# Modelling climate change impacts on marine fish populations: Process-based integration of ocean warming, acidification, and other environmental drivers

*Stefan Koenigstein[1,2], Felix C. Mark[2], Stefan Gößling-Reisemann[1,3], Hauke Reuter[4,5], Hans-Otto Pörtner[2,5]*

[1] Sustainability Research Center (artec), University of Bremen; [2] Integrative Ecophysiology section, Alfred Wegener Institute (AWI) Helmholtz Centre for Polar and Marine Research; [3] Department of Resilient Energy Systems, University of Bremen; [4] Dept. of Theoretical Ecology and Modelling, Leibniz Center for Tropical Marine Ecology; [5] Faculty of Biology and Chemistry, University of Bremen

Correspondence:
Stefan Koenigstein, University of Bremen, artec Sustainability Research Center, Enrique-Schmidt-Str. 7, D-28359 Bremen, Germany. E-mail: koenigstein@uni-bremen.de

## Abstract

Global climate change affects marine fish through drivers such as warming, acidification and oxygen depletion, causing changes in marine ecosystems and socio-economic impacts. Experimental and observational results inform about anticipated effects of different drivers, but linking between these results and ecosystem level changes requires quantitative integration of physiological and ecological processes into models to advance research and inform management.

We give an overview of important physiological and ecological processes affected by environmental drivers. We then provide a review of available modelling approaches for marine fish, analysing their capacities for process-based integration of environmental drivers. Building on this, we propose approaches to advance important research questions.

Examples of integration of environmental drivers exist for each model class. Recent extensions of modelling frameworks have a greater potential for including detailed mechanisms to advance model projections. Experimental results on energy allocation, behaviour and physiological limitations will advance the understanding of organism-level trade-offs and thresholds in

response to multiple drivers. **More explicit representation of life cycles and biological traits can improve description of population dynamics and adaptation, and data on food web topology and feeding interactions help detail the conditions for possible regime shifts. Identification of relevant processes will benefit the coupling of different models to investigate spatial-temporal changes in stock productivity and responses of social-ecological systems.**

**Thus, a more process-informed foundation for models will promote the integration of experimental and observational results and increase the potential for model-based extrapolations into a future under changing environmental conditions.**

**Key words:** ecosystem modelling, environmental drivers, climate change, ocean acidification, fish ecophysiology, process understanding

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## Introduction

The productivity of marine fish stocks is influenced by a multitude of environmental factors. In the near future, many stocks will be increasingly affected by climate change including global ocean warming, ocean acidification, oxygen loss and other long-term and more regional environmental changes such as salinity, nutrient redistribution or eutrophication and pollution (Roessig et al., 2005, Cochrane et al., 2009, Hollowed et al., 2013, Pörtner et al., 2014). Environmental drivers affect marine ecosystems, marine organisms and fish stocks through direct impacts on individual physiology and life history, and/or indirectly via changes in primary productivity or ecological (mainly food web) interactions, spatial configuration of habitats, or planktonic larval transport (Doney et al., 2012, Metcalfe et al., 2012).

Responses to these environmental drivers, e.g. through changes in productivity and spatial distribution will co-determine the future development of fish stocks and fisheries (Perry et al., 2005, Lehodey et al., 2006). For instance, periodic changes between anchovy and sardine regimes in the North Pacific can be explained by different optimum growth temperatures (Takasuka et al., 2007, Lindegren and Checkley, 2013), and warming temperatures have contributed to recently high stock levels in Barents Sea cod (Ottersen et al., 2006, Kjesbu et al., 2014). In tropical and upwelling areas, and due to the general warming trend, low oxygen availability can set physiological limits to fish stocks (Ekau et al., 2010, Stramma et al., 2010). Across marine ecosystems, ocean acidification has emerged as an additional threat for marine fish populations e.g. through impacts on larval behaviour and associated mortality as seen in coral reef fish (Munday et al., 2010).

Climate change impacts different hierarchical levels of biological organization, from individual physiology and population level changes to community and ecosystem shifts (Le Quesne and Pinnegar, 2012). Many of the direct effects on organisms can only be observed and investigated at the cellular or individual level, and to assess their overall stock effects, they have to be scaled up to population and community level, thus integrating processes on the different levels (Rijnsdorp et al., 2009, Pörtner and Peck, 2010). Physiological processes link the physical environment to individual-level responses and thus help to gain principal mechanism-based understanding of climate change impacts on populations and ecosystems (Pörtner and Farrell, 2008, Denny and Helmuth, 2009, Chown et al., 2010).

To anticipate climate change effects in marine ecosystems, ecological simulation models allow for the inclusion of processes on different hierarchical levels of biological organization, and an analysis of their mutual feedbacks. Models may integrate the impacts of multiple drivers on fish from the physiological to the community and ecosystem levels, and to analyse stock dynamics under different scenarios of environmental change. To improve model projections and test hypotheses about environmental determinants for fish stocks, it is necessary to investigate mechanisms underlying stock dynamics and distribution (Hollowed et al., 2009, Hare, 2014). As empirical or statistical descriptions are based on the observed range of the combined underlying factors, historical data and identified patterns for fish stocks may fail to resolve uncertainties of projections if the underlying processes, e.g. life history, energetics, and recruitment patterns, change and causalities are not understood (Mangel and Levin, 2005).

