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Discussion

Forecasting marine invasions under climate change: Biotic interactions and demographic processes matter

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ABSTRACT

Biological invasions are one of the most significant threats to marine biodiversity, and can be facilitated and amplified by climate change. Among all aspects of invasion biology, biotic interactions between invaders and native species are of particular importance. They strongly influence the invasion velocity as well as species responses to climate-induced stressors. Yet the effects of biotic interactions and other important demographic processes remain overlooked among most studies of climate-mediated invasions. We critically assessed current modelling techniques for forecasting marine invasions under climate change, with a particular focus on their ability to account for important biotic interactions and demographic processes. We show that coupled range dynamics models currently represent the most comprehensive and promising approach for modelling and managing marine invasions under climate change. We show, using the crown-of-thorns seastar (*Acanthaster planci*), why model architectures that account for biotic interactions and demographic and spatial processes (and their interaction) are required to provide ecologically realistic predictions of the distribution and abundance of invader species, both under present-day conditions and into the future. We suggest potential solutions to inform data-poor situations, such as Bayesian parameter estimation and meta-analysis, and identify strategic and targeted gaps in marine invasion research.

1. Introduction

Marine invasive species are a major threat to biodiversity worldwide and can have profound ecological and economic impacts on marine ecosystems (Bax et al., 2003). Although the criteria that categorise a species as invasive remain somewhat controversial, invaders are commonly characterised as species that undergo rapid increases in abundance and/or spatial occupancy with adverse effects on recipient ecosystems (Valery et al., 2008). This definition includes the case of ‘native invaders’ that can spread within their historical range by exploiting niche opportunities resulting from human activities and/or loss of other species: by attaining extreme abundances and exerting severe per-capita effects on local communities, native invaders can indeed cause ecological impacts that rival those of non-native invaders (Valery et al., 2009; Carey et al., 2012). Whether native or not, invaders can impact recipient communities directly through competition, predation, and hybridization, and indirectly by modifying habitats and potentially disrupting their suitability. Over 1500 species have invaded locations throughout the world's oceans, and more are discovered every year (European Environment Agency, 2012). The potential economic costs incurred by even a single marine invasive species can reach US$250 million yr^{-1} (Williams & Grosholz, 2008) and eradication seems possible only in highly constrained situations (Bax et al., 2002). Future climate change is predicted to increase the introduction and spread of invasive species, accelerating marine invasions and resulting in widespread biodiversity loss (Garcia Molinos et al., 2016).

The ecological traits that commonly characterize marine invasive species are disproportionately favoured under climate change, potentially exacerbating future impacts of marine invasions (Poloczanska et al., 2013). This is because marine invaders often tend to be generalist and/or opportunists with relatively plastic life histories (Clavel et al.,

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2011), making them able to better adapt to rapidly changing environmental conditions and fare better in warming waters than native species (Sorte et al., 2013; Bates et al., 2013). By relaxing some of the physiological constraints on temperature-dependent growth and survival while also altering connectivity, human-induced climate change has already enabled some non-native invasive species to expand into regions where they previously could not survive and reproduce, as exemplified by the green 'killer' algae *Caulerpa taxifolia* in the Mediterranean (Walther et al., 2009). Additional climate-related factors that might enhance a species' invasive ability include: extensions of spawning periods and increases in per capita reproductive output (Walther et al., 2009); altered timing of recruitment and faster growth in warmer years (Stachowicz et al., 2002); faster developmental rates (Walther et al., 2009); and modified local dispersal patterns due to altered hydrodynamic conditions (Diez et al., 2012). In the case of native invaders, climate-driven environmental changes at local scales (e.g. eutrophication, altered connectivity due to changes in ocean currents) can favour the dominance of invaders in parts of their historical range where they previously could not survive or reproduce (Carey et al., 2012).

Despite these established physiological and demographic responses to climate change, there have been few attempts to forecast the potential impact of invasive species under climate change and test the efficacy of alternative management actions (Sorte, 2014). Most existing knowledge is based on local field observations or mesocosm experiments (e.g., Cockrell & Sorte, 2013) that are often conducted at small scales and/or do not necessarily represent realistic environmental conditions. More integrated approaches that combine empirical data on local and regional ecological processes with simulation models are urgently needed in marine invasion biology to improve our knowledge of impending invasions and to manage existing and future invasive species (Fordham, 2015).

