



Physiology-based modelling approaches to characterize fish habitat suitability: Their usefulness and limitations



Lorna R. Teal ^a, Stefano Marras ^b, Myron A. Peck ^c, Paolo Domenici ^{b,*}

^a Institute for Marine Resources and Ecosystem Studies, Wageningen IMARES, PO Box 68, IJmuiden 1970 AB, The Netherlands

^b IAMC-CNR, Istituto per l'Ambiente Marino Costiero, Consiglio Nazionale delle Ricerche, Località Sa Mardini, 09170, Torregrande, Oristano, Italy

^c Institute for Hydrobiology and Fisheries Science, University of Hamburg, Olbersweg 24, 22767 Hamburg, Germany

ARTICLE INFO

Article history:

Received 6 May 2015

Received in revised form

5 October 2015

Accepted 12 November 2015

Available online 17 November 2015

Keywords:

Physiology-based models

Dynamic Energy Budget

Aerobic scope

Species distribution

Fish

Conservation biology

ABSTRACT

Models are useful tools for predicting the impact of global change on species distribution and abundance. As ectotherms, fish are being challenged to adapt or track changes in their environment, either in time through a phenological shift or in space by a biogeographic shift. Past modelling efforts have largely been based on correlative Species Distribution Models, which use known occurrences of species across landscapes of interest to define sets of conditions under which species are likely to maintain populations. The practical advantages of this correlative approach are its simplicity and the flexibility in terms of data requirements. However, effective conservation management requires models that make projections beyond the range of available data. One way to deal with such an extrapolation is to use a mechanistic approach based on physiological processes underlying climate change effects on organisms. Here we illustrate two approaches for developing physiology-based models to characterize fish habitat suitability. (i) Aerobic Scope Models (ASM) are based on the relationship between environmental factors and aerobic scope (defined as the difference between maximum and standard (basal) metabolism). This approach is based on experimental data collected by using a number of treatments that allow a function to be derived to predict aerobic metabolic scope from the stressor/environmental factor(s). This function is then integrated with environmental (oceanographic) data of current and future scenarios. For any given species, this approach allows habitat suitability maps to be generated at various spatiotemporal scales. The strength of the ASM approach relies on the estimate of relative performance when comparing, for example, different locations or different species. (ii) Dynamic Energy Budget (DEB) models are based on first principles including the idea that metabolism is organised in the same way within all animals. The (standard) DEB model aims to describe empirical relationships which can be found consistently within physiological data across the animal kingdom. The advantages of the DEB models are that they make use of the generalities found in terms of animal physiology and can therefore be applied to species for which little data or empirical observations are available. In addition, the limitations as well as useful potential refinements of these and other physiology-based modelling approaches are discussed. Inclusion of the physiological response of various life stages and modelling the patterns of extreme events observed in nature are suggested for future work.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Global change is altering the distribution of aquatic and terrestrial species worldwide (Sunday et al., 2012). In the marine environment, one of the main environmental factors driving distribution changes is the climate-driven rise in sea water

temperature (Harley et al., 2006), which is predicted to continue throughout the 21st century (IPCC, 2013). As ectotherms, fish in particular are being challenged to adapt or track changes in their environment, either in time through a phenological shift (Asch, 2015; Sims et al., 2005) or in space by a biogeographic shift in productivity (Petitgas et al., 2012). In recent decades many poleward movements have been recorded across the globe (Perry et al., 2005; Sunday et al., 2015) as well as shifts towards deeper waters (Dulvy et al., 2008). Field time series indicate that spring phenology has been advancing at a rate of 4.3 days per decade

* Corresponding author.

E-mail address: paolo.domenici@cnr.it (P. Domenici).

(Burrows et al., 2011; Thackeray et al., 2010). The ability to transfer knowledge on historical observations to make robust projections of future distributions is a challenge that ecologists need to overcome to provide the advice required for good management decisions.

Empirical observations have played a major role in assessing the effect of warming on the distribution of marine organisms (Perry et al., 2005). In the last decade, eco-physiological studies have focused on linking the effect of climate change on species distributions based on organisms' physiological limits (Deutsch et al., 2015; Sunday et al., 2012) and, in some cases, with the overall relationship between environmental factors and physiological performance (Eliason et al., 2011; Pörtner and Knust, 2007; Pörtner and Peck, 2010). In addition to experimental (physiological or ecological) studies and meta-analyses, modelling is required to project the future effects of climate change on marine organisms. Species distribution models (SDMs) provide a widely applied approach for making projections of species range shifts required for conservation of biodiversity and natural resource management as well as assessing the threat and potential spread of invasive species (Albouy et al., 2012, 2013; Ben Rais Lasram et al., 2010; Franklin, 2013; Guillera-Arroita et al., 2015; Guisan and Thuiller, 2005; Guisan et al., 2013; Newbold, 2010).

Correlative SDMs, also known as “bioclimatic envelope models”, “ecological niche models” or “habitat suitability models” use associations between aspects of climate and known occurrences of species across landscapes of interest to define sets of conditions under which species are likely to maintain populations (Araújo and Peterson, 2012) (Fig. 1). The practical advantages of this correlative approach are its simplicity, the flexibility of the data requirements and the range of interactions (biotic/abiotic) which can be incorporated (Kearney et al., 2010). However, the effective conservation management response depends on reliable predictions of species range shifts, which often requires projection beyond the range of available (historical) data. This is problematic because the information is simply lacking and the response of species to changes in environmental factors is highly complex. A second issue is how well model predictions transfer to different regions (Randin et al., 2006; Torres et al., 2015). The output from correlative SDMs can be considered to be specific to the location from which it was derived as the field data will implicitly capture local ecological processes potentially modifying the broader occurrence-environment

relationship (see Table 1 for details on SDMs). Some available studies suggest that spatial extrapolation may be limited and that knowledge of local habitat availability and preferences is necessary to understand and successfully predict realized distribution patterns within any region (Randin et al., 2006; Torres et al., 2015).