A more mechanistic formulation of models could be based on the explicit consideration of physiological and ecological processes that determine observed phenomena (Baskett, 2012, Metcalfe et al., 2012). This could increase the

projection capacities of models under new combinations of environmental drivers (Jørgensen et al., 2012, Russell et al., 2012). These models could make better use of results from advanced experiments on multiple drivers (Denman et al., 2011, Dupont and Pörtner, 2013) and be tested with observations on stock dynamics in already changing environments, facilitating development of early-warning signs for productivity changes in fish stocks (Brander, 2010). In the light of recently increased efforts to establish ecosystem-based fisheries management approaches and the growing importance of societal climate adaptation, an integration of knowledge about ecological and physiological processes seems necessary more than ever before (Cury et al., 2008, Miller et al., 2010, Persson et al., 2014).

Although models for use in climate change projections and ecosystem-based fisheries management have been reviewed for general strengths and weaknesses (Keyl and Wolff, 2007, Plagányi, 2007, Stock et al., 2011, Hollowed et al., 2012) and some approaches for better integration of physiological data and mechanistic concepts have been proposed (Metcalfe et al., 2012, Persson et al., 2014), a systematic inspection of possible directions for advancement is currently lacking. An up-to-date and comprehensive review of modelling approaches for marine fish and options for direct integration of environmental effects therefore seems timely and may facilitate better interdisciplinary exchange and well-coordinated progress in this fast-developing field.

In this article, we will provide an overview of potentially relevant physiological and ecological processes to understand climate change impacts on fish stocks (section two). We then review available modelling approaches and present examples for marine fish species, analysing them for their potential and limitations to incorporate environmental impacts on the identified processes (section three). In the closing section, we exemplify the challenges and potential for the advancement of models by addressing five key questions in regard to climate change impacts on marine fish, in the context of changes in their ecosystems and in human resource uses.

## From drivers to processes: Physiological and ecological processes affected by environmental drivers

Physiological processes act from the cellular to the organism level, and can be used to explain direct effects of environmental drivers and individual tolerance towards changes. They affect and are affected by higher levels of biological organization, such as the population or community and ecosystem interactions, where ecological processes can serve to extrapolate the impacts of climate change, ocean acidification and other drivers (Pörtner and Peck, 2010, Monaco and Helmuth, 2011, Gaylord et al., 2015). As a framework for structuring our analysis of modelling approaches, we will consider physiological and ecological key processes, organized by the level of biological organization on which they act primarily (Fig. 1). This is intended to help the reader identify potentially relevant processes as the basis for choosing an appropriate model.

| Ecosystem (spatio-temporal) | Migration | Dispersal | Habitat availability | → | *Spatial heterogeneity* *Temporal fluctuation* |
| Community | Predation | Competition | Mutualism & facilitation | → | *Trophic structure* *Community diversity* |
| Population | Reproduction | Recruitment | Population adaptation | → | *Population dynamics* |
| Organism (and suborganismal) | Plasticity & acclimation — Growth & development — Maturation — Metabolism — Energy allocation | Behavioral adaptation — Foraging & assimilation — Mortality — Activity — Physiological limitations | | → | *Individual tolerance* |

+ / - Temperature     - pH + CO₂     - O₂     Other drivers (e.g. salinity, toxins)

Figure 1: Overview over physiological and ecological processes, as a framework to assess potential effects of environmental drivers on fish stocks. Processes are separated among different levels of biological hierarchy, from organism and suborganismal (cell and tissue or organ) processes to population, community, and spatio-temporal ecosystem processes. Environmental drivers such as warming, acidification, hypoxia and others (bottom) act directly on organisms and indirectly affect processes on higher levels, shaping the characteristics resulting at each level of description (right). Higher-level processes are aggregate descriptions of processes on lower levels, and this framework is proposed to represent an easily observable and quantifiable description, but alternative descriptions are possible (e.g., recruitment can be described as the product of growth, foraging and mortality of early life stages, and evolution is the product of individual plasticity, acclimation and adaptations, and population adaptation). For details on processes and effects, see section two.

## Organism level processes, and suborganismal processes interacting on the individual level

Environmental drivers can affect a range of processes at the organismal level, and individual tolerance of fish is co-defined by suborganismal (i.e. tissue and cellular) level capacities and processes (cf. Fig. 1). Basic organism processes such as routine activity, growth and reproduction are sustained only in a limited range of temperatures, indicating thermal specialization. Through its effects on metabolic processes in ectothermic animals, temperature modifies development and growth rates. Elevated temperatures entail increased metabolic rates and energy turnover (Clarke and Johnston, 1999). However, when a critical temperature is reached, aerobic physiological performance fails to increase further or is even reduced, due to limited oxygen availability and capacities of respiratory, ventilatory, and cardiovascular systems. Sustained performance relies on aerobically produced metabolic energy, thus oxygen availability sets general limits to fish metabolism and growth (Pauly, 2010). Organismal capacities vary between behavioural types and habitat adaptations, e.g. active pelagic swimmers *vs.* benthic ambush predators, eurythermal *vs.* stenothermal habitats (Pörtner et al., 2004). Individual fish behaviour thus has consequences for population, community and ecosystem processes, and behavioural adaptation may also buffer impacts of environmental drivers on individuals and populations (Mittelbach et al., 2014).

