



Food for Thought

How to make progress in projecting climate change impacts

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Scientific modelling has become a crucial tool for assessing climate change impacts on marine resources. Brander *et al.* criticize the treatment of reliability and uncertainty of such models, with specific reference to Cheung *et al.* (2013, *Nature Climate Change*, 3: 254–258) and their projections of a decrease in maximum body size of marine fish under climate change. Here, we use the specific criticisms of Brander *et al.* (2013, *ICES Journal of Marine Science*) on Cheung *et al.* (2013) as examples to discuss ways to make progress in scientific modelling in marine science. We address the technical criticisms by Brander *et al.*, then their more general comments on uncertainty. The growth of fish is controlled and limited by oxygen, as documented in a vast body of peer-reviewed literature that elaborates on a robust theory based on abundant data. The results from Cheung *et al.* were obtained using published, reproducible and peer-reviewed methods, and the results agree with the empirical data; the key assumptions and uncertainties of the analysis were stated. These findings can serve as a step towards improving our understanding of climate change impacts on marine ecosystems. We suggest that, as in other fields of science, it is important to develop incrementally (or radically) new approaches and analyses that extend, and ultimately improve, our understanding and projections of climate change effects on marine ecosystems.

Keywords: climate change, marine, fish, modelling, projection, body size.

Introduction

The Swedish physicist Svante Arrhenius suggested, based on first-order consideration (or a “toy model”) that the carbon dioxide released by the burning of large quantities of coal would eventually result in more of the sun’s energy being trapped in the Earth’s atmosphere, leading to a global increase in temperature (Arrhenius, 1896), which can be considered the beginning of climate change research. Since then, the development of improved conceptual, mathematical and computer models of atmospheric phenomena have modified Arrhenius’ first-order considerations almost beyond recognition. These advancements assimilated an immense amount of empirical data, and also enabled a wide range of descriptions to be produced, tests of important hypotheses, and increasingly realistic scenarios to be generated for policy makers (Edwards, 2010). With each advance and new model, the previous models were shown to be wanting—although the older models (including Arrhenius’ toy model) were not “wrong” at the time they were published. Rather, they became

“wrong” because they triggered the development of the improved models that replaced them. Indeed, models which do not trigger further developments, and hence their eventual replacement, are, to cite the celebrated phrase of Wolfgang Pauli, “not even wrong”.

Scientific modelling has also become a crucial tool for assessing and analysing climate change impacts on the biological (including human) components of marine resources (Stock *et al.*, 2010), and as has occurred with their counterpart in the physical sciences, these efforts will progress from toy model to complex constructs, capable of incorporating (and hence explaining) more data from different domains, and making projections of increased usefulness. One example is the Dynamic Bioclimate Envelope Model (Cheung *et al.*, 2008a, 2008b), whose scope was gradually extended, like that of the physical models alluded to above, to consider processes not part of the original model formulation, such as poleward migrations of fish and the implication for biodiversity (Cheung *et al.*, 2009), the potential impact of these migrations on fisheries (Cheung *et al.*, 2010), shifts

in phytoplankton size distribution, effects of changes in ocean chemistry (Cheung *et al.*, 2011) and, recently, the effects of higher temperatures and lower oxygen availability on fish size distribution (Cheung *et al.*, 2013) and trophic interactions (Fernandes *et al.*, 2013).

Criticisms of scientific modelling include “philosophical” and “technical” issues of science as well as non-scientific issue, as exemplified by Brander *et al.* (2013). In this paper, we use the specific criticisms of Brander *et al.* (2013) on Cheung *et al.* (2013) as examples to illustrate these points. At the philosophical level, Brander *et al.* suggest that scientific modelling should deal at length with issues of reliability and uncertainties, while their claim, at the technical level, is that the model used by Cheung *et al.* (2013) is unreliable and that it overestimates the decreases in maximum body size of fish likely to occur under climate change. Additionally, they suggest that Cheung *et al.* (2013) overplayed their result through the press—a non-scientific issue.

