of their recommendations and acquire an understanding of the functioning of the system and its interacting components. This skill is a prerequisite for successful adaptive management.

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Chapter twenty-nine

Bayesian decision analysis and uncertainty in fisheries management

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ABSTRACT

Large variability and estimation errors in data create challenges for estimating risks and identifying appropriate fisheries management strategies. The formal quantitative method of decision analysis, sometimes referred to as statistical decision theory, can help deal with this challenge because it explicitly considers uncertainties in quantities such as parameters of dynamic processes in fish populations or fishing fleets. Field data can be used in conjunction with Bayesian statistical analysis to calculate probabilities associated with different estimates of the uncertain parameters. These probabilities can then be used as part of a decision analysis to identify the optimal management action for each specified management objective. We illustrate this approach of decision analysis with three examples. (1) The optimal decision for opening an in-river sockeye salmon fishery depended, among other things, on the assumed functional form (not just parameter values) of the stock–recruitment relationship, i.e. whether it was a Ricker model or a more flexible Shepherd model, which can take on various shapes, including a Ricker shape. (2) When uncertainties in density-dependent growth and in size-dependent vulnerability to fishing