Limitations to an animal's performance and tolerance to unfavourable environmental conditions will eventually become visible at the whole animal level, but are co-defined at the cellular level. While temperature may be the most important factor in setting these limits (Pörtner and Peck, 2010), further environmental factors such as ocean acidification or hypoxia (low $O_2$ levels) can modify aerobic capacity and temperature limits (Pörtner, 2010, 2012). Hypoxia has for instance been shown to reduce food uptake and limit metabolic and growth rates and development of early life stages in fish (Ekau et al., 2010). More recently, ocean acidification (declining oceanic pH and elevated $CO_2$ levels) has been identified as an additional driver, underscoring the necessity to integrate physiological responses and experimental results on interactions among drivers into models and projections (Fabry et al., 2008, Riebesell and Gattuso, 2015).

High seawater $CO_2$ levels increase $CO_2$ diffusion into the bloodstream of marine fish, which is generally compensated within hours to days by an active accumulation of bicarbonate ($HCO_3^-$) to maintain the extracellular pH required for efficient cellular functioning (e.g. Heisler, 1984, Brauner and Baker, 2009, Melzner et al., 2009b). The increased energy demand of compensatory metabolic processes such as acid-base regulation (Deigweiher et al., 2008, Melzner et al., 2009a) can entail shifts in the animal's energy budget, and lead to acclimatory responses in various physiological processes. Consequently, ocean acidification will act in addition to, or synergistically with, ocean warming, leading to decreased upper critical temperatures (Pörtner and Peck, 2010). Recent studies have demonstrated a considerable chronic impact of ocean acidification, e.g. on cellular metabolism (Strobel et al., 2012, Strobel et al., 2013), metabolic rate (Michaelidis et al., 2007, Enzor et al., 2013), respiratory performance (Couturier et al., 2013) and aerobic scope (Rummer et al., 2013).

Thus, consideration of the physiological processes involved in individual responses can serve to integrate the effects of multiple drivers (increasing temperature, acidification, hypoxia) and to assess the combined effect on the organism and the energetic cost of individual acclimation.

## Population level processes: recruitment, reproduction, population adaptation

Processes at the population level, such as recruitment, determine the dynamics of fish stocks and can be strongly influenced by the physical environment (Rothschild et al., 1989, Myers, 1998, Ottersen et al., 2013, Szuwalski et al., 2014). Increasing temperatures lead to faster development of fish larval stages, earlier maturation at smaller sizes and reduced *per-capita* fecundity, affecting population productivity (Rijnsdorp et al., 2009, Baudron et al., 2014).

Embryos and larval stages do not yet express the fully developed capacities for acid-base regulation of juvenile and adult fish. Thus, additional stressors such as ocean acidification, hypoxia or pollution can lead to increased mortality and impaired growth performance (Franke and Clemmesen, 2011, Baumann et al., 2012, Frommel et al., 2012, Nikinmaa, 2013). Increased temperature and ocean acidification can also affect reproductive output and gamete survival, impacting reproduction of the population (Inaba et al., 2003, Frommel et al., 2010, Miller et al., 2015). Thus, egg and larval stages are potential bottlenecks in life history and in adaptation of fish to multiple environmental drivers (Melzner et al., 2009b, Rijnsdorp et al., 2009).

Whether adaptation of fish populations can keep pace with future changes in environmental conditions is an important open research question (Rijnsdorp et al., 2009). Population adaptation can happen within the range of phenotypic plasticity, e.g. through behavioural adaptation, developmental and trans-generational acclimation (Crozier and Hutchings, 2014), or by evolution of adaptive genetic divergence (Nielsen et al., 2009, Reusch, 2014). While genomic markers have been linked to ecological differentiation e.g. in Atlantic cod (Hemmer-Hansen et al., 2013), most available studies have found plastic responses, and studies reporting trans-generational plasticity under conditions of climate change are relatively scarce for large and long-lived fish species (Crozier and Hutchings, 2014, Munday, 2014). However, some laboratory and in situ experiments demonstrate that heritable effects can significantly enhance tolerance to environmental drivers and involve metabolic readjustments (Donelson and Munday, 2012, Miller et al., 2012, Shama et al., 2014). Effects of climate change at the population level may also act synergistically with impacts of human exploitation, as fishing pressure can lead to a reduction in size at maturation (Law, 2000, Jørgensen et al., 2007) and to a higher sensitivity towards environmental fluctuations in exploited stocks (Perry et al., 2010).

## Community level processes: predation, competition, mutualism & facilitation

Direct environmental effects on fish are influenced by species interactions in the food web, and can lead to indirect effects on other species (e.g. Link et al., 2009, Engelhard et al., 2014, Bogstad et al., 2015). The response of a marine ecosystem to changes of one stock depends on the type of trophic control, i.e. bottom-up or top-down (Frank et al., 2006), and the characteristics of predator-prey interactions are a primary determinant of marine community resilience (Hunsicker et al., 2011). Cascading effects triggered by direct impacts on one element of the food web may be especially relevant in top-down controlled systems (Frank et al., 2006), can lead to regime or phase shifts, and therefore have to be considered when discussing effects of climate change (Mangel and Levin, 2005, Link et al., 2009).