Philosophically, we agree that understanding the reliability and uncertainties of scientific modelling is very important and that all analyses should account for and acknowledge major sources of uncertainty—this is true for any scientific investigation, and it is one of the functions of peer-review to filter out papers whose authors do not acknowledge and deal properly with uncertainties. However, it is impossible to truly assess the uncertainty of any predictions until the occurrence, or non-occurrence, of the events in the future. Secondly, we note with Donald Rumsfeld that while it is relatively straightforward to deal with “known unknowns” (or known uncertainties), it is far more difficult to deal with “unknown unknowns”. In fact, the latter are the reason why models that seemed correct upon publication (including in their treatment of uncertainty) turn out to be “wrong” some time later. We think that is the main reason why (post-peer review) critiques of the way models deal with “uncertainty” (i.e. “known unknowns”) are not the most effective way to advance science. Rather, we believe that the most effective way to criticize a published model is to propose a better one: one that, at a minimum, identifies one or several of the previously “unknown unknowns”.

We will address the technical criticisms by Brander *et al.*, and show that the model of Cheung *et al.* (2013) is robust. As for Brander *et al.*'s comment on non-scientific issues, we will not engage in an argument about the “kudos” gained by scientists communicating their research with the public. There is no need to cast aspersions on anyone here, as the level of science communication in which scientists engage is entirely dependent on their institutional culture and personal preferences. The broader issue related to the quality of science journalism is also beyond the scope of the discussion here. On the issue of publishing in high profile journals (in addition to publishing highly technical papers that refine existing findings, e.g. through studies that improve treatment of uncertainty), there is a need to publish studies that use unconventional or new approaches to raise important issues. Cheung *et al.* (2013) clearly falls in the latter category as they report surprisingly strong effects of climate change on fish size, which they demonstrate using scientifically sound methods. Such a finding deserves the greater attention that a high visibility journal can bring to it, as agreed by the reviewers and editors of *Nature Climate Change*, even if the uncertainty is high—which was stated explicitly and is always the case for complex natural systems.

Reliability of projections by Cheung *et al.* (2013)

Cheung *et al.* (2013) applied the Dynamic Bioclimate Envelope Model (DBEM) initially documented in Cheung *et al.* (2008a,

2009) to assess how changing ocean conditions, particularly temperature and oxygen level, would affect maximum body size of fish under climate change. Their approach is based on fundamental ecological and physiological theory, and has two interconnected components: (i) an ecophysiology model that predicts changes in growth and body weight, and (ii) a species distribution model that predicts changes in distribution of fish based on changes in ocean conditions. Driven by changes in ocean physical and biogeochemical conditions projected from two different global earth system models, the DBEM was applied to 610 species of exploited marine fish.

Cheung *et al.* (2013) reported two main findings: one that maximum body size in individual fish populations is projected to decrease by a median rate of around 10% by 2050 relative to 2000 under the SRES A2 scenario, the other that, because of the decrease in maximum body size of fish populations and invasion of smaller, low-latitude fish, the fish assemblage is projected to decrease its average maximum body size by 14–24%.

The relationship between seawater temperature, oxygen and maximum body size of fish are supported by first-order considerations and abundant empirical evidence, starting with Pütter (1920) and highlighted in Pörtner (2010). While Brander *et al.* cite Brett (1979) to suggest that oxygen is a limiting factor for growth, and not a controlling factor, there is abundant theoretical and empirical support in the peer-reviewed literature for oxygen being both a limiting and controlling factor for the growth of fish and aquatic invertebrates (Pauly, 1981; Peck and Chapelle, 2003; Kolding *et al.*, 2008; Pörtner, 2010; Pörtner and Peck, 2010; Verberk and Bilton, 2011; Verberk *et al.*, 2011), although the degree of sensitivity may vary between species. The growth equations incorporating relationships linking temperature, oxygen, thermal niche and maximum body size of fish were detailed in Cheung *et al.* (2013) and have been previously published in the peer-reviewed literature (Cheung *et al.*, 2011).

Brander *et al.* also argue that fish growth is inversely related to reproductive investment. However, this “reproductive drain hypothesis” cannot explain why female fish (which have a much larger reproductive investment than male fish) reach larger sizes than males in the majority of fish species, and why sterile fish (i.e. fish that never invest in reproduction) grow asymptotically. Moreover, a review of published experiments comparing diploid (reproductively active) and triploid (sterile) fish show very similar growth patterns despite large differences in reproductive investment (Maxime, 2008). Indeed, the “reproductive drain hypothesis”, which is usually perceived as a truism and not as the hypothesis that it is, was thoroughly refuted 40 years ago (Iles 1974; see also Pauly, 1984, 2010).