One way to deal with these issues of extrapolation is to use a mechanistic approach (Fig. 2). Physiological processes undoubtedly underpin an individual's response to its environment and understanding the physiology underlying climate change effects on organisms is a major and urgent challenge (Pörtner and Farrell, 2008). Physiological measurements can be fundamental to assess the differential responses of endotherms vs. ectotherms, and those of mobile vs sedentary species (Bozinovic and Pörtner, 2015). As ectotherms, temperature has a particularly strong influence on fish (Pörtner and Peck, 2010) and thermal gradients are important determinants of fish distribution (Schram et al., 2013). There is an increasing effort, therefore, to incorporate physiology not only into distribution modelling (Buckley et al., 2011), but also into research on invasive species and conservation management (Lennox et al., 2015). Lennox et al. (2015) point out that only 6% of articles published in *Biological Invasions* incorporate physiological knowledge but it is clear from the broader literature that fundamental and applied physiology can support invasive species management (Lennox et al., 2015) as well as conservation applications (Jørgensen et al., 2012). In addition, physiology-based models, such as Monahan (2009), overcome the circularity of predicting species response to climate change (Figs. 1, 3A) using range filling of potential distributional areas (Araújo and Peterson, 2012).

Here, we discuss the potential to add more physiological realism to models predicting species distributions and habitat suitability. Particularly, we focus on how laboratory experiments have been used to collect physiological data and the theoretical frameworks behind models incorporating these physiological data. We argue that such mechanistic approaches can increase the reliability of future projections to underpin better management decisions.

2. Physiology-based models

2.1. Experimental data based approach

A number of physiology-based models utilise data collected from laboratory experiments (Peck et al., submitted for publication). Normally, these data were collected for two reasons including to: (1) derive physiological limits (Monahan, 2009) for generalised mechanistic niche models that evaluate species' responses to seasonal temperature gradients and (2) establish a relationship between a set of environmental factors and a physiological performance trait in order to evaluate the habitat suitability for a given species (Marras et al., 2015) (Fig. 3B). Physiological limits can be related to either an acute endpoint such as death or more chronic endpoints such as the loss of basic functions (e.g. growth and development). Whilst knowledge of physiological tolerance limits is an important first step towards making predictions of the effect of climate change on presence/absence of a given species, knowledge of the full performance curve of particular physiological traits of a species has the added value of revealing how the environment relates to a species' performance (Fig. 3B).

A recent approach used for habitat suitability modelling in marine fish has been based on the relationship between environmental factors and aerobic scope (aerobic scope models, ASM). Aerobic scope can be defined as the energetic potential of an organism to accomplish all of its tasks and is measured as the difference between the maximum and the standard (i.e. maintenance) metabolic rate (Fry, 1971). Typically, maximum metabolic rates are measured immediately after exhaustive activity, while standard

Correlative Species distribution models

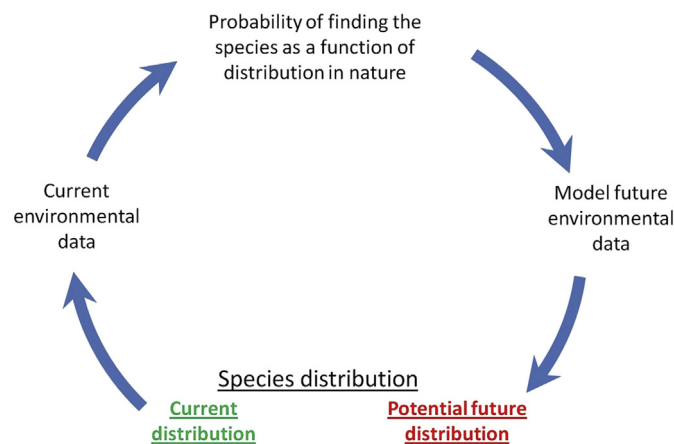


Fig. 1. Correlative species distribution models are based on the statistical association between environmental data and the current distribution of a given species records to predict future distributions based on future environmental projections.

Table 1
Characteristics of the three modelling approaches.

Characteristics of the model	SDM approach	DEB approach	ASM approach
Data requirements	Species presence and absence data from field surveys conducted across the geographical range of the target species Environmental (oceanographic) data of current and future scenarios	Literature and/or laboratory data on life history parameters of species Temperature tolerance limits Food availability Environmental (oceanographic) data of current and future scenarios	Laboratory data on the relationship between aerobic scope and one or more environmental factors Environmental (oceanographic) data of current and future scenarios
Fundamental assumptions	Abiotic factors explain the habitat niche	Underlying assumptions of DEB theory Optimum temperatures decrease as size increases Relative performance between areas is due to interaction between food availability and temperature	The metabolic responses to the environmental variables observed in the laboratory determine the limits of the distribution and the relative performance in the field
Main processes included	Most are purely correlative and do not include mechanistic processes	Bio-energetics: energy intake and utilization within organism (temperature dependant processes)	Aerobic metabolism and its relationship with environmental factors
Main processes excluded	Intra and inter-specific competition and predation Foraging. Dispersal mechanisms Physiological processes.	Intra and inter-specific competition and predation, dispersal mechanisms and cost of migration	Intra and inter-specific competition and predation; foraging; dispersal mechanisms
Strengths	They are simple and have well defined metrics to gauge how well the model explains the field data	Mechanistic models that can be applied also to data-limited species; cover the full life cycle DEBs are able to deal with multiple stressors Able to provide projections of the relationships environmental factors beyond those currently observed in the field	Can produce estimates of relative performance when comparing different locations or different species Potentially able to deal with multiple stressors Able to provide projections of the relationships environmental factors beyond those currently observed in the field
Weaknesses	Not mechanistic, projections from most SDMs do not account for 1) processes (prey/predator overlap) impacting population demographics and 2) limits to dispersal Extrapolation beyond historical observations can lead to spurious estimates Evolutionary response to climate change is not included	Relies on knowledge of upper and lower temperature tolerances and assumptions on how these change with size – this is not yet mechanistically implemented in DEB Biotic interactions and migration costs are not considered Evolutionary response to climate change is not included	Biotic interactions such as predator-prey relationships and competition are not considered The fully complexity of the environment cannot be fully reproduced in the laboratory Challenging to apply to various life stages Evolutionary response to climate change is not included