Changes in prey biomass and composition can influence the energy uptake for fish due to different energy content or size of food particles (Beaugrand et al., 2003, Beaugrand and Kirby, 2010). Regional changes in zooplankton

communities are correlated to rising water temperatures and may facilitate range shifts of fish stocks, which follow the occurrence of their preferred prey (Brander, 2010, Dalpadado et al., 2012). Calcifying zooplankton species, e.g. pteropods, may be vulnerable to ocean acidification and warming (Lischka and Riebesell, 2012). Non-calcifying zooplankton, such as copepods, have displayed a reduced overall energy content under warming and acidification (Hildebrandt et al., 2014), and may also be impacted indirectly through reduced food quality of phytoplankton (Rossoll et al., 2012).

Changes in trophic interactions and energy transfer will be modulated by individual animal feeding behaviour. Behaviour and sensory systems of fish can be influenced by elevated $CO_2$ levels putatively through interaction with neuronal receptors (Briffa et al., 2012, Nilsson et al., 2012, Hamilton et al., 2014). Effects have been shown to occur in all life stages in laboratory and field experiments mostly of tropical reef fish (but see Jutfelt et al., 2013, Jutfelt and Hedgarde, 2013) and include impaired olfactory, visual and hearing abilities (Simpson et al., 2011, Leduc et al., 2013, Chung et al., 2014), reduced capacities for learning, homing and decision-making (Devine et al., 2012, Ferrari et al., 2012), and reduced or delayed behavioural responses towards predators (Ferrari et al., 2011, Munday et al., 2013a, Nagelkerken et al., 2015).

In sharks, warming and acidification can impair growth and hunting behaviour (Pistevos et al., 2015).

Thus, changes in planktonic community composition and predator-prey interactions point at probable changes in food composition for fish and in marine community dynamics. Other interactions, such as mutualism, facilitation or parasitism, may also be affected by changed occurrences and sensitivities of species, and influence the response at the community level.

## Spatial ecosystem level processes: migration, dispersal, habitat availability

The spatial heterogeneity of marine habitats influences the range of environmental conditions experienced by individuals, and interacts with population and community processes (Ciannelli et al., 2008). Changes in distribution ranges of marine fish species under climate change, are based on the spatial processes migration and dispersal, and on the availability of suitable habitat (Roessig et al., 2005). For instance, vertical foraging migrations or large-distance seasonal migrations can be linked to characteristic temperature corridors (e.g. Kitagawa et al., 2000, Stensholt, 2001). Spatial structure and distribution of stocks can be shaped by migratory behaviour and larval dispersal, as governed by oceanic currents and bottom topography (e.g. Rindorf and Lewy, 2006, Knutsen et al., 2007). Local impacts of climate change e.g. in spawning or nursery grounds can thus disrupt spatial life cycles via recruitment success (Petitgas et al., 2012, Llopiz et al., 2014). Spatial structure of fish stocks also influences the response to harvesting (Ciannelli et al., 2013).

Ocean warming may reduce dispersal distances and decrease population connectivity due to faster larval development, and can lead to shifts in seasonal spawning timing (O'Connor et al., 2007, Asch, 2015). Experimental and empirical data can elucidate these spatial-temporal organism-habitat connections. Processes such as migration and recruitment can in principle be described as a result of behavioural responses to the spatial environment, governed by physiological capabilities and limitations (cf. Fiksen et al., 2007). Observational and telemetry data can be used to inform about population movements (Metcalfe et al., 2012), and genomic methods can reveal fine-scale population structuring and local or regional adaptive differentiation in fish species (Nielsen et al., 2009).

## From processes to models: Modelling approaches and their capacity for process-based integration of environmental drivers

In this section, the main types of models used to investigate marine fish are analysed for their capacity to incorporate the effects of environmental drivers on specific physiological and ecological processes. For clarity, we divide the models into seven categories: 1) single-species population dynamic models, 2) multi-species population dynamic models, 3) trophodynamic & mass-balanced models, 4) species distribution models (SDMs), 5) trait-based & size-spectrum models, 6) individual-based models (IBMs), and 7) bioenergetic models. These categories represent historical developments, but no definitive functional distinctions. Modelling approaches are under rapid development and continuously incorporating new possibilities, sometimes originating from other model classes. Finally, we describe approaches and issues for the coupling of models and coupled end-to-end models.

We aim to explain the underlying concepts, and review recent applications and extensions with regard to the incorporation of environmental drivers, to give a guideline in the choice of a suitable modelling approach. Furthermore, we present relevant freely available software packages, to encourage the reader to try out models and gain a better understanding of the underlying assumptions.

### Single-species population dynamic models

Single-species population dynamic models descend from models used for traditional fisheries stock assessment (Ricker, 1954, Beverton and Holt, 1957). These models rely on catch and survey data to estimate fish stock size, and simulate stock dynamics based on estimated population-level parameters like biomass, growth rate, recruitment, fishing and natural mortality (Hilborn, 2012). Extensions have divided stocks into age and/or size classes that can possess varying mortalities and growth (Deriso et al., 1985, Fournier et al., 1990), and 'matrix population' models consider both factors e.g. by describing stages within age classes (Caswell, 2001).

