Towards landscape ecological modelling of marine reserves

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Abstract: The dispersal of propagules is a critical process for most terrestrial and marine systems. For example, it has been shown that larval dispersal enables to connect fish populations in networks of marine reserves. However, most current marine reserves models include an over-simplified representation of dispersal. The major limitation to using more sophisticated approaches has traditionally been the uncertainty surrounding larval dispersal patterns. We report recent improvements in methods and tools for modelling and measuring larval dispersal and show how they will allow integrating modelling of marine reserves into the wider field of landscape modelling.

Keywords: fish egg; fish larva; ichthyoplankton; marine reserve; marine protected area; dispersal; connectivity

Introduction

Most of the questions and methods used in landscape ecology for terrestrial ecosystems are also relevant for marine ecosystems. For example, there is a large body of literature on landscape connectivity in terrestrial systems (recently reviewed by Kindlmann and Burel, 2008), which has many natural parallels with fragmented marine systems like coral reef ecosystems. A landscape is composed of suitable habitats and a non suitable matrix that connects them. In a coral reef system habitats are reefs and the matrix is the water and sandy habitats not suitable for settlement. The distinction between structural and functional landscape connectivity is also essential for reef systems: the spatial distribution of reefs and water movements determine the structural connectivity, while the behaviour of organisms (within the matrix) contribute to the functional connectivity. Despite these parallels between terrestrial and marine ecosystems, there are only a limited number of studies where the concepts of landscape ecology are applied to marine ecosystems (Hinchey et al., 2007). And except for a few attempts to relate patterns and processes in oceanic systems (e.g., Bakun 1996), marine landscape ecology has traditionally focused on littoral systems (e.g., intertidal systems). Yet some questions and concepts of landscape ecology apply to oceanic systems too. Here we focus on one of them, the connectivity of populations via the dispersal of propagules. In the following sections, we briefly compare the relative importance of propagules dispersal within terrestrial and marine reserves and underline two limitations of most current marine reserves models in the way they include dispersal. We then report recent improvements in our ability to model and measure larval dispersal and show how they will allow us to integrate modelling of marine reserves into the wider field of landscape modelling.

1. Dispersal in terrestrial and marine reserves

Though some terrestrial plants seeds are dispersed by water or animals, most of them are wind-dispersed. There are therefore many parallels between terrestrial plant seed dispersal and marine larval dispersal. For example, in both cases dispersal occurs in three-dimensions and is largely influenced by a physical process, wind for seed dispersal, oceanic currents for larval dispersal. However, there are also significant differences between dispersal of plants and fish. An important difference is the spatial scale at which dispersal occurs. According to Kinlan and Gaines's (2003) comparative review of propagule dispersal in marine and terrestrial environments, the genetically-estimated dispersal scales of demersal fish species (in the range 1–1000 km) is typically orders of magnitude larger than the estimated dispersal scale of terrestrial plants species (0.1 m–10 km). Terrestrial and marine reserves typical sizes are between a few 100 m to a few 10 km (e.g., Halpern, 2003), which is relatively large compared to the typical scale of dispersal in terrestrial systems but small compared to the typical scale of dispersal in marine systems. There is therefore a global view that terrestrial reserves would be relatively closed systems, with little exchanges between them, whereas marine reserves would be more open (Carr et al., 2003), with significant exchanges between them. Another major difference between seed dispersal and fish larval dispersal is that during their dispersal phase fish eggs and larvae develop into different life stages. Most fish develop from egg to yolk-sac larva where individuals carry their own food reserves, to early larva where they have developed a functional jaw and pigmented eyes that allow them to catch food, to late larva where they have fins and are therefore able to swim.

2. Dispersal in marine reserves models

In the previous section we stressed the importance of the larval dispersal process on connectivity of populations between marine reserves. However, prevailing methods for designing marine reserves networks remain strictly habitat based (e.g., Klein et al., 2008; Watts et al., 2009) and do not take into account concepts such as population connectivity. In their review of marine reserves models, Gerber et al. (2003) noted that few models have attempted to explicitly consider the dispersal process. We also underlined the importance of ichthyoplankton ontogeny during dispersal. Depending on their development stage, fish eggs and larvae face very different risks of starvation and movement abilities. Yet in most marine reserve models the size or age structure of the population is not taken into account

(Gerber et al. 2003). A number of authors have recently developed spatial metapopulation models of marine reserves networks (e.g., Walter et al., 2007; Kaplan et al., 2009). The major limitation to using more sophisticated modelling approaches is the considerable uncertainty surrounding larval dispersal patterns (Shanks et al., 2003). However, methods and tools for modelling and measuring and larval dispersal are now available, as we report in the next two sections.