Moreover, while Brander *et al.* cited an older book chapter (Brett, 1979) to support their argument, they criticized Cheung *et al.* (2013) for citing a recent book (Pauly, 2010) to support their own case. The journal in which Cheung *et al.* (2013) was published has a strict limit on the number of references that can be cited. Pauly (2010), although not being a peer-reviewed book, provides a detailed synthesis of published literature supporting the relationship between growth and oxygen, based on peer-reviewed research by its author (Pauly, 1981, 1984, 1997, 1998a, b), and other colleagues (e.g. Chiba, 1988; Bejda *et al.*, 1992; Chabot and Dutil, 1999; Chapelle and Peck, 1999; Burleson *et al.*, 2001; Peck and Chapelle, 2003; Pörtner and Knust, 2007; Kolding *et al.*, 2008).

Contrary to what Brander *et al.* assert, all of the scaling relationships in Cheung *et al.* (2013) were based on intraspecific comparisons, or on abundant empirical supports for the relationships between and within species. Thus, the metabolic scaling for temperature was based on intraspecific comparisons (Clarke and Johnson, 1999), as

mentioned explicitly. Moreover, the body-mass scaling used for their growth model is widely applicable across and within fish species (Pauly, 1981, 2010).

Brander *et al.* question the legitimacy of earlier, published temperature–size relationships for North Sea haddock (*Melanogrammus aeglefinus*) (Baudron *et al.*, 2011) and Atlantic cod (*Gadus morhua*) (Taylor, 1958), and their use for comparison with the projections from Cheung *et al.* (2013). Regarding the former species, Brander *et al.* argued that the temperature–size relationship presented by Baudron *et al.* (2011) was so strong that other unaccounted factors were likely to have been involved. While we cannot refute that hypothesis, we point out that the projection from Cheung *et al.* (2013) was much more conservative than the temperature–size relationship reported in Baudron *et al.* (2011). Changes in body size projected by Cheung *et al.* (2013) were only those driven by oceanographic changes. If fishing effects were to be included in the study, the projected decrease in body size would be higher and likely to be closer to the observed changes reported in Baudron *et al.* (2011). Regarding the latter species, we suggest that there is nothing inherently unreliable in using the growth parameters and temperature data measured early in the 20th century and reported in Taylor (1958). Fish age determination using otoliths was routine in the early 20th century, including for cod (see e.g. bibliographies in Mohr 1927, 1930, 1934), and temperature and fish sizes were routinely measured. In fact, it could be argued that datasets originating from the first decades of industrial fisheries should document the relationship between growth and temperature better than more recent ones, as fishing itself has modified the growth pattern of fish, notably cod (Swain *et al.*, 2007). The fact that some stocks are migratory will add variance to the data, but this potential confounding effect will not affect the strong temperature–size relationship demonstrated in Taylor (1958). The inverse relationship between terminal body size and temperature has been known since the work of Pütter (1920), from which von Bertalanffy (1951) derived his widely used growth equation, and has also been observed in other species such as Atlantic herring (*Clupea harengus*) (Brunel and Dickey-Collas, 2010). This relationship is also known to fish taxonomists, for example Randall *et al.* (1993), who noted that “tropical fish living near the limit of their tolerance for low temperature grow to larger size at such temperatures” or Smith-Vaniz *et al.* (1999) who noted that “[m]any fishes live longer and grow larger in the cooler parts of their range”. We therefore disagree with Brander *et al.* that the temperature–size relationship of fish populations can only be studied by using recently developed electronic storage tags.

Brander *et al.* also contrasted the use of sea surface temperature by Taylor (1958) to the use of sea bottom temperature in Cheung *et al.* (2013). For shelf seas such as those in the North Atlantic, the Earth System Model predicts that sea surface temperature (SST) is strongly correlated with sea bottom temperature (SBT) (Figure 1). Cheung *et al.* (2013) acknowledge the potential uncertainty associated with predictions from the Earth System Models. Notwithstanding such uncertainty, the results here suggest that whether the projections from Cheung *et al.* (2013) are reported with SST or SBT in the comparison with data from Taylor (1958) will have no effect on the conclusion that the projected decreases in body size of cod are consistent with observations.