**Organism:** Stock models with both size- and age-structure can integrate adjustments of size-dependent or age-dependent processes (e.g. growth, mortality, development as shift to the next stage) based on environmental effects. The effects of temperature have been incorporated by tuning the growth function, e.g. for climate-dependent variations in Atlantic cod stocks (Brander, 1995, Clark et al., 2003), and by adjusting natural mortality, e.g. in an age-structured model for Pacific saury (*Cololabis saira*, Scomberesocidae; Tian et al., 2004). Assumed effects of changes in temperature, salinity and hypoxia on growth, mortality and reproduction have been integrated in a matrix projection model for Atlantic croaker (*Micropogonias undulatus*, Sciaenidae; Diamond et al., 2013).

**Population**: Stock assessment models aggregate early life stages in an empirical stock-recruitment relationship (Needle, 2001), which determines critical characteristics of the produced stock dynamics (e.g. Cabral et al., 2013). Environmental drivers have been incorporated into recruitment functions (Hollowed et al., 2009), e.g. as temperature effects on North Sea and Baltic cod (Köster et al., 2001, Clark et al., 2003), on tropical rock lobster (*Panulirus ornatus*, Palinuridae; Plaganyi et al., 2011) and on Baltic sprat (*Sprattus sprattus*, Clupeidae; Voss et al., 2011). The influences of atmospheric oscillations and regional oceanographic regimes on recruitment have been incorporated e.g. for Atlantic cod (Brander and Mohn, 2004), Northern rock sole (*Lepidopsetta polyxystra*, Pleuronectidae;

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Hollowed et al., 2009) and jackass morwong (*Nemadactylus macropterus*, Cheilodactylidae; Wayte, 2013).

Simpler, non stage-structured 'surplus production' models have investigated stock dynamics as driven by temperature regimes and climate oscillations (Rose, 2004, Holsman et al., 2012). Matrix projection models can incorporate more process detail, integrating reproduction and estimating recruitment from growth, maturation and cannibalism processes, as applied for Atlantic cod (Frøysa et al., 2002, Andrews et al., 2006) and Atlantic croaker (Diamond et al., 2013).

**Community:** Food web interactions are not explicitly incorporated in single-species assessment models (see 'multi-species population dynamic models'), but are indirectly considered through model fitting to stock observations. Stock models could take into account changes in community level processes via adjusting stock growth or an additional mortality parameter.

**Spatial consideration:** Movement of stocks has been integrated through grid cells connected by advection and diffusion e.g. for albacore (*Thunnus alalunga*, Scombridae; Fournier et al., 1998) and for Atlantic cod (Andrews et al., 2006). By modelling the dynamics of metapopulations with distinct sub-stocks, differences in population parameters and more detailed spatial processes such as migration, spatially disaggregated spawning, and larval diffusion can be incorporated (Goethel et al., 2011).

## Multi-species population dynamic models

Multi-species population dynamic models originate from the extension of single-species stock assessment models (Pope, 1979, Gislason, 1999, Lewy and Vinther, 2004). These models use diet data to couple several species via their feeding interactions, whereby the mortality rate of a stock is determined from its consumption by other species (Pope, 1991, Magnússon, 1995, Rose and Sable, 2009). Selection of the included species can be based on abundance, relevance from an economic or management perspective, or because of key interactions with the target species (Rindorf et al., 2013, Plaganyi et al., 2014b). Models include up to six species and often aim to evaluate interdependent fluctuations of fish stocks in response to environmental changes (e.g. Bogstad et al., 1997, Livingston, 2000).

**Organism:** Due to an underlying structure equivalent to single-species population dynamic models, multi-species models have essentially the same capacities and limitations for integrating organism-level processes. The explicit consideration of species interactions may allow a more realistic parameterization e.g. of natural mortality and growth (Hollowed, 2000).

**Population:** Restrictions apply as for single species stock models. However, multi-species models can include impacts of predation by other species on early life stages, as demonstrated e.g. for Atlantic cod and interacting species (Lewy and Vinther, 2004, Lindstrøm et al., 2009, Speirs et al., 2010). This would in principle allow for integration of food-web mediated environmental effects on recruitment success.

**Community**: Multi-species models incorporate predation and competition processes among the included species, with a moderate number of species assumed to be sufficient to describe regional food web dynamics (Rindorf et al., 2013). The predation process is formulated as a statistical 'functional response' between predator consumption and prey abundance (Holling type functions; Holling, 1959), where prey suitability is usually based on data from stomach content analysis (Magnússon, 1995). Environmental influence on the predation process has been incorporated by dynamically modelling stomach content and the impact of temperature on evacuation rates to represent

metabolic activity, in a study with Atlantic menhaden (*Brevoortia tyrannus*, Clupeidae) and its predators (Garrison et al., 2010).