Physiology-based models

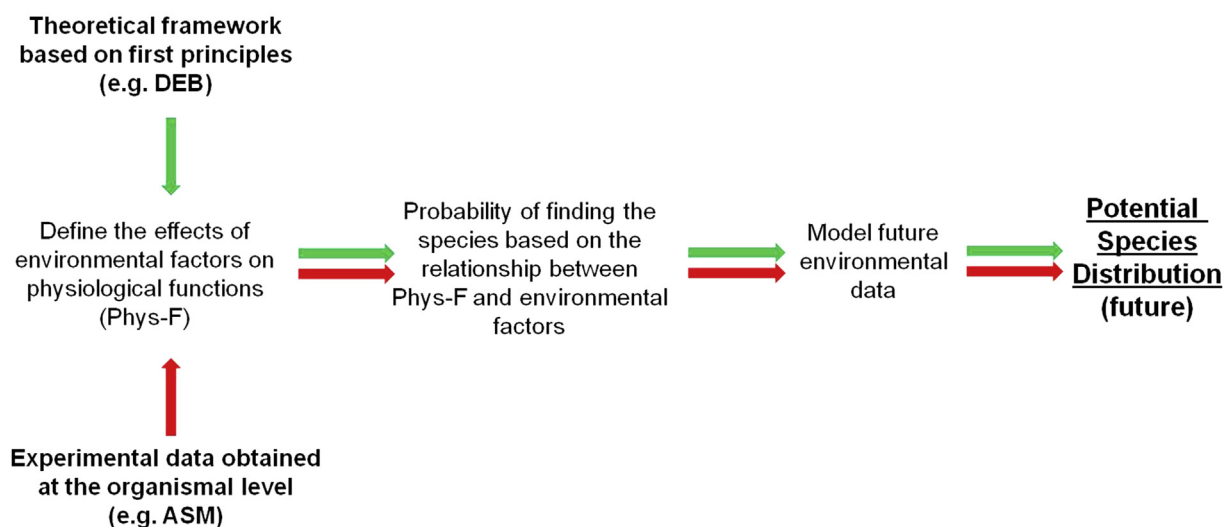


Fig. 2. Physiology-based models can be based on (i) theoretical framework derived from first principles (green arrows) or (ii) the relationship between environmental factors (e.g. temperature) and a key organismal functions such as growth or metabolic scope (red arrows). Both approaches are then coupled with environmental future projections to make predictions on the species distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