A commonly overlooked consequence of climate change affecting marine invasions is the way climate change alters ecological interactions in native communities (Sorte et al., 2010). Climate-driven changes in invasive ability affect the way native communities are organised, facilitating the formation of novel ecological communities characterised by new arrangements and ecological interactions (Lurgi et al., 2012). Such new configurations can create ecological vacuums that facilitate future invasions, especially if top predators are depleted (as frequently reported in response to global change; Cheung et al., 2015). Other anthropogenic stressors such as fisheries exploitation, terrestrial runoff, and eutrophication can act in synergy with climate change to facilitate not only invasions by alien species but also state-shifts of species dominance, as for example, in the case of invasive jellyfish (gelatinous plankton; Fig. 1) (Licandro et al., 2010; Lynam et al., 2011). These interactions can be complex, with climate change and other anthropogenic stressors having both direct and indirect effects on the strength of biotic interactions (e.g. competition, predation). Consequently, not only is the dominance of invasive species likely to change owing to synergies between anthropogenic stressors, but also the number and strength of their biotic interactions between invasive and other species, with potentially multiplying effects brought about by trophic cascades (Lynam et al., 2011).

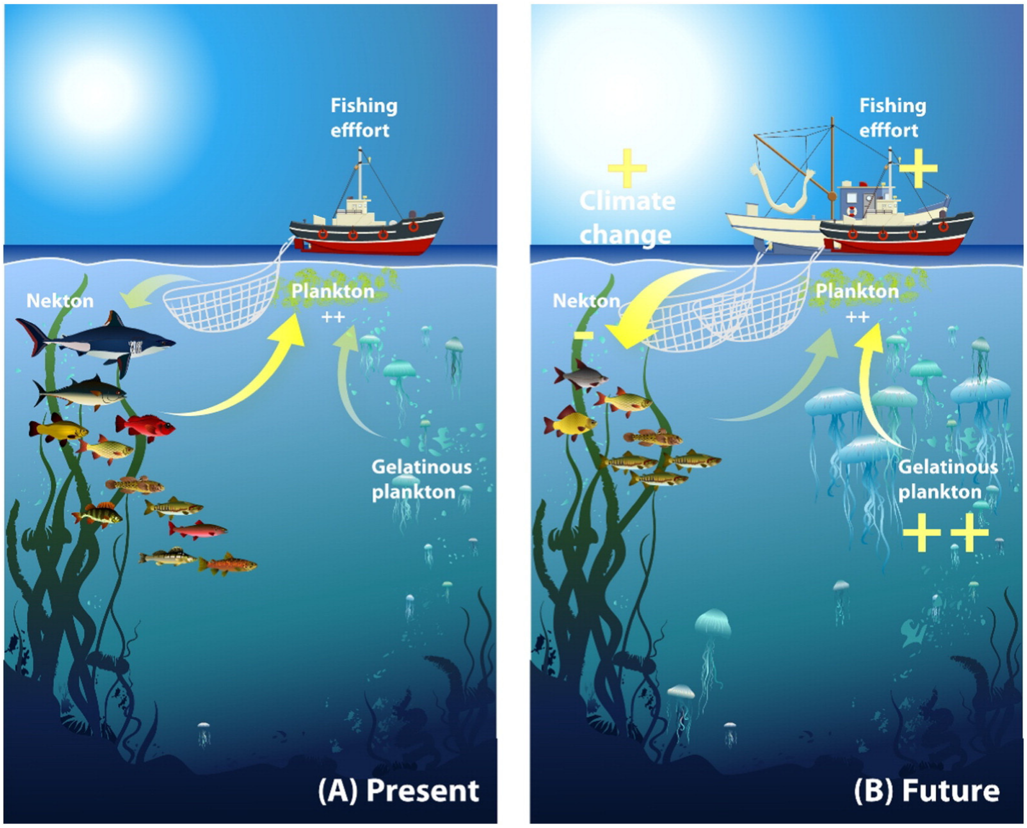

Fig. 1. One conceptual model of mutually reinforcing effects of climate change and other anthropogenic stressors on native invasive jellyfish (*gelatinous plankton*), with biotic interactions (i.e., predator-prey relationships) represented by the arrows. **(A)** Increasing terrestrial runoff and nutrients loads contribute to eutrophication, leading to unusually high phytoplankton (*plankton*) concentrations associated with low oxygen concentrations (Miller & Graham, 2012). These conditions promote the growth of jellyfish populations, sustained by plankton resources usually consumed by fish stocks and fish larvae (*nekton*). Fish stocks are subsequently impacted by this reduced availability of plankton resources, as well as by continuously increasing *fishing effort* (e.g. Pauly et al., 2002). The reduced size of fish stocks results in a reduced uptake of planktonic resources, thus made available to sustain further jellyfish blooms (Licandro et al., 2010; Lynam et al., 2011). **(B)** *Climate change* favours gelatinous plankton species that are able to adapt to new environmental conditions and increase in abundance rapidly (Lynam et al., 2011). The composition of nekton communities and fish stocks is altered not only as increasing fishing efforts remove fish predators (Pauly et al., 2002) but also as surface temperature increases leading to the dominance of (sub)tropical species (Cheung et al., 2013). Because these subtropical species are unlikely to prey on the same plankton species as their temperate peers, planktonic resources not consumed by fish are more readily available to sustain increasingly frequent and extensive jellyfish blooms.

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