Comparing model parameterizations of the biophysical impacts of ocean acidification to identify limitations and uncertainties

Travis C. Tai[a,*], Christopher D.G. Harley[a,b], William W.L. Cheung[a]

[a] Institute for the Oceans and Fisheries, The University of British Columbia, Vancouver, B.C., V6T 1Z4, Canada
[b] Department of Zoology, The University of British Columbia, Vancouver, B.C., V6T 1Z4, Canada

A B S T R A C T

Ocean acidification (OA) driven by anthropogenic CO_2 emissions affects marine ecosystems, fisheries and aquaculture. Assessing the impacts of OA using projection models facilitates the development of future scenarios and potential solutions. Here, we explored various ways to incorporate OA impacts into a multi-stressor dynamic bioclimatic envelope model to project biogeographic changes of ten commercially exploited invertebrate species. We examine three dimensions of uncertainties in modelling biophysical OA effects: model structure, parameterization, and scenario uncertainty. Our results show that projected OA impacts are most sensitive to the choice of structural relationship between OA and biological responses, followed by the choice of climate change emission scenarios and parameterizations of the size of OA effects. Species generally showed negative effects to OA but sensitivity to the various sources of uncertainty were not consistent across or within species. For example, some species showed higher sensitivity to structural uncertainty and very low sensitivity to parameter uncertainty, while others showed greatest sensitivity to parameter uncertainty. This variability is largely due to geographic variability and difference in life history traits used to parameterize model simulations. Our model highlights the variability across the sources of uncertainty and contributes to the development of integrating OA impacts in species distribution models. We further stress the importance of defining the limitations and assumptions, as well as exploring the range of uncertainties associated with modelling OA impacts.

1. Introduction

Carbon dioxide (CO_2) emissions from human activities such as the burning of fossil fuels largely contributes to the rapid rate of ocean acidification (OA) since the industrial revolution (IPCC, 2013). OA is the chemical process driven by elevated atmospheric CO_2 that results in reduced pH and increased acidity. Global sea surface pH has already decreased by 0.1 units since the pre-industrial average of 8.17, a 26% increase in acidity (Caldeira and Wickett, 2003; Feely et al., 2009; Pörtner et al., 2014). Under our current emissions trajectory, sea surface pH is projected to decrease by an additional 0.3 units by the end of the 21st century (Ciais et al., 2013; IPCC, 2013). Some areas are experiencing much larger changes in pH. For example, the Northeast Pacific Ocean has naturally fluctuating pH levels due to upwelling, and the uptake of anthropogenic CO_2 is elevating acidification across these areas (Feely et al., 2014; Haigh et al., 2015).

Ocean acidification is expected to impact marine organisms, communities and ecosystems (Branch et al., 2013; Cooley et al., 2009; Doney et al., 2012; Guinotte and Fabry, 2008; Haigh et al., 2015; Le

Quesne and Pinnegar, 2012; Mathis et al., 2015), with variations in sensitivity across populations, taxonomic groups and ecosystem types (Heuer and Grosell, 2014; Kroeker et al., 2013; Nagelkerken and Connell, 2015). Most notably, OA compromises the ability of organisms to efficiently build and retain calcium carbonate structures (e.g. coral reefs, oyster and mussel shells, coccolithophore exoskeletons) due to the under-saturation of calcium carbonate (Fabry et al., 2008; Feely et al., 2004; Kleypas et al., 2006; Nienhuis et al., 2010; Ries et al., 2009). Beyond calcification, OA affects a wide range of physiological processes such as acid-base balance, basal metabolic rates, aerobic scope, oxygen consumption, thermal tolerance, fertilization rates, and development, among others (detailed in Le Quesne and Pinnegar, 2012). Direct impacts of OA on changes in species abundance will result in important changes to competitive, facilitative, and trophic relationships (Dutkiewicz et al., 2015; Queirós et al., 2015; Sunday et al., 2017; Trenkel et al., 2005). Overall, changes in physiology and behaviour lead to changes in growth and abundance, and when considered across multiple interacting species, results in important changes in community structure and ecosystem function (Kroeker et al., 2013; Nagelkerken

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and Connell, 2015).

OA coincides with other anthropogenic CO_2 driven stressors including ocean warming and decreases in dissolved oxygen concentration. Increases in temperature affects physiological processes such as metabolism, increasing the demand for oxygen and reducing aerobic scope (Pörtner and Lannig, 2009). Decreases in oxygen content further exacerbates this effect, and is projected to lower the metabolic capacity of marine habitats potentially leading to decreased body size (Cheung et al., 2013a; Deutsch et al., 2015; Pauly and Cheung, 2017). Biogeographic responses to ocean warming and decreased oxygen content have been observed as shifts in distributions to deeper and higher latitudinal waters (Cheung et al., 2013b; Dulvy et al., 2008; Perry et al., 2005). While isolating the effects of OA is important for understanding the mechanisms in which OA effects operate, integrating OA with other stressors provides a more real-world application of the effects of anthropogenic-influenced global changes on species distribution and abundance.