Finally, and most importantly, Brander *et al.* suggested that a recent meta-analysis of empirically observed responses by Forster *et al.* (2012) demonstrates that the rate of change of body mass in response to the temperature and oxygen changes applied in Cheung *et al.* (2013) was overestimated by one order of magnitude. If true,

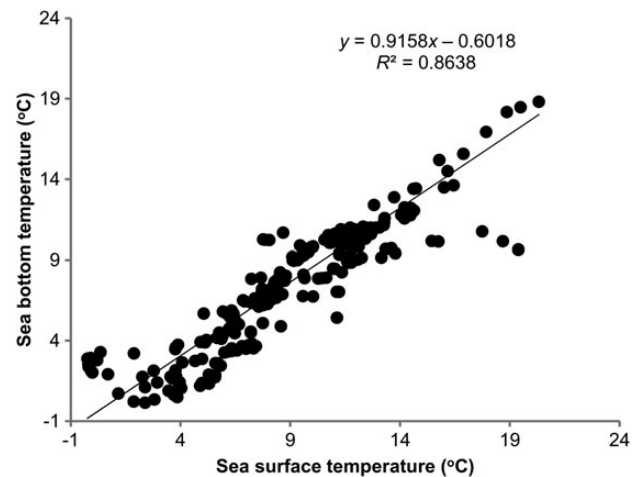


Figure 1. Relationship between modelled sea surface temperature and sea bottom temperature in the year 2000 from NOAA’s GFDL Earth System Model 2.1 (used by Cheung *et al.* 2013) for shelf seas (<200 m depth) in the North Atlantic.

this would indeed be a devastating argument. However, Brander *et al.* overlooked two important aspects of the study by Forster *et al.* (2012). First, Brander *et al.* did not distinguish the assemblage-level decrease in body size changes (14–24%) with the individual population level decreases ($\sim 10 \pm 6\%$) by 2050 relative to 2000 projected by Cheung *et al.* (2013). Results from Forster *et al.* (2012) should be compared only with the latter, as they did not account for distribution shifts in their study. Second, while Forster *et al.* (2012) suggested that the average temperature–body size response of the aquatic ectotherms they studied was around $-5\%^{\circ}\text{C}^{-1}$ when mean species dry body mass is about 100 mg, they also showed that the temperature–body size response is size-dependent over a range of body size from 10^{-10} – 10^3 mg dry mass, which does not overlap with the range of body size of exploited fish included in Cheung *et al.* (2013), i.e. from 10^3 to 10^8 mg dry mass. Extrapolating the significant relationship presented by Forster *et al.* (2012) to the size range of exploited marine fish, the temperature–size responses were predicted to be 0 – $13\%^{\circ}\text{C}^{-1}$, generally overlapping with the $\sim -10 \pm 6\%$ estimate of the projected changes of individual body size in Cheung *et al.* (2013) (Figure 2). There is uncertainty associated with the extrapolation of the empirical relationship beyond the data. On the other hand, it is invalid to compare biological responses between organisms that differ in body size by orders of magnitude when significant body size effect is demonstrated in such responses. Thus, if an example is required, the percentage change in body mass of Atlantic cod projected from Cheung *et al.* (2013; Figure 4) is $-13\%^{\circ}\text{C}^{-1}$, while the prediction based on extrapolating the regression lines reported in Forster *et al.* (2012) is between -12 and $-3\%^{\circ}\text{C}^{-1}$ (Figure 2, 95% prediction intervals). Notwithstanding the admitted uncertainties associated with both analyses, the prediction from Cheung *et al.* is similar to the extrapolation from Forster *et al.* (2012).

Cheung *et al.* (2013) specified the key assumptions and uncertainties associated with their study, such as uncertainties of climate projections, assumption of stationary trophic effects, and the lack of evolutionary adaptation, while they examined sensitivity of the analysis to alternative values of key parameters. Also, the algorithms and data sources used by Cheung *et al.* (2013) are described and published (e.g. Cheung *et al.* 2008b, 2011, 2013 supplementary information), allowing for the reproduction of the models and