**Spatial consideration:** Multi-species models can divide stock representations into several regional areas to include connecting processes such as seasonal migration patterns and larval dispersal, as realized for the Barents Sea (Tjelmeland and Bogstad, 1998, Lindstrøm et al., 2009).

## Trophodynamic & mass-balance models

Trophodynamic or mass-balance models (also termed whole system or aggregate system models) build on the analysis of mass or energy flows in ecological networks (Polovina, 1984, Ulanowicz, 1985). Exchange of biomass as wet weight or energy equivalents is modelled among functional groups or 'compartments' (usually species or ecologically similar groups of species) in marine food webs. Available software packages include *Econetwrk* (Ulanowicz, 2004), which focuses on network analysis, *Ecotroph* (Gascuel and Pauly, 2009), which analyses biomass flow through trophic levels, and the multifunctional and widely utilised *Ecopath with Ecosim* package (EwE; Christensen and Walters, 2004).

**Organism**: Effects of temperature, acidification and hypoxia on physiological performance of organisms have been incorporated in Ecosim by forcing functional groups or by adjusting their aggregate production, consumption or mortality values (e.g. Ainsworth et al., 2011, Cornwall and Eddy, 2015). The spatial EwE extension *Ecospace* (Walters et al., 1999) permits specifying habitat quality based on various environmental factors, which then determines foraging capacity (Christensen et al., 2014a), and can divide life stages into smaller packages to approach 'individual-based' functionality (Walters et al., 2010).

**Population:** The ‚multi-stanza' feature in EwE facilitates the representation of life stages to describe recruitment (Christensen and Walters, 2004, Walters et al., 2010), but reproduction is not explicitly represented. As the underlying parameters are on functional group level, the analysis of plasticity and adaptation of populations is limited (Christensen and Walters, 2004).

**Community:** Energy flow over trophic levels can inform about general ecosystem characteristics and functioning (e.g. Link et al., 2008, Gascuel et al., 2011). The differentiation of represented compartments (species or functional groups) can be adjusted to optimize between food web resolution and data availability and reliability (Prato et al., 2014), informed by general ecological knowledge and sensitivity analyses (Link, 2010, Lassalle et al., 2014).

Predation is represented by a functional response depending on predator and prey biomasses (Christensen and Walters, 2004). In principle, vulnerability settings for each compartment provide an aggregate measure to integrate e.g. risk-sensitive foraging or predation behaviour (Ahrens et al., 2012). Via forcing functions, consumption and vulnerability parameters, or zooplankton groups and primary production can be adjusted to represent impacts of climate change on feeding interactions or food availability (e.g. Shannon et al., 2004, Field et al., 2006, Araújo and Bundy, 2012).

**Spatial consideration:** The *Ecospace* module of EwE can represent spatial-temporal distribution of biomass, including probability functions of movement (Walters et al., 2010). Habitat suitability, seasonal migrations and larval dispersal have been integrated e.g. for areas in the Mediterranean (Libralato and Solidoro, 2009, Fouzai et al., 2012). Two recently added features enable dynamic spatial-temporal environmental data input (Steenbeek et al., 2013a) and more

detailed integration of variable habitat suitability factors (Christensen et al., 2014a).

## Species Distribution Models (SDMs)

Species Distribution Models (SDMs, also termed niche-based models, climate envelope models, or predictive habitat distribution models) link observed geographical species distributions to environmental parameters, classically through regression analysis (Guisan and Zimmermann, 2000, Elith and Leathwick, 2009). Besides a wealth of applications in the terrestrial realm, SDMs are increasingly used for projecting future distributions of marine fish stocks from regional projections of environmental factors (Cheung et al., 2008, Cheung et al., 2009, Lenoir et al., 2010). Dedicated SDM software platforms enable the application and comparison of different algorithms (e.g. Thuiller et al., 2009).

**Organism:** Organism level effects of environmental drivers can readily be incorporated into SDMs as performance curves dependent on physical factors. To integrate multiple environmental variables, different suitability factors can be multiplied (e.g. Kaschner et al., 2006). Aerobic scope has been used to integrate effects of temperature, oxygen, pH and food energy into the population growth function for marine fish stocks (Cheung et al., 2011).

SDMs which aim to increase detail by including functional relationships between physical variables and species performance, e.g. thermodynamic energy transfer principles, have been termed mechanistic SDMs or mechanistic niche models (Dormann, 2007, Kearney and Porter, 2009). Under changing environmental conditions, increased care has to be taken in the choice of environmental variables, species-specific data, and applied algorithms to supply ecologically meaningful and robust projections (Araújo and Guisan, 2006, Heikkinen et al., 2006, Austin, 2007).

**Population:** A logistic population growth model incorporates temperature effects on population carrying capacity to model the global distribution of fish species (Cheung et al., 2008). As environmental correlations are usually based on the occurrence of adults, it is difficult to include ontogenetic shifts in environmental tolerance or preference in different life stages (Robinson et al., 2011), but more detailed, stage-structured representations of population processes have been achieved in terrestrial models (e.g. Fordham et al., 2013).

