



# Projecting changes in the distribution and productivity of living marine resources: A critical review of the suite of modelling approaches used in the large European project VECTORS



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## ABSTRACT

We review and compare four broad categories of spatially-explicit modelling approaches currently used to understand and project changes in the distribution and productivity of living marine resources including: 1) statistical species distribution models, 2) physiology-based, biophysical models of single life stages or the whole life cycle of species, 3) food web models, and 4) end-to-end models. Single pressures are rare and, in the future, models must be able to examine multiple factors affecting living marine resources such as interactions between: i) climate-driven changes in temperature regimes and acidification, ii) reductions in water quality due to eutrophication, iii) the introduction of alien invasive species, and/or iv) (over-)exploitation by fisheries. Statistical (correlative) approaches can be used to detect historical patterns which may not be relevant in the future. Advancing predictive capacity of changes in distribution and productivity of living marine resources requires explicit modelling of biological and physical mechanisms. New formulations are needed which (depending on the question) will need to strive for more realism in ecophysiology and behaviour of individuals, life history strategies of species, as well as trophodynamic interactions occurring at different spatial scales. Coupling existing models (e.g. physical, biological, economic) is one avenue that has proven successful. However, fundamental advancements are needed to address key issues such as the adaptive capacity of species/groups and

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ecosystems. The continued development of end-to-end models (e.g., physics to fish to human sectors) will be critical if we hope to assess how multiple pressures may interact to cause changes in living marine resources including the ecological and economic costs and trade-offs of different spatial management strategies. Given the strengths and weaknesses of the various types of models reviewed here, confidence in projections of changes in the distribution and productivity of living marine resources will be increased by assessing model structural uncertainty through biological ensemble modelling.

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## 1. Introduction

Marine habitats provide resources critical for the wellbeing of society including food security and energy (Lam et al., 2012; Merino et al., 2012). For the effective stewardship of living marine resources, it is critical to understand the factors and processes that may have interacted to cause historical changes in distribution and productivity (Simpson et al., 2011; Sumaila et al., 2011; Blanchard et al., 2012). Furthermore, it is important to develop tools and approaches that provide robust projections of future changes (Metcalfe et al., 2012; Jørgensen et al., 2012), particularly within regional seas and their coastal habitats (Luisetti et al., 2011). Nearly one third of our burgeoning human population inhabits areas surrounding regional seas. Multiple drivers (e.g., the need to maintain food security, requirements to increase renewable energy sources, maintaining viable shipping routes) have made coastal areas and shelf seas hotspots of pressures (Doney, 2010) such as, the potential for over-fishing, increased nutrient runoff/inputs causing eutrophication, physical alteration/loss of marine habitats, continued risk of introduction and spread of invasive alien species). Given the diversity of anthropogenic activities and effects, the development of tools that can examine the interaction among various pressures such as climate and overfishing (Perry et al., 2010; Griffith et al., 2012), will be important for projecting impacts and providing effective management advice for living marine resources.

Changes in the productivity and changes in the distribution of a species are likely to be strongly coupled (Blanchard et al., 2011) but the processes causing the former and latter may differ. Patterns in distribution result from interactions between physical (ocean currents/inflow, temperature, salinity, or substrate type) and biological processes (e.g., predator-prey relationships, competition) and both are influenced by anthropogenic activities. Changes in the distribution of marine organisms, including shifts towards higher latitudes or deeper waters in response to ocean warming, are well documented (Dulvy et al., 2008; Rijnsdorp et al., 2009; Sunday et al., 2012; Hiddink et al., 2015). At temperate latitudes, these shifts are associated with the appearance of Lusitanian fauna (organisms traditionally distributed in warmer waters) and reduced extent or loss of boreal species (Sunday et al., 2012). In most cases, species move (or disappear) from areas after critical thresholds in abiotic factors (temperature, salinity, dissolved oxygen and pH) are exceeded (Pörtner and Peck, 2010; Pörtner, 2012). In European waters and elsewhere, these climate-driven shifts (Beaugrand and Reid, 2003; Beare et al., 2004; Perry et al., 2005; Rijnsdorp et al., 2009) as well as the increasing number of alien species introduced via ballast waters, released from aquaculture (Hulme et al., 2008) or migrating through man-made waterways such as the Suez Canal (Galil et al., 2014) are creating novel mixtures of species with unforeseen consequences to the structure and function of marine food webs (i.e. Hobbs et al., 2009).

In contrast to changes in distribution, changes in the productivity of a species can result from a mixture of trophodynamic (bottom-up and top-down) processes. Bottom-up processes can

alter growth performance and the reproductive potential of adults (Marshall et al., 2000; Kraus et al., 2002) as well as the rates of survival of their progeny (e.g. Sundby, 2000) whereas top-down processes can regulate lower trophic levels (Shurin et al., 2002; Frank et al., 2005; Mueter et al., 2006). A further complication is that the strength of these various trophodynamic processes can be influenced by changes in key abiotic factors on species such as changes in life history scheduling and match-mismatch dynamics between predators and their prey resources (Clark and Frid, 2001; Hunt et al., 2002; Beaugrand et al., 2003; Kempf et al., 2013). It is critical to track changes in the productivity of different populations since changes in productivity of local populations can be misinterpreted as an active migration of species to higher latitude (Petitgas et al., 2012a).

A variety of modelling tools has been utilized to examine historical changes in distribution and/or productivity of living marine resources (Fig. 1). Often designed for specific objectives, these tools differ markedly in complexity, from simple statistical descriptions of trends in historical field data to more complex physiological models attempting to understand the mechanisms underlying habitat requirements of species, trophic groups or any other kind of assemblage (Jørgensen et al., 2012). Another sub-set of modelling approaches has focused on providing spatially explicit representations of trophodynamic structure and function of ecosystems. Finally, the most complex, “end-to-end” models create virtual ecosystems incorporating industries, allowing trade-offs between various, competing economic sectors and activities (e.g., fisheries, renewable energy, conservation) to be examined in a management evaluation framework (Fulton et al., 2011). These various tools can offer insight, to a greater or lesser extent, on the mechanisms acting to cause historical changes in distribution and productivity of living marine resources and some allow projection of future trajectories. Plagányi (2007) provided a thorough review of the merits of various modelling tools in the context of ecosystem-based fisheries management while Travers et al. (2007) provided a retrospective on various modelling approaches leading to the design of size-based food web and end-to-end models. From the perspective of informing policy, Piroddi et al. (2015) reviewed the ability of ecosystem models to provide information on indicators of good environmental status established for EU waters while Hyder et al. (2015) reviewed 14 different ecosystem models currently operational in the UK with regard to their applicability to provide advice on five sets of policy questions including spatial management issues in the North Sea and NE Atlantic.

In this study, we compared four modelling approaches developed to estimate changes in the distribution and/or productivity of living marine resources. The suitability of each method for understanding and projecting changes that arise from interacting drivers is also discussed. Model approaches considered were: 1) statistical modelling of habitat associations including bioclimate envelope models; 2) biophysical models of single species and/or life stages; 3) spatially explicit food web models; and 4) end-to-end models. Some of these approaches rely heavily on the statistical analysis of historical observations (1), while others are coupled physical-

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