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Towards developing a general framework for modelling vertical migration in zooplankton

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HIGHLIGHTS

- Existing models of diel vertical migration (DVM) in zooplankton assume that animals should optimize a certain 'universal' criterion.
- The choice of the optimization criterion is often subjective and this would strongly affect predictions of models.
- We show that DVM can be unambiguously obtained as an outcome of selection in the underlying equations of genotype/trait frequency dynamics.
- We consider four generic DVM models and demonstrate that in each model we need to maximize a different functional.
- The infinite dimensional trait space of strategies can be projected onto a low dimensional subspace of generalized parameters and the evolution dynamics can be followed using this subspace.

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ABSTRACT

Diel vertical migration (DVM) of zooplankton is a widespread phenomenon in both oceans and lakes, and is generally considered to be the largest synchronized movement of biomass on Earth. Most existing mathematical models of DVM are based on the assumption that animals maximize a certain criterion such as the expected reproductive value, the venturous revenue, the ratio of energy gain/mortality or some predator avoidance function when choosing their instantaneous depth. The major shortcoming of this general point of view is that the predicted DVM may be strongly affected by a subjective choice of a particular optimization criterion. Here we argue that the optimal strategy of DVM can be unambiguously obtained as an outcome of selection in the underlying equations of genotype/traits frequency dynamics. Using this general paradigm, we explore the optimal strategy for the migration across different depths by zooplankton grazers throughout the day. To illustrate our ideas we consider four generic DVM models, each making different assumptions on the population dynamics of zooplankton, and demonstrate that in each model we need to maximize a particular functional to find the optimal strategy. Surprisingly, patterns of DVM obtained for different models greatly differ in terms of their parameters dependence. We then show that the infinite dimensional trait space of different zooplankton trajectories can be projected onto a low dimensional space of generalized parameters and the genotype evolution dynamics can be easily followed using this low-dimensional space. Using this space of generalized parameters we explore the influence of mutagenesis on evolution of DVM, and we show that strong mutagenesis allows the coexistence of an infinitely large number of strategies whereas for weak mutagenesis the selection results in the extinction of most strategies, with the surviving strategies all staying close to the optimal strategy in the corresponding mutagenesis-free system.

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1. Introduction

One of the most intriguing features of marine and freshwater zooplankton is the phenomenon of regular diel vertical migration (DVM) which is often considered to be the largest synchronized movement of biomass on our planet (Hays, 2003; Kaiser et al., 2005).

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DVM plays a major role in the carbon exchange between the surface waters and deeper layers and potentially has a strong influence on Earth's climate (Ducklow et al., 2001; Buesseler et al., 2007). A typical DVM pattern consists in ascending to food rich surface waters for feeding on phytoplankton at night, then descending to deep layers and remaining there during the day (Ohman, 1990; Hays, 2003). Currently, the most supported explanation for DVM in the literature is that it is an adaptive behavioral response allowing animals to both feed in food rich shallow waters and escape from visual predators such as planktivorous fish, which are more efficient in the day time (Bollens and Frost, 1989; Ohman, 1990; Lampert, 1989; Fortier et al., 2001; Pearre, 2003). It has also been pointed out that zooplankton may perform DVM for some other reasons, such as saving energy in deep waters due to the low temperature, avoiding solar radiation or increasing genetic exchange (McLaren, 1963; Mangel and Clark, 1988; Pearre, 2003). Despite the fact that the phenomenon of DMV in zooplankton has been extensively studied both empirically and theoretically, there is still a rather poor understanding of the key factors which shape this migration behaviour (Mangel and Clark, 1988; Pearre, 2003; Ringelberg, 2003; Morozov et al., 2011).

Various mathematical models have been proposed in the literature, which explains the emergence of DVM as a trade-off between food consumption and predator avoidance. A number of models use elements of game theory, assuming that organisms maximise their gain based on a certain pay-off matrix which can differ from model to model (Iwasa, 1982; Gabriel and Thomas, 1988; Gabriel et al., 1988). Other related approaches are based on the idea that organisms should maximize some fitness function, for instance, the expected individual reproductive value (Fiksen and Giske, 1995; Fiksen and Carlotti, 1998; Mangel and Clark, 1988), the 'venturous revenue' (Liu et al., 2003, 2006), the ratio of energy gain/mortality (De Robertis, 2002) or minimize instantaneous changes in some particular types of predation pressure (Han and Straskraba, 1998; Han and Straškraba, 2001). Models using different optimization criteria generally predict similar patterns of migration, in the sense that the optimal strategy is to stay in deep waters during the day and feed at night near surface, as is widely observed in real plankton systems. However, when more specific features are considered, for instance, the optimal choice of the instantaneous depth by animals through the day, or the dependence of the amplitude of migration and the average depth on the key parameters (e.g. the amount of predators, food, light intensity, etc), the implementation of different models can predict different outcomes (Fiksen and Giske, 1995; Han and Straškraba, 2001; Liu et al., 2003).