The inclusion of OA in assessing impacts of anthropogenic CO_2 emissions is important in developing scenarios of future global change for marine systems. Published syntheses and meta-analyses are extremely useful for providing baseline parameters for modelling and assessing the biological impacts of OA (Kroeker et al., 2013; Nagelkerken and Connell, 2015; Sunday et al., 2017). They also provide a basis for linking complex physiological responses to life history traits that have direct implications on population dynamics. For example, Cheung et al. (2011) incorporated physiological models into a dynamic bioclimatic envelope model (Cheung et al., 2008) to assess climate change effects on species distribution and abundance. This model was then applied to a socioeconomic analysis of climate change and OA impacts in the Arctic Ocean (Lam et al., 2014). Empirical models of OA effects have also been used to estimate changes in the growth rates of mollusc species and thereby impacts on US mollusc fisheries (Moore, 2015; Ries et al., 2009). Another promising approach incorporates information about marine food webs by using an ecosystem model to model the impacts of OA on functional groups that include harvested taxa (Ainsworth et al., 2011).

Projection models provide valuable insight to potential future scenarios but are subject to various sources of uncertainty. Uncertainty when modelling ocean acidification arises from the choice of model parameterizations, which produce a range of possible impact pathways. We define three sources of uncertainty when modelling OA impacts: 1) structural, 2) parameter, and 3) scenario uncertainty (Hawkins and Sutton, 2009). Structural uncertainty refers to the underlying construction of the model, such as the mathematical formulation of a model to represent ecological relationships, or the processes modelled using correlative versus mechanistic approaches (e.g. Pauly et al., 2000). Parameter uncertainty stems from the inherent variability and our limited ability to accurately and precisely measure biological processes and relationships (e.g. Kremer, 1983). Scenario uncertainty results from the different possible future pathways due to many socioeconomic factors (e.g. governmental policies, technological development) that affect biophysical drivers. This includes the various greenhouse gas concentration trajectories used to drive climate and biophysical models (IPCC, 2013). The combined uncertainties produce the full range of future trajectories, providing valuable insight to the sensitivities of modelling OA impacts.

In this study, we explored various ways to incorporate OA impacts into a multi-stressor dynamic bioclimatic envelope model to project changes in the biogeography of ten commercially exploited invertebrate species. We examined the structural, parameterization and scenario uncertainties in modelling OA effects. To eventually improve our confidence in forecasting future scenarios, we explored the variability of model outputs and discussed the utilities and limitations of different ways to incorporate OA impacts in spatial biogeographic models.

2. Methods

We incorporated the impacts of OA into a previously developed dynamic bioclimatic envelope model (DBEM) (Cheung et al., 2016a, 2011, 2008) to estimate changes in species distribution and abundance. The DBEM uses earth system models as inputs (e.g. Dunne et al., 2013) and links species distribution models (Jones et al., 2012), advection-diffusion movement models (Sibert et al., 1999), growth models (Pauly, 1980), physiological models (Pauly, 1981), and population dynamics models (Hilborn and Walters, 1992; O'Connor et al., 2007; Pauly, 1980) to predict how species will move geographically across time (annual time step) and space (on a 0.5° latitude x 0.5° longitude grid) with climate change. We outline the specifics of modelling the effects of OA and how it interacts with effects from other stressors (i.e. temperature and oxygen) below, while other details on the DBEM can be found in the Supplementary material (Supplementary Fig. S1).

2.1. Modelling the effects of global change

Global change effects on organisms and populations include changes in temperature, oxygen and pH. We integrated the biological impacts of OA on exploited populations through the effects on somatic growth and mortality rates. We define the effects on somatic growth as a mechanistic process, and the effects on survival as a correlative process. First, the model uses the von Bertalanffy growth function (von Bertalanffy, 1951) to simulate changes in growth in response to ocean warming, decreases in dissolved oxygen concentration, and ocean acidification (Cheung et al., 2011). Growth rate (change in biomass, B, as a function of time, t) is determined with the derived equation from a growth function:

$$\frac{dB}{dt} = HW^d - kW^b \tag{1}$$

where H and k represent the coefficients for anabolism and catabolism, respectively. Anabolism scales with body weight (W) to the exponent $d < 1$, catabolism scales linearly with (W), i.e. $b = 1$, and their difference determines the growth rate of species biomass (B). Solving for $dB/dt = 0$ when asymptotic weight (W_∞) is reached, we obtained $H = kW_\infty^{(1-d)}$. Thus, growth rate is dependent on the available oxygen (anabolism) and oxygen demand for maintenance metabolism (catabolism).

Integrating Eq. (1) into a generalized von Bertalanffy growth function:

$$W_t = W_\infty \left[1 - e^{-K(t-t_0)}\right]^{1/(1-d)} \tag{2}$$

where K is the von Bertalanffy growth parameter where $K = k(1-d)$. The von Bertalanffy growth parameter K represents the rate at which maximum body size is reached. We assume $d = 0.7$, although values typically range from 0.5 and 0.95 across invertebrate species (Hughes, 1983; Johnson and Rees, 1988; Jones et al., 1992). Sensitivity of maximum body size to changes in temperature and acidity show that low values of d (< 0.7) results in slight decreases in sensitivity, while larger values of d (> 0.7) results in major increases in sensitivity (Supplementary Table S1) (Pauly and Cheung, 2017). Effects of multiple stressors show an antagonistic interaction for the effects on body size. Therefore, the use of 0.7 for all species considered here are conservative as smaller values of d do not considerably change temperature and acidity effects on maximum body size, while larger values of d only increase sensitivity.

The effects of temperature were modelled to affect metabolism—described in Eqs. (3) and (4)—through the H and k coefficients following the Arrhenius equation, $e^{-j/T}$, where $j = E_a/R$, with E_a and R equal to the activation energy and Boltzmann constant, respectively. Furthermore, oxygen availability affects aerobic scope (i.e. oxygen supply) while acidification affects maintenance metabolism (i.e. oxygen demand). We modelled the impacts of decreases in oxygen and ocean