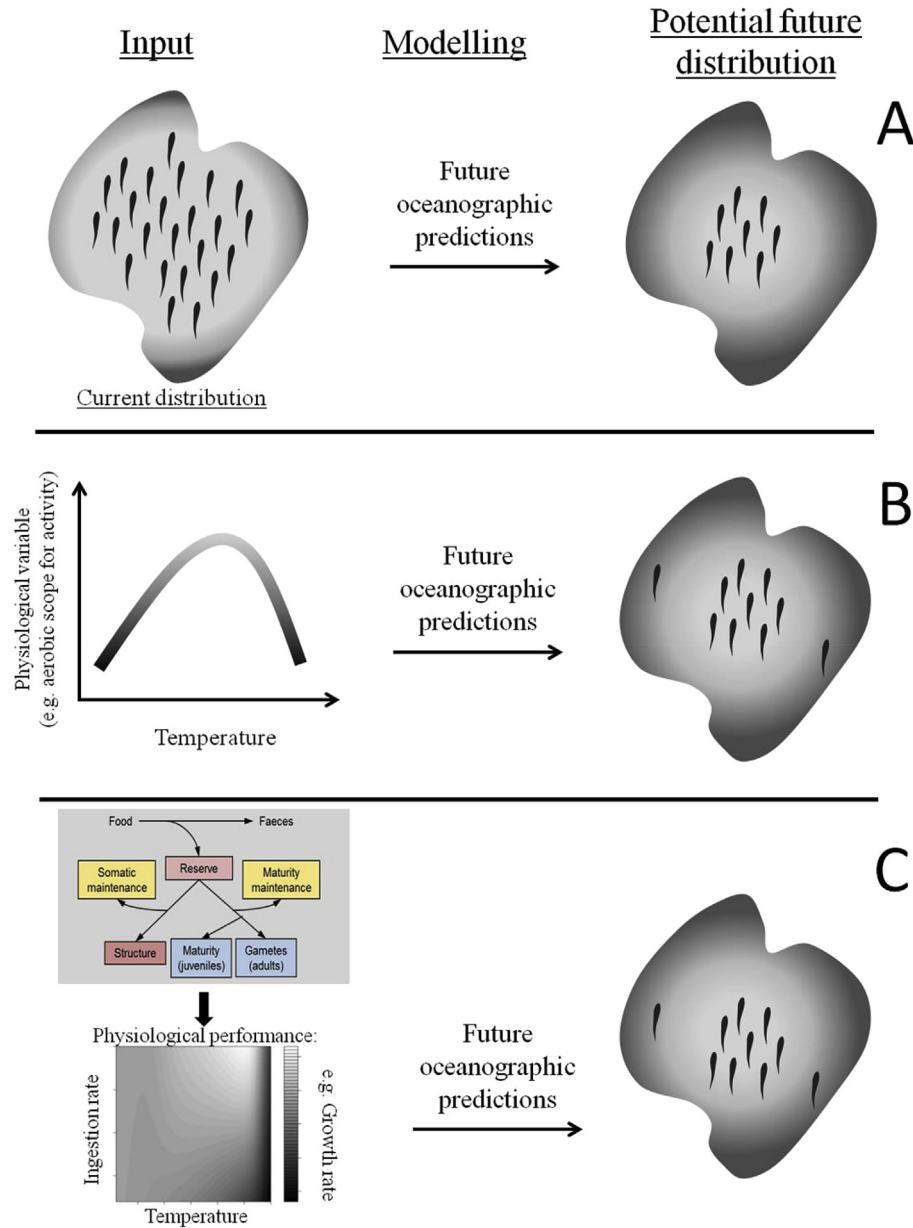


Fig. 3. (A) In the correlative species distribution models the input is represented by the occurrences of species across landscapes of interest. This presence/absence study defines the sets of conditions under which species are likely to maintain populations in those areas. Using output from ecosystem models the suitability of habitat can be mapped in terms of the future conditions. (B) In the physiology-based ASM the input is the establishment of a relationship between a set of environmental factors and a physiological performance trait in order to evaluate the habitat suitability for a given species. Using output from ecosystem models the suitability of habitat can be mapped in terms of the physiological performance in question. (C) In the physiology-based DEB model the input is the theoretical framework of the physiological functions within an organism developed from common patterns detected across species. The development of such a framework relies on fundamental measurements across many species to detect commonalities in physiology from which theory can be developed. The framework presented is based on the Dynamic Energy Budget theory and model described by [Kooijman \(2010\)](#).

metabolic rates are measured after a period of rest that leads to complete recovery from exercise. Aerobic scope, therefore, measures the metabolic confines within which aerobic activities (including mechanical work such as locomotion, growth, digestion, fighting diseases or other stresses) can be carried out ([Claireaux and Lefrançois, 2007](#)). Aerobic scope is related to growth and can be used as a proxy of the general conditions of an organism ([Claireaux and Lefrançois, 2007](#)). Reductions in aerobic scope have been found to correspond with declines in species abundance and it has thus been argued that one of the first processes to cause local extinction or relocation of fish to cooler waters is the reduction in aerobic scope in warming conditions ([Pörtner and Knust, 2007](#)).

The physiological relationship between environmental factors and metabolic scope have led to the concept of oxygen and capacity-limited thermal tolerance, which provides access not only to understanding the physiological mechanisms behind the performance of organisms but also integrates those at whole-organism and tissue levels with the underlying biochemical and genomic mechanisms ([Pörtner, 2010](#)).

The steps used in the ASM approach to habitat modelling are illustrated in [Fig. 2, 3B](#) and [Table 1](#). First, experiments are carried out using either one or multiple stressors. These experiments are conducted using a number of treatments that allow a regression function to be derived between the stressor/environmental factor

and aerobic metabolic scope (Killen et al., 2013). This function is then integrated with environmental (oceanographic) data of current and future scenarios, in order to allow hind- and forecasting of the species performance at various locations (habitat suitability) and at different time points. Hind-casting allows validation of model performance based on the comparison between model output and observational data of species distribution. For any given species, this approach allows habitat suitability maps to be generated at both small and large spatial (and temporal) scales. The strength of the ASM approach relies on the estimate of relative performance when comparing for example different locations or different species.

As a first example of ASM, experiments were conducted on a coastal fish species (grey mullet, *Mugil cephalus*) that undergoes annual migration into and out of coastal lagoons in order to obtain a function relating aerobic scope to temperature and dissolved oxygen concentration (Cucco et al., 2012). These relationships were then coupled with oceanographic data in order to compare the habitat suitability of this species inside the lagoon with that outside the lagoon (in a gulf). The relative habitat suitability matched well with the seasonal differences in occurrence of the species inside and outside the lagoon, suggesting that aerobic scope is maximized at any given time. In a second example of ASM, Marras et al. (2015) compared the relative aerobic performance of two species that are known to compete for resources, the rabbit fish *Siganus rivulatus* (a species from the Red Sea that has invaded the Mediterranean Sea) and the salema *Sarpa salpa* (a species native to the Mediterranean Sea). Laboratory experiments were carried out in order to obtain a relationship between aerobic scope and temperature for the two species. Temperature was used as the main stressor because changes in Mediterranean Sea temperature were claimed to be a critical factor influencing invasion success by affecting the physiological mechanisms responsible for invader superiority in a global warming scenario (Albouy et al., 2012, 2013; Ben Rais Lasram et al., 2010). These experiments on the relationship between aerobic scope and temperature allowed a full function to be derived that included thermal limits as well as optimal temperatures for each species. Standardization of these functions allow the relative performance of each species to be compared across the large range of temperatures relevant for these areas, thus estimating “winners” and “losers” for various locations and at different times, i.e. by coupling the experimentally-derived function with current oceanographic data as well as future projections. The results show a good match between the model scenarios of the current environmental situation and the ecological data of the distribution of the two species. In addition, the model allows projections to be made for the future invasion of the western side of the Mediterranean Sea by *Siganus rivulatus*. Although in a warming scenario, species distribution shifts are likely to depend on a number of factors in addition to metabolic scope, such as food availability, predation and competition (Marras et al., 2015), these modelling efforts represent a potential tool for evaluating the relative performance of species in different locations.

Recent work employed a metabolic approach to compare the current distribution of various fish species with their metabolic index (i.e. the ratio of O_2 supply to resting metabolic O_2 demand) (Deutsch et al., 2015). The results showed that the minimum metabolic index, where these fish species were present varied between 2 and 5, indicative of a critical energetic requirement for organismal activity. This approach was also used to project future changes in metabolic index as a result of climate change (warming and decrease in O_2 concentration). The upper ocean metabolic index was projected to be reduced by 20% globally and by 50% in northern regions, forcing poleward shifts of metabolically suitable habitats (Deutsch et al., 2015).

2.2. First principles approach

In addition to an experimental approach, physiological tolerances of species to environmental factors can also be estimated based on *first principles* (Buckley et al., 2011; Elith et al., 2010; Kearney and Porter, 2004; Kearney et al., 2010). Knowledge of the fundamental physiology underpinning a species response to their environment is a prerequisite for reliable projections of climate change impacts. At the same time, the experimental data-based approach is not practical for many species as they may be intractable for experimentation. In cases where laboratory studies are not feasible, bio-energetics modelling can provide a flexible theoretical framework based on physiological mechanisms that can be parameterised using experiments or empirical observations (Table 1). The challenge for bio-energetics modelling is to capture enough physiological realism whilst remaining simple enough so that detailed species-specific measurements for parameterisation are not required (Fig. 3C).

