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Review

Modelling swimming aquatic animals in hydrodynamic models

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ABSTRACT

Aquatic life exists between very small passive floating objects such as spores, eggs or seeds which are at the mercy of currents through to animals which swim powerfully enough to overcome most natural currents. There is a corresponding scale of cognitive and sensory capability. Coupling hydrodynamic with Lagrangian particle modelling is well established, as is individual based modelling of animal behaviour. These areas have developed rapidly, due to availability of faster computers. These different disciplines have fundamentally different conceptual frameworks, but the combination of techniques offers an unparalleled opportunity to model swimming animals in water more accurately. More accurate models of dispersion, migration and other spatial dynamics would support a better informed ecosystem management and provide methods to define protected areas that are linked in coherent networks. Development plans for tidal power schemes and offshore wind farms mean that predictive models of migrating fish are needed urgently. Statistical models based on correlations become inaccurate as the environments move to previously unobserved states. This is where models based on rules such as individual based models have a unique advantage. I briefly review Eulerian, Lagrangian, coupled Eulerian–Lagrangian water models, water quality models and individual based models of animal movements, navigation and interactive behaviour.

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1. Introduction

The aim of this review is to summarise the state of the art of different scientific fields in order to justify and inform further combined approaches in the future. This review supports the contention that there is a gap and an opportunity in our existing modelling capability which essentially is the coupling of models of physics and chemistry to ones of animal behaviour. The intention is to review several scientific fields in a way that is fresh and interesting to either a hydrodynamic modeller or an aquatic ecologist. I have attempted to identify pertinent issues and examples which relate to the main objective without replicating excellent existing reviews within multiple disciplines. A secondary aim is to collect together examples of directed swimming behaviour of aquatic organisms and modelling approaches which may be used to inform future studies. Tidal power, offshore wind power, coastal squeeze, climate change, agricultural intensity, and many other human activities will put aquatic life in situations for which there has been no precedent. The combined environmental and behavioural models discussed in this review show potential to predict the most likely response of aquatic animals to future environmental changes, including cumulative pressures, by examining fundamental causes in a rule-based approach.

The ways in which populations of animals distribute themselves over suitable habitat has been the subject of extensive study, developing through theoretical constructs such as ideal free distribution, optimal foraging theory, game theory and artificial neural networks ultimately to Stochastic Dynamic Programming (SDP) (Reviewed for fish in Giske et al., 1998). SDP provided the basis for a set of tools for ecologists to study movement, fitness and behaviour using sound evolutionary theory (Mangel, 2006). Giske et al. (1998) summarised; "Probably the road forward for SDP modelling is to utilize these possibilities by transferring the optimal solutions found by SDP into IBM [individual based model] ecosystem models and physical transportation models", and this review charts the continuation of the development of IBM's and physical transport models. Thus recently the focus has been on IBMs which encode parameters and behaviours of individuals to predict outcomes of relevance at the individual and population level (Camazine et al., 2003; Grimm and Railsback, 2005). IBMs are advantageous because models based on causal rules offer the opportunity to predict outcomes from first principles, whereas, models based on statistical correlations to past conditions become progressively less accurate as we move far from the existing data. IBM's combined with transportation models are important in aquatic contexts, where perhaps they are rarely so useful in terrestrial ecology, because they can model explicit paths of aquatic animals through complex and dynamic (often chaotic) environments and thus tease out the balance between passively moving at the mercy of currents (environmental context) and powered swimming (evolved behaviour). In addition to the transportation role mentioned above, hydrodynamic models can offer predictions of future habitat availability without necessarily linking transportation to currents (often through aggregated output such as mean bed shear stress, or maximum flow rate, etc.) and, as such, they can be directly used in combination with classical theoretical methods for animal movement. However, here I will focus on more tightly coupled models of individual animal behaviour with hydrodynamic models aimed at predicting how individual animals directly respond to water currents (or substances carried in currents) both actively through swimming and passively through advection.

This review continues with an outline of what is not covered followed by an introduction to hydrodynamic models, particle type models and the combination of the two. Then the review moves on to the potential swimming behaviour of living things. This serves as a reminder of the extraordinary range of possibilities and may aid the formulation of null hypotheses for future ecological models. First discussed are examples of vertical movement of larvae and eggs before addressing fisheries recruitment modelling and related examples. From this point the review moves to more complex models of animals moving vertically and horizontally and covers the emerging potential of models to capture both individual and population dynamics. Navigation, orientation and movement methods are defined and reviewed before exploring the potential of interactive behaviour (where modelled individuals respond directly to others in the same model). Models of interactive behaviour have been particularly successful in capturing natural patterns in terrestrial biology and, on a few occasions, aquatic biology. Finally the review is summarised with a section on uncertainty and a brief overview of future directions and requirements.

Most examples of modelling given here are combinations of:

(1) hydrodynamic modelling, directed at the physics of the movement of water,
(2) water quality models, which predict the fate of physical substances, chemicals, and simple organisms, such as algae or phytoplankton and
(3) ecological models which target animal behaviour.

In order to provide a framework for explanation and a roadmap through some of the nomenclature in this review the connections and dependencies between these models (or sub-models) can be represented diagrammatically (Fig. 1). Some generality is inevitable in such a simplification. There is little consensus in some of the naming schemes, and there are many examples of excellent approaches that deviate from this simple structure. This review is roughly organised in sequence from the bottom right to the top left of this diagram, and covers existing approaches of combining such sub-models which have been developing over at least 20 years.

1.1. What is not covered

1.1.1. End-to-end ecosystem models

This review does not cover end-to-end ecosystem models (reviewed in Fulton, 2010) which can encompass all the elements