**Community:** The incorporation of community shifts under climate change represents a challenge for SDMs, as species interactions are only implicitly included in the empirically based response function. Depending on the scale of projections, changes in species interactions may significantly influence the performance of SDMs (Araújo and Rozenfeld, 2014). Mechanistic SDMs aim to exclude biotic interactions from the response function and consider them separately (Guisan and Thuiller, 2005) to take into account differential preferences of prey and predator for environmental factors (Robinson et al., 2011),

An SDM for the North Atlantic has been extended with community size-spectra to represent competition between species as a division of available food energy (Fernandes et al., 2013). For the Mediterranean Sea, a niche model has been coupled to a trophic network model to derive temperature-induced shifts in food webs (Albouy et al., 2014).

**Spatial consideration:** SDMs can provide high spatial resolution, but correlations are often limited by the availability of species occurrence data. Larval dispersal, adult migrations, habitat availability and regional primary production changes have been included into projections of worldwide distribution changes of marine fish (Cheung et al., 2009, Cheung et al., 2010). Seasonal migrations and other spatio-temporal processes governed by factors other than current

environmental parameters (e.g. genetic) are more difficult to include (Robinson et al., 2011), but have been included e.g. in a habitat prediction model for southern Bluefin tuna (*Thunnus maccoyii*, Scombridae) under changing oceanographic conditions (Hartog et al., 2011).

## Trait-based & size-spectrum models

Trait-based models constitute a relatively new approach, focusing on the description of individual characteristics and processes (traits), e.g. size, morphology or weight, which are defined to govern performance of organisms in a specific environment (Chown, 2012). These traits can be used together with metabolic scaling and predation rules to describe life histories and interactions (Brown et al., 2004, Andersen and Beyer, 2006) and to construct community size-spectrum models for fish (Benoit and Rochet, 2004, Pope et al., 2006). A multi-species size spectrum modelling package, is available with an example parameterized for the North Sea (Scott et al., 2014).

**Organism:** Trait-based models can incorporate considerable detail on organism-level processes such as growth, foraging, reproduction and basal metabolism, modelling organismal trade-offs via energy allocation (Jørgensen and Fiksen, 2006). For Atlantic cod larvae, optimal vertical migration and life history strategies have been derived from responses to the environmental variables food, temperature and light (Kristiansen et al., 2009, Fiksen and Jorgensen, 2011). Recently, individual energy and oxygen budgets have been used to derive changes in growth, mortality and reproduction rates under ocean warming and project impacts on population characteristics and optimal behavioural and life history strategies (Holt and Jørgensen, 2014, Holt and Jørgensen, 2015).

**Population**: Trait-based models have high potential to describe processes shaping population dynamics, such as reproduction and recruitment, by basing them on individual life histories. These can be resolved for size, growth and maturation (e.g. Hartvig et al., 2011, Holt and Jørgensen, 2014). However, trait-based models usually include an empirical stock-recruitment relationship to determine recruitment and represent closure of life cycles (Jacobsen et al., 2014). Adaptation of fish populations to size-selective drivers (e.g. fisheries exploitation) can be quantified based on changes of individual growth, reproduction and mortality processes (Andersen and Brander, 2009). Eco-genetic or adaptive dynamics models investigate plasticity and evolutionary rates within populations (Dunlop et al., 2009).

**Community**: In size spectrum models, community interactions and food webs are usually constructed bottom-up, based on the realized interactions as governed by the integrated traits, e.g. 'size at maturation' (e.g. Jennings and Brander, 2010, Hartvig et al., 2011). Simple size spectrum models can investigate community shifts under temperature effects on growth (Pope et al., 2009). Behavioural, energy allocation and foraging processes can connect individual processes in more detail (Andersen and Beyer, 2013), and functional separation in interactions can be integrated by using coupled size spectra, as exemplified for pelagic predators and benthic detritivores (Blanchard et al., 2009).

**Spatial consideration:** Size spectrum models can use spatial input from oceanographic and biogeochemical models to incorporate e.g. temperature effects on feeding and mortality (Blanchard et al., 2012) and to simulate movement (Watson et al., 2014).

## Individual-based models (IBMs)

Individual-based models (also termed agent-based models) are a bottom-up modelling approach, based on the simulation of individuals as separate entities. Their status is determined by internal state variables and changed by interactions with other individuals and the environment (e.g. foraging and predation),

generating population and higher-level system properties (Huston et al., 1988, Judson, 1994, Grimm, 1999). Various IBM programming packages focus on agent-environment interactions (Railsback et al., 2006, Arunachalam et al., 2008). More specialized software tools model environmental impacts on the dispersal of planktonic fish larvae (Lett et al., 2008, e.g. Huebert and Peck, 2014).

**Organism:** IBMs for larval fish describe growth, development and mortality as dependent on environmental parameters (Hinckley et al., 1996, Hermann et al., 2001, Gallego et al., 2007). Behavioural rules can link environmental factors (e.g. light, temperature, oxygen) to metabolism, energy use, and predation risk (Fiksen et al., 2007). Energy allocation principles can be used to describe connections and trade-offs among internal processes in IBMs (Sibly et al., 2013). More detailed environmental and experimental data is needed for further advances in larval IBMs (Lett et al., 2010, Peck and Hufnagl, 2012).