One such bio-energetic model, which has been successfully applied for modelling species distributions, is the Dynamic Energy Budget (DEB) model (Pecquerie et al., 2009; Raab et al., 2013; Teal et al., 2012), which is based on first principles described in the Dynamic Energy Budget theory (Kooijman, 2010). The underlying idea of DEB theory is that metabolism is organised in the same way within all animals and the (standard) DEB model aims to describe the empirical patterns which can be found consistently across the animal kingdom (Kooijman, 2010). Well known examples of such general patterns are the van Bertalanffy growth curve and Kleiber's rule, but there are many more (Sousa et al., 2008). The standard DEB is therefore applicable to all animals, but describes each species individually using species-specific parameters. The energy flow through the organism can be quantified for each species allowing physiological performance (e.g. growth, reproduction) to be calculated taking into account body size, temperature and food intake. The effects of climate change (specifically changes in temperature and food availability) on the individuals performance can therefore be calculated by using output from ecosystem models (e.g. ERSEM) as input for the DEB model. The suitability of a habitat can be then be assessed by how well an individual may perform given the environmental conditions (Fig. 3C).

The mechanistic method of modelling climate change effects on fish distribution was adopted to study the effects of climate on physiology-based habitat suitability of two commercially important flatfish species in the North Sea, plaice, *Pleuronectes platessa*, a more northern species, and sole, *Solea solea*, which prefer warmer temperatures (Teal et al., 2012). By combining Dynamic Energy Budget (DEB) models with the temperature and food conditions estimated by an ecosystem model (ERSEM), spatial differences in habitat quality were estimated under contrasting temperature and food conditions (Teal et al., 2012). The resulting habitat quality maps were in broad agreement with observed ontogenetic and seasonal changes in distribution and showed that whilst warming sea temperatures can enhance growth of sole (a more southern species), the coastal habitats of juvenile plaice in the southern North Sea are likely becoming too warm. Juvenile plaice are shown to respond by shifting distributions offshore confirming previous observations (Van Keeken et al., 2007). It seems that for plaice, the driving force behind distribution shifts is an avoidance of summer temperature peaks in coastal areas.

The DEB approach may also be used to explore other hypothesis apart from avoidance of unsuitable areas. The expansion of anchovy (*Engraulis encrasicolus*) in the North Sea in recent years for example, has been hypothesised to be due to an increased winter survival rate, allowing anchovy to remain in the southern North Sea rather than retracting south. Using again a combination of ERSEM output

and a DEB model parameterised for European anchovy, a previous study calculated the potential for this species to reach a large enough body size after the first year of growth to allow them to survive the winter (Raab et al., 2013). The model predicted that, over the past 30 years, the area where anchovy are able to reach this critical survival length increased from 0.2% of the North Sea in 1988 to 10.7% of the North Sea in 2003. Using the DEB approach it is possible to explore the mechanisms behind changes in patterns of distribution in greater detail and determine the relative roles played by temperature and food availability in governing habitat suitability. The DEB does not mechanistically output temperature tolerance limits and therefore still relies heavily on this knowledge being available per species. Current examples of applications of DEB for modelling distributions (e.g. Teal et al., 2012) have also relied on the assumption that optimum temperatures decrease with increasing size of fish [based on laboratory experiments (Fonds, 1975)]. To make the approach purely mechanistic, the underlying physiology of these temperature relationships should be parameterised within the DEB structure.

A second example of the bio-energetics approach can be found in individual-based models (IBM) parameterized for the marine fish larvae and applied in the North Sea for species such as sprat (*Sprattus sprattus*) and Atlantic cod (*Gadus morhua*) (Daewel et al., 2011). A recent physiology-based IBM for fish larvae was a generic model (Huebert and Peck, 2014) which embraced the fact that many bio-energetics rates remain unmeasured and some parameters of balanced energy budgets can be combined to simplify the input data required to obtain estimates of growth potential of larvae. This generic approach was able to explain considerable variability in growth rates observed across species such as Atlantic cod, sprat, Atlantic herring (*Clupea harengus*) and European anchovy (*Engraulis encrasicolus*).

In the terrestrial environment Physiologically Based Demographic Models (PBDM) have also been applied to tri-trophic systems and deal with resource acquisition and allocation within organisms and energy flow across trophic levels as well as population dynamics (Gutierrez et al., 2008, 2009).

The advantages of the bio-energetics-based models are that they makes use of the generalities found in terms of animal physiology and, therefore, can be applied to species for which little data or empirical observations are available. Regardless of any shortcomings in terms of availability of fundamental measurements, the model can therefore provide a consistent framework for modelling the physiology of all species, improving the comparability of results. Furthermore, the DEB model and IBM approaches are also able to deal with multiple stressors and other environmental parameters that are expected to affect the individual through physiological processes (e.g. salinity, oxygen, pH).

3. Discussion

As pointed out by Araújo and Peterson (2012), a physiology-based approach is not practical for many species, because either their ecology is poorly studied which limits *first principles approaches* or they are not suitable for laboratory experimentation. However, for species in which physiological experiments can be conducted, knowledge of physiological limits and relationships between environmental factors and physiological functions can provide additional knowledge for making predictions on the effect of climate change (such as in the ASM examples presented above: Cucco et al., 2012; Marras et al., 2015). As demonstrated in Teal et al. (2012) and Raab et al. (2013), in cases where such fundamental measurements are not available for given species, there are clear advantages of a *first principles* approach using a bio-energetics model such as the DEB model. DEB theory makes use of the

generalities found in terms of physiology across the animal kingdom and can therefore be applied to species for which little data or empirical observations are in fact available. Furthermore, once parameterised, the DEB model describes all life stages of the species, from egg to reproducing adult. Such a bio-energetics model can thus provide a consistent framework for modelling the physiology of all species, improving the comparability of results and allowing different measures of physiological performance (growth, reproduction) to be studied.