3. Fish larval dispersal models

There are many modelling studies that have focused explicitly on fish larval dispersal (reviewed in Miller, 2007, Werner et al., 2007, Metaxas and Saunders, 2009). These models incorporate a description of both the physical environment and the biological properties of the eggs and larvae. The physical environment is simulated using regional circulation models (RCM) like ROMS (Shchepetkin and McWilliams, 2005) or MARS (Lazure and Dumas, 2008) and the biological processes are described using an individual-based model (IBM). The approach that is generally used to implement fish larval dispersal models is the following. First the RCM is run to provide 3D dynamic fields of physical variables like current velocity and temperature (and potentially other variables like phytoplankton concentration if a hydrodynamic-biogeochemical coupled model is used). Then these fields are used as inputs to the IBM that tracks the location of a collection of individuals over time (and potentially other variables like their size). In the IBM, the processes generally included for the eggs and larvae are transport, growth, behaviour and mortality. The behavioural processes considered are mainly movement of eggs and larvae in the vertical dimension, due to egg buoyancy and larval vertical migration. As an example, a suite of larval dispersal modelling studies was applied to anchovy (*Engraulis encrasicolus*) in the southern Benguela upwelling system off South Africa. Spawning areas of several fish species, including anchovy, are mainly located along the south coast of South Africa, whereas the nursery areas of these species, where the larvae find phytoplankton and zooplankton to feed on, are located on the west coast. The modelling studies therefore aimed at investigating the physical and biological processes that allow the eggs and larvae being transported from the south coast to the west coast. Results showed the critical importance of a coastal jet current in this transport (Huggett et al., 2003) but also of biological properties like egg density (Parada et al., 2003) and larval behaviour (Mullon et al., 2003). This is an example of a simple study of connectivity between two habitats (spawning and nursery) using a dispersal model. Similar studies have been conducted in more fragmented landscapes like coral reefs ecosystems. For example, Cowen et al. (2006) used a GIS to identify the potential settlement habitats for reef fish in the Caribbean Sea. They then used a larval dispersal model to estimate the connectivity between these different habitats, and could identify major biogeographic breaks in the region and, conversely, areas with particularly strong connections. Tools for easily implementing fish larval dispersal models are now available (e.g., Ichthyop, Lett et al., 2008).

4. Fish larval dispersal data

Direct validation of results obtained from larval dispersal models has traditionally been challenged by the difficulty of following a multitude of small individuals, such as fish eggs and larvae, in the field. But again in coral reef ecosystems, new microchemical and genetic techniques have been developed to overcome this challenge. Using these techniques, different authors (Jones et al., 2005; Almany et al., 2007; Planes et al., 2009) could build a connectivity matrix showing the number of larvae exchanged between 5 lagoons. This was at a very small scale (~1 km), but the same approach was also used at larger scale (~100 km) to estimate the connectivity between islands. One surprising result of these empirical studies is the relatively high degree of self-recruitment, suggesting that the typical terrestrial assumption of a closed reserve system may be applicable to coral reef systems as well. While these techniques show great promise, they have yet to be applied to larger population sizes, such as the temperate species of greatest interest to industrial fisheries.

Conclusion

According to several authors (Levin 2006; Jones et al., 2009), the challenge that remains now is to integrate modelling and experimental studies of marine population connectivity into a single coherent approach. This is precisely the objective of a project that we submitted to the “French Research National Agency” for funding. In this project we propose to conduct experimental and modelling studies of larval connectivity among reefs in New Caledonia, some of which are within marine reserves. We have shown how two major limitations of current marine reserves models (an over-simplified representation of larval dispersal and the absence of size-structure for dispersing individuals) could be overcome by using a better representation of larval dispersal patterns coming from larval dispersal models. The goal of this proposed project is to test our ability to make these improvements in a real, spatially-heterogeneous marine landscape that poses significant managerial questions regarding the protection of sensitive marine resources.

The main human threat to terrestrial systems is likely habitat degradation, whereas it is fishing pressure for marine systems (Carr et al. 2003). Therefore, terrestrial and marine reserves have been historically developed with different goals, maintaining biodiversity for terrestrial reserves, maintaining commercial fish biomass for marine reserves. However, habitat degradation is also becoming an issue in marine systems and therefore maintaining both commercial fish biomass and biodiversity is a concern today. However, most models of marine reserves are still single-species models and can therefore not be used to answer questions about biodiversity. But there is a strong movement of the modelling community towards multi-species models within the framework of an ecosystem approach to fisheries. The three limitations of current marine reserves models mentioned above lead Gerber et al. (2003) to the conclusion that most marine reserves models are “strategic” models, in the sense that they are simple models developed to answer broad questions, rather than “tactical”, more complex models appropriate to specific situations and designed to make local decisions. It is clear that we are moving from strategic to tactical models, and it is in this sense that we conclude that we are moving towards landscape ecological modelling of marine reserves.

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