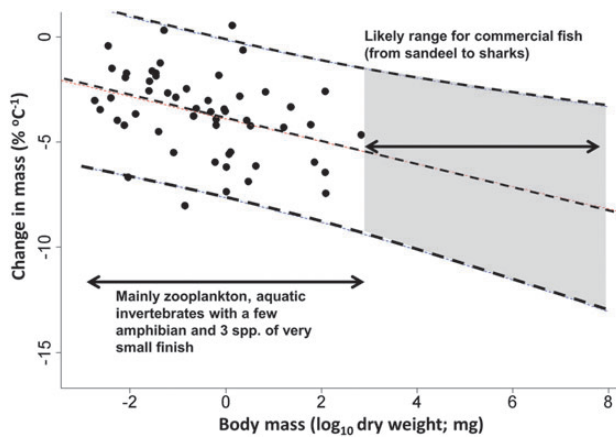


Figure 2. Comparison of predicted responses of individual body size decrease under warming between Forster *et al.* (2012: Figure 2) and Cheung *et al.* (2013). Data on temperature and body size relationship for a range of taxonomic groups of aquatic animals were extracted from Forster *et al.* (2012). A linear regression was performed following Forster *et al.* (2012) and the 95% prediction intervals of the regression (dotted lines) were included. The range of body size of species included in Forster *et al.* (2012) does not overlap with those of the commercially exploited fish. The regression model was extrapolated for the body size range that corresponds with the exploited marine fish included in Cheung *et al.* (2013). The shaded area represents the range of temperature–size sensitivity that is expected from the analysis by Forster *et al.* (2012).

results. Based on fundamental ecological theory, the DBEM leads to results that can be duplicated, and which thus can be revised when better data or hypotheses become available. Cheung *et al.* (2013) also clearly stated that their results should be viewed as a step towards better understanding of climate change impacts on marine ecosystems.

Brander *et al.* objected to Cheung *et al.* (2013) having used only one species distribution model. However, at the time Cheung *et al.* (2013) was published, the DBEM was the only published model that simultaneously evaluated the effects of temperature and oxygen on ecophysiology, growth, population dynamics and species distribution, and which had been applied globally to a wide range of exploited fish. When other models that integrate changes in body size and species distributions become publicly available, we will be able to apply multimodel and ensemble comparisons.

Advancing the science in modelling climate change impacts

Brander *et al.* bring up the important philosophical question of what “models” are and what they should do. Models are a representation of complex systems that allow for investigation of the properties of such systems and, in some cases, prediction of future outcomes. Models, therefore, are usually designed for a specific objective e.g. to characterize the energy flow of a marine ecosystem, or to develop hypotheses of how climate change may affect marine biodiversity. Thus, by definition, models are not a replication of all of the components of such systems, nor are they ever complete. Rather they remain abstractions, involving numerous assumptions and uncertainties, both explicit and implicit. Scientific communities are generally aware of the limitations of models and are cautious in interpreting their outputs, because they know, with Box and Draper (1987), that “[a]ll models are wrong, but some are useful.”

We suggest that marine and fisheries biologists should emulate our colleagues who study the physics of climate change by relying, as Cheung *et al.* (2013) did, on incremental models, rooted in first principles, and to which, in a gradual and collective process, elements can be added which enable them to assimilate more data, and thus extend their domain. When multiple models addressing similar questions start to become publicly available, multimodel comparisons and ensembles can then be conducted (e.g. Jones *et al.*, 2012, 2013). This would both improve the characterization of their uncertainty, and increase their usefulness. Modelling climate change impacts on marine ecosystems, particularly at large spatial scales, is difficult, both in terms of developing computational methods and obtaining the data required for parameterization. This requires progressive development and refinement of models and improved data acquisition systems—a point that is also suggested by Brander *et al.*

The advancement made from incremental progression of modelling approaches could be illustrated by the study of Sarmiento *et al.* (2004) referred to by Brander *et al.* This paper was originally designed to build on previous efforts (e.g. Bopp *et al.*, 2001; Christian *et al.*, 2002) in analysing how projected physical atmospheric and oceanographic changes would alter ocean primary productivity. Sarmiento *et al.* (2004) developed and applied alternative statistical approaches to predict biological responses, which would then allow further comparisons between different models (e.g. Steinacher *et al.*, 2010). Thus, the advances made in developing different models gradually improved our understanding of biological responses to ocean and atmospheric changes, and, ultimately, revealed the overall uncertainty of those predictions.

Scientific studies that describe the methodology and assumptions clearly, and are reproducible (making it possible for peers to provide critiques), are important components of the scientific approach. The study presented in Cheung *et al.* (2013), as illustrated in this discussion, clearly fulfils these criteria. We suggest that the most effective way to make progress in our scientific understanding and ability to predict the climate change response of these extraordinarily complex systems is through a continual process of model development and improvement, and we encourage our colleagues to join us in the process.

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