Although these approaches go some way towards a better mechanistic underpinning of predictions of climate change effects, it must be recognised that, because the complexity of climate change effects cannot be fully captured in the laboratory, physiology-based models are limited in this respect (Table 1). Whilst some laboratory studies coupled with modelling have attempted to capture interacting effects of multiple environmental drivers [e.g. temperature \times O₂ (Cucco et al., 2012)], the majority of studies still take into account only one environmental factor at a time (e.g. temperature). Whether based on single or multifactorial effects, it needs to be acknowledged that laboratory studies are ultimately small-scale idealisations of the real world, and as such they may not be realistic when scaled up to the field. Experimental designs need to be adequate for robust statistical inference (Cornwall and Hurd, 2015), which may be practically challenging in many marine laboratory facilities.

Furthermore, in nature, multiple drivers interact continuously. It can be particularly challenging to predict how many possible interactions exist among drivers, and this complexity escapes our imagination until it is observed in the field (Parmesan et al., 2013; Wernberg et al., 2013). Physiology-based models are able to deal with multiple stressors and other environmental parameters that are expected to affect the individual through physiological processes (e.g. salinity, oxygen, pH, various toxicants) and have frequently been applied in eco-toxicological studies to deal with interacting stressors (Jager and Klok, 2010). However, in order for these multiple stressors to be incorporated, additional experiments are required to measure responses to different combinations of stressors and detect the generalities in the underlying physiological responses that can then be applied across species.

The end result of interactions among factors to an organism may be synergistic (cumulative or multiplicative) or antagonistic (Davis et al., 2013). In addition to the complexity of interactions among multiple stressors, natural populations may also show evolutionary responses to climate change (Thomas et al., 2001) and/or adapt by phenotypic plasticity. Transgenerational effects have also been documented which change physiological responses to changes in climate-driven factors such as pH (Thor and Dupont, 2015). In physiology-based models, the species-specific parameters are currently assumed to be stable over time. Although the responses to climate change can be studied in the laboratory (Gonzalez and Bell, 2013), the extrapolation of the evolutionary responses, measured in the laboratory, to the field is a challenging task (Gonzalez and Bell, 2013). Therefore, phenotypic plasticity and potential evolutionary responses to climate change are not considered in physiology-based models which are clear limitations of their present approach. Future work should incorporate adaptation of a species metabolic functioning into physiology-based models by allowing the parameters of the model to adjust over time in accordance with the adaptation of the species. Differences in physiological performance, such as growth and reproduction, would then not only reflect changes in the environment (temperature and food availability) but also phenotypic plasticity in response to environmental changes. Disentangling these confounding effects in such a way that they can be mechanistically implemented within physiology-based models may prove

challenging.

Some life stages will be more sensitive to specific climate-driven factors than other life stages which will be important to assess when projecting future changes in distribution and productivity of marine fishes (Petitgas et al., 2013). Embryo and larval stages may have a different range in upper and lower tolerable temperatures compared to later (larger) life stages. In addition, larvae may be particularly vulnerable to changes in seawater chemistry (e.g. due to ocean acidification) because larvae lack functioning gills and therefore do not have the same osmoregulatory capacity as juveniles and adults (Llopiz et al., 2014). To explore the impacts of climate change on fishes and other organisms with complex life histories, it will be necessary to conduct laboratory experiments not only on juveniles and adults but also on earlier life stages and/or during phases of reproduction and to translate this information into full life cycle physiology-based models (Peck et al., 2013). This is a challenging task because of large differences in methodology often needed to measure specific parameters such as metabolic scope in young larvae, juveniles and adults (Killen et al., 2007), and represents a current limitation for the predictive capacity of some physiology-based models such as the ASMs.

In contrast to long-term warming trends, a key aspect of climate change will be projected changes in peak and extreme temperatures and the frequency with which these will be encountered. It is not sufficient to gauge the impact of a subtle (few degree) increase in mean temperature; knowledge of how frequently and by how much environmental variables such as temperature may surpass critical limits is needed. For example, some physiology-based models for fish employ relatively short (mins to hrs) time steps (e.g. IBMs constructed for larvae) and only include simple depictions of mortality (e.g. larvae die when they experience temperatures above or below pre-defined limits). However, the short-term survival of fish at extreme temperatures depends on both the duration and the magnitude of exposure (Pörtner and Peck, 2010). Physiology-based models such as the DEB and ASMs employ longer time steps (days to weeks) and neither are formulated to capture the small-scale (seasonal) changes in internal processes. Studying these physiological mechanisms acting at different time scales requires more in depth knowledge of species biology and the environmental triggers which are central to population survival. The DEB model is designed to fit patterns of growth displayed across life stages of an animal and the impacts of broad-scale, long-term processes on resource partitioning. When considering, for example, metabolic scope or allocation of energy to reproduction under different environmental scenarios, seasonal processes are critical. Field data collected among years with markedly different temperature regimes can help inform models on how allocation strategies of income or capital breeders change with temperature (Haslob et al., 2012), but patterns observed in the field result from a complex interplay of temperature-dependent phenomena such as changes in the quality or availability of prey (Hufnagl et al., 2015). The effects of temperature on reproductive partitioning and other physiological details require further study in the laboratory if we hope to supply models with the data needed to capture processes acting on short (hours, days, months) time scales. Similarly, current ASMs do not take into account food availability, biotic interaction such as predator-prey relationships and interspecific competition. Future work should therefore focus on including such factors, especially when aimed at predicting the effect of climate change on the future distribution of competing species. The role of physiological experiments in predicting the effects of climate change would be strengthened by using the experimental results in conjunction with both modelling and manipulation of natural or semi-natural (e.g. enclosures) systems (Parmesan et al., 2013). In addition, laboratory work coupled with

modelling could be designed to better represent the pattern of extreme events observed in nature (e.g. severe hypoxic events, short-term extreme warming events) in order to quantify and better simulate with models the organism's response to those phenomena. Taking advantage of relatively short-term events such as heat waves that can significantly alter the ecosystem structure and species abundance of large coastal areas (Wernberg et al., 2013), would allow predictions from physiology-based models to be better validated.