One of the main shortcomings of the existing models of DVM, as in many other models of animals' optimal strategies, is that the choice of optimization criterion is often subjective and based on conventional wisdom or even individual preference of the researcher (cf. Mangel and Clark, 1988). As a result, the fact that the optimal behaviour predicted can be strongly affected by the choice of optimization criterion is a serious shortcoming. As an alternative approach, we can make a natural assumption that the organisms follow Darwin's idea of the survival of the fittest (Darwin, 1964; Wright, 1986), which can be formalized by means of mathematical modeling. In the case where we have model equations adequately describing the given biological system, we can expect that the fittest genotypes will be those which will persist in the system whereas the others will go extinct. Mathematically, this would signify that the relative frequency of unsuccessful genotypes should vanish compared with the that of better fitted individuals (Gorban, 2007; Karev, 2010; Kuzenkov and Ryabova, 2015). In the long run, the best animal strategies will dominate less efficient strategies. Note that a similar concept is the basis of the adaptive dynamics paradigm, where evolution of genotypes/strategies is the result of consecutive invasions by small amounts of genetically close mutants, and the eventual outcome is a strategy which cannot be invaded by nearby mutants (Dieckmann et al., 2002; Geritz et al., 1998; Parvinen et al., 2006; Hoyle and Bowers, 2008).

In this paper, we explore the patterns of optimal zooplankton DVM obtained from the dynamics of the genotype/ functional trait distribution in the strategy space. Unlike earlier models, the optimal strategy of DVM is now an emerging property of the given model, i.e. it is independent of any the optimization criterion. Here we are interested in finding the optimal trajectory of an animal in terms of the instantaneous depth $x(t)$ of a zooplankter in the water column throughout the day. The choice of a particular strategy $x(t)$ will automatically determine the population dynamics of the given zooplankton cohort and its eventual evolutionary outcome. Each strategy can be considered as a function-valued trait, and so mathematically the space of available genotypes is infinite-dimensional. We demonstrate how the optimal strategy of DVM can be found in such a space, and how we can follow the dynamics of strategy distributions across the space of genotypes/ functional traits. Unlike some previous works considering function-valued traits (Parvinen et al., 2006; Dieckmann et al., 2006), we do not implement the adaptive dynamics formalism here. This allows us to consider a system with long-range mutation (strong mutagenesis) in the genotype space as well as the possibility of invasion by individuals with any possible genotype structure.

As insightful examples, we derive the optimal DVM for four zooplankton models: three single-species models (one of which explicitly includes developmental stages) and a predator–prey model. In each case, we unambiguously define a generalized fitness function R, maximisation of which gives the optimal strategy of migration $x(t)$; all other genotypes eventually go extinct. We consider the effects of key parameters such as predation pressure, food abundance, metabolic cost of migration, etc., on the optimal strategy of DVM. We demonstrate that although the models predict broadly qualitatively similar patterns (i.e. feeding at upper layers at night and staying in deeper layers during the day), variation of food availability may affect the response of optimal strategy differently, both in terms of the amplitude and the average depth. Finally, we show that the infinite dimensional space of DVM strategies can be projected onto a low dimensional space of generalized traits. Considering such a space allows us to model evolution of strategies both for a weak and a strong mutagenesis. In particular, we show that a weak mutagenesis results in extinction of most of strategies, except for those in the vicinity of the optimal strategy in the mutagenesis-free scenario.

The paper is organized as follows. Section 2 introduces the generalized variational principle of biological selection. In Section 3, four basic models of zooplankton dynamics are introduced and the expression for the generalized fitness is derived in each case. In Section 4, the optimal strategies of DVM for all models are analyzed and then compared and the role of mutagenesis in the on selection process is investigated. In Section 5, the main results are summarized and further ideas are considered for finding optimal DVM strategies in more complex models.

2. General variational principle of natural selection

Here we discuss the generic mathematical framework of modelling a process of natural selection which will be further applied to modelling DVM of zooplankton.

Let us assume that the behavioural strategy v of an organism is genetically inherited and belongs to a certain space V of genotypes or functional traits (finite or infinite dimensional). In terms of DVM, V can include the amplitude of migration, the average depth throughout the day or the instantaneous spatial location of

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