Acknowledgements

This work was supported by the European Community's Seventh Framework Programme (FP7/2007–2013) under Grant Agreement No. 266445 for the project Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS).

References

- Albouy, C., Guilhaumon, F., Araújo, M.B., Mouillot, D., Leprieux, F., 2012. Combining projected changes in species richness and composition reveals climate change impacts on coastal Mediterranean fish assemblages. *Glob. Change Biol.* 18, 2995–3003.
- Albouy, C., Guilhaumon, F., Leprieux, F., Ben Rais Lasram, F., Somot, S., Aznar, R., Velez, L., Le Loc'h, F., Mouillot, D., 2013. Projected climate change and the changing biogeography of coastal Mediterranean fishes. *J. Biogeogr.* 40, 534–547.
- Araújo, J.O., Peterson, T., 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93, 1527–1539.
- Asch, R.G., 2015. Climate change and decadal shifts in the phenology of larval fishes in the California current ecosystem. *Proc. Natl. Acad. Sci.* 112, E4065–E4074.
- Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., Mouillot, D., 2010. The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change. *Glob. Change Biol.* 16, 3233–3245.
- Bozinovic, F., Pörtner, H.O., 2015. Physiological ecology meets climate change. *Ecol. Evol.* 5, 1025–1030.
- Buckley, L.B., Waaser, S.A., MacLean, H.J., Fox, R., 2011. Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology* 92, 2214–2221.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., et al., 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334, 652–655.
- Claireaux, G., Lefrançois, C., 2007. Linking environmental variability and fish performance: integration through the concept of scope for activity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362, 2031–2041.
- Cornwall, C.E., Hurd, C.L., 2015. Experimental design in ocean acidification research: problems and solutions. *ICES J. Mar. Sci.* <http://dx.doi.org/10.1093/icesjms/fsv118>.
- Cucco, A., Sinerchia, M., Lefrançois, C., Magni, P., Ghezzi, M., Umgieser, G., Perilli, A., Domenici, P., 2012. A metabolic scope based model of fish response to environmental changes. *Ecol. Modell.* 237–238, 132–141.
- Daewel, U., Peck, M.A., Schrum, C., 2011. Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modelling approach. *Can. J. Fish. Aquat. Sci.* 68, 426–443.
- Davis, A.R., Coleman, D., Broad, A., Byrne, M., Dworjanyn, S.A., Przeslawski, R., 2013. Complex responses of intertidal molluscan embryos to a warming and acidifying ocean in the presence of UV radiation. *PLoS One* 8, e55939.
- Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O., Huey, R.B., 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348, 1132–1135.
- Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* 45, 1029–1039.
- Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., Farrell, A.P., 2011. Differences in thermal tolerance among sockeye salmon populations. *Science* 332 (6025), 109–112.
- Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. *Methods Ecol. Evol.* 1, 330–342.
- Fonds, M., 1975. The influence of temperature and salinity on growth of young sole *Solea solea* L. In: *Proceedings of the 10th European Symposium on Marine Biology* 1, pp. 109–125.
- Franklin, J., 2013. Species distribution models in conservation biogeography: developments and challenges. *Divers. Distrib.* 19 (10), 1217–1223.
- Fry, F.E., 1971. The effect of environmental factors on the physiology of fish. In: Hoar, W.S., Randall, D.J. (Eds.), *Fish Physiol.* Academic Press, New York, pp. 1–98.
- Gonzalez, A., Bell, G., 2013. Evolutionary rescue and adaptation to abrupt environmental change depends upon the history of stress.
- Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R., Wintle, B.A., 2015. Is my species distribution model

- fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* 24 (3), 276–292.
- Guisan, A., Thuiller, W., 2005. Predicting species distributions: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., et al., 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16 (12), 1424–1435.
- Gutierrez, A.P., Ponti, L., d'Utrement, T., Ellis, C.K., 2008. Climate change effects on poikilotherm tritrophic interactions. *Clim. Change* 87 (Suppl. 1), S167–S192.
- Gutierrez, A.P., Ponti, L., Zossu, Q.A., 2009. Effects of climate warming on olive and olive fly (*Bactrocera oleae*) in California and Italy. *Clim. Change* 95, 195–217.
- Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett.* 9, 228–241.
- Haslob, H., Hauss, H., Petereit, C., Clemmesen, C., Kraus, G., Peck, M.A., 2012. Temperature effects on vital rates of different life stages and implications for population growth of Baltic sprat. *Mar. Biol.* 159, 2621–2632.
- Huebert, K.B., Peck, M.A., 2014. A day in the life of fish larvae: modeling foraging and growth using quirks. *PLoS One* 9, e98205.
- Hufnagl, M., Peck, M.A., Nash, R.D.M., Dickey-Collas, M., 2015. Unravelling the Gordian knot! Key processes impacting overwintering larval survival and growth: a North Sea herring case study. *Prog. Oceanogr.* 138, 486–503.
- IPCC, 2013. Climate Change 2013: the Physical Science Basis. Working Group 1 Contribution to the Fifth Assessment Report of the International Panel on Climate Change. Cambridge, New York.
- Jager, T., Klok, C., 2010. Extrapolating toxic effects on individuals to the population level: the role of dynamic energy budgets. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 3531–3540.
- Jørgensen, C., Peck, M.A., Antognarelli, F., Azzurro, E., Burrows, T., Cheung, W.W.L., Cucco, A., Holt, R.E., Huebert, K.B., Marras, S., et al., 2012. Conservation physiology of marine fishes: advancing the predictive capacity of models. *Biol. Lett.* 8, 900–903.
- Kearney, M., Porter, W.P., 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85, 3119–3131.
- Kearney, M., Wintle, B.A., Porter, W., 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conserv. Lett.* 3, 203–213.
- Killen, S.S., Costa, I., Brown, J., Gamperl, K., 2007. Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. *Proc. R. Soc. B Biol. Sci.* 274, 431–438.
- Killen, S.S., Marras, S., Metcalfe, N.B., McKenzie, D.J., Domenici, P., 2013. Environmental stressors alter relationships between physiology and behaviour. *Trends Ecol. Evol.* (0)
- Kooijman, S.A.L.M., 2010. *Dynamic Energy Budget Theory for Metabolic Organization*. Cambridge University Press, Cambridge, UK.
- Lennox, R.J., Choi, K., Harrison, P.M., Paterson, J.E., Peat, T., Ward, T., Cooke, S.J., 2015. Improving science-based invasive species management with physiological knowledge, concepts, and tools. *Biol. Invasions*. <http://dx.doi.org/10.1007/s10530-015-0884-5>.
- Llopiz, J.K., Cowen, R.K., Hauff, M.J., Ji, R., Munday, P., Muhling, B., Peck, M.A., Richardson, D.E., Sogard, S., Sponaugle, S., 2014. Early life history and fisheries oceanography: new questions in a changing world. *Oceanography* 27 (4), 26–41.
- Marras, S., Cucco, A., Antognarelli, F., Azzurro, E., Milazzo, M., Bariche, M., Butenschön, M., Kay, S., Di Bitetto, M., Quattrocchi, G., et al., 2015. Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. *Conserv. Physiol.* <http://dx.doi.org/10.1093/conphys/cou059>.
- Monahan, W.B., 2009. A mechanistic niche model for measuring species' distributional responses to seasonal temperature gradients. *PLoS One* 4, e7921.
- Newbold, T., 2010. Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Prog. Phys. Geogr.* 34, 3–32.
- Parmesan, C., Burrows, M.T., Duarte, C.M., Poloczanska, E.S., Richardson, A.J., Schoeman, D.S., Singer, M.C., 2013. Beyond climate change attribution in conservation and ecological research. *Ecol. Lett.* 16, 58–71.
- Peck, M.A., Arvanitidis, C., Butenschön, M., Melaku Canu, D., Chatzinikolaou, E., Cucco, A., Domenici, P., Fernandes, J.A., Gasche, L., Huebert, K.B., et al., 2015. Understanding and projecting changes in the distribution and productivity of living marine resources: a critical review of modelling approaches. *Estuar. Coast. Shelf Sci.* (submitted for publication).
- Peck, M.A., Reglero, P., Takahashi, M., Catalán, I.A., 2013. Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Prog. Oceanogr.* 116, 220–245.
- Pecquerie, L., Petitgas, P., Kooijman, S.A.L.M., 2009. Modeling fish growth and reproduction in the context of the Dynamic Energy Budget theory to predict environmental impact on anchovy spawning duration. *J. Sea Res.* 62, 93–105.
- Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915.
- Petitgas, P., Alheit, J., Peck, M.A., Raab, K., Irigoien, X., Huret, M., van der Kooij, J., Pohlmann, T., Wagner, C., Zarraonaindia, I., et al., 2012. Anchovy population expansion in the North Sea. *Mar. Ecol. Prog. Ser.* 444, 1–13.
- Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K., Drinkwater, K., Huret, M., Nash, R.D.M., 2013. Impacts of climate change on the complex life cycles of fish. *Fish. Oceanogr.* 22, 121–139.
- Pörtner, H.O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* 213, 881–893.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–692.
- Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97.
- Pörtner, H.O., Peck, M.A., 2010. Climate change impacts on fish and fisheries: towards a cause and effect understanding. *J. Fish. Biol.* 77, 1745–1779.
- Raab, K., Lope, M., Nagelkerke, L.A.J., Rijnsdorp, A.D., Teal, L.R., Licandro, P., Ruardij, P., Dickey-Collas, M., 2013. Influence of temperature and food availability on juvenile European anchovy *Engraulis encrasicolus* at its northern boundary. *Mar. Ecol. Prog. Ser.* 488, 233–246.
- Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? *J. Biogeogr.* 33 (10), 1689–1703.
- Schram, E., Bierman, S., Teal, L.R., Haenen, O., van de Vis, H., Rijnsdorp, A.D., 2013. Thermal preference of juvenile dover sole (*Solea solea*) in relation to thermal acclimation and optimal growth temperature. *PLoS One* 8, e61357.
- Sims, D.W., Wearmouth, V.J., Genner, M.J., Southward, A.J., Hawkins, S.J., 2005. Low-temperature-driven early spawning migration of a temperate marine fish. *J. Anim. Ecol.* 73, 333–341.
- Sousa, T., Domingos, T., Kooijman, S.A.L.M., 2008. From empirical patterns to theory: a formal metabolic theory of life. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 363, 2453–2464.
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* 2 (9), 686–690.
- Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Smith, R.S., Barrett, N., Wernberg, T., et al., 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* 18 (9), 944–953.
- Teal, L.R., van Hal, R., van Kooten, T., Ruardij, P., Rijnsdorp, A.D., 2012. Bio-energetics underpins the spatial response of north sea plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to climate change. *Glob. Change Biol.* 18, 3291–3305.
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., et al., 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Change Biol.* 16 (12), 3304–3313.
- Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., Conrad, L., 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411 (6837), 577–581.
- Thor, P., Dupont, S., 2015. Transgenerational effects alleviate severe fecundity loss during ocean acidification in a ubiquitous planktonic copepod. *Glob. Change Biol.* <http://dx.doi.org/10.1111/gcb.12815> (in press).
- Torres, L.G., Sutton, P.J.H., Thompson, D.R., Delord, K., Weimerskirch, H., Sagar, P.M., Sommer, E., Dilley, B.J., Ryan, P.G., Phillips, R.A., 2015. Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. *PLoS One*. <http://dx.doi.org/10.1371/journal.pone.0120014>.
- Van Keeken, O.A., Van Hoppe, M., Grift, R.E., Rijnsdorp, A.D., 2007. Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries. *J. Sea Res.* 57, 187–197.
- Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat. Clim. Change* 3 (1), 78–82.