**Population**: IBMs allow for consideration of inter-individual variation in fish responses and the resulting environmental selection (Van Winkle et al., 1993) and can thus be used to investigate population adaptation to changing environmental drivers (e.g. Anderson et al., 2013). While representing both detailed early life stages and closed life cycles of populations produces considerable model complexity and computational demands, IBMs can be used to integrate variation into more aggregate models (Rose et al., 2001).

IBMs have been used to investigate early life stage dynamics, connectivity between stocks and environmental impact on recruitment potential of marine fish (Mullon et al., 2002, Miller, 2007, Hinrichsen et al., 2011). Demographic changes under climate change have been investigated for Atlantic salmon (*Salmo salar*, Salmonidae; Piou and Prévost, 2012).

**Community**: IBMs are successful in detailing the predation of larval fish on zooplankton based on spatial co-occurrence, the environment and behavioural processes, e.g. investigating match-mismatch dynamics (Kristiansen et al., 2011). Thus, growth and mortality can be described as emergent properties of individual interactions, providing the predation functional response with ecological detail (Huse and Fiksen, 2010).

Changes in lower trophic levels can be integrated as 'prey fields' (aggregated prey densities in a defined space) into larval models (Hermann et al., 2001, Daewel et al., 2008). Size-governed predation processes have been resolved in a multi-species IBM for pelagic fish communities (OSMOSE; Shin and Cury, 2001, 2004; for this and other multi-species IBMs, see section on 'coupled and end-to-end models').

**Spatial consideration:** Biophysical IBMs can model impacts on larval dispersal, based on output from three-dimensional oceanographic models, as realized e.g. for larvae of walleye pollock (Theragra chalcogramma, Gadidae; Hermann et al., 2001), Southern African anchovy (Engraulis capensis, Engraulidae; Mullon et al., 2002), Atlantic cod (Vikebo et al., 2007, Heath et al., 2008) and Atlantic herring (Vikebo et al., 2010). A mechanism-based, not species-explicit model has been used to investigate climate change impacts on adult fish and mammal migrations (Anderson et al., 2013).

## Bioenergetic models

Bioenergetic models simulate the internal energy budget of organisms by using rules for energy allocation. Metabolic processes such as feeding, respiration, growth and reproduction are linked to external parameters, e.g. food and temperature, to determine the organism's performance (Brown et al., 2004, Hartman and Kitchell, 2008). Classic bioenergetic models have been applied to a variety of fish species (Hansen et al., 1993). In Dynamic Energy Budget (DEB) models (Kooijman, 2000, van der Meer, 2006),

individuals are characterized by the state of different energy compartments such as structure, reserves and reproduction (Lika and Kooijman, 2011, Nisbet et al., 2012). Energy budget representations have also been integrated into other model types (see 'Organism' subsections of 'Trait-based & size-spectrum models', 'Individual-based models' and 'Coupled and end-to-end models' sections).

**Organism:** Energy budgets have been used to compare temperature-dependent organism performances and sensitivities among different fish species (van der Veer et al., 2001, Sousa et al., 2008, Freitas et al., 2010). While this provides the base for a mechanistic understanding of diverging organism performances under climate change, further research will be required to incorporate life history and behavioural detail, activity costs, and seasonal and ontogenetic variations in energy allocation (Beauchamp et al., 2007, Sibly et al., 2013) as well as the treatment of oxygen supply for metabolism (Pauly, 2010).

**Population:** Bioenergetic models have been scaled up to population level to determine parameters such as biomass, consumption and growth of fish stocks, based on changes in metabolic and feeding rates (Beauchamp et al., 2007, Perez-Rodriguez and Saborido-Rey, 2012). To include more detail on population level processes, DEBs have been integrated into matrix population models (e.g. Klanjscek et al., 2006) and energy allocation patterns adapted to the life-history of the organism (Nisbet et al., 2012).

Spawning dynamics resulting from temperature and food effects on energy budgets have been investigated for European anchovy (Pecquerie et al., 2009) and Atlantic Bluefin tuna (*Thunnus thynnus*, Scombridae; Chapman et al., 2011).The integration of energy budget models into IBMs allows more detailed upscaling of individual-level processes to population level (Hölker and Breckling, 2005, Sibly et al., 2013),

and for DEB-IBM integration a software framework is available (Martin et al., 2011, Martin et al., 2013).

**Community:** Predator-prey interactions in bioenergetic IBMs determine energy transfer between individuals, and can therefore include changes in prey composition or energy content (Martin et al., 2011). Behavioural aspects of foraging are more difficult to include (Beauchamp et al., 2007). Dynamic Energy Budgets have been used to derive thermal ranges of fishes in the North Sea (Freitas et al., 2010), and can be integrated into size-spectra models to investigate community dynamics (Maury and Poggiale, 2013).

**Spatial consideration:** A DEB model has been coupled to biogeochemical and lower trophic level models to investigate the spatial distribution of North Atlantic flatfish species (Teal et al., 2012). To investigate detailed spatial processes, bioenergetic models have been integrated into size-structured models (e.g. Maury, 2010; see 'Coupled and end-to-end models'), and can be incorporated into individual-based and species distribution models, but data availability and the complexity of organismal plasticity and ontogenetic changes may limit their up-scaling to the ecosystem level (Freitas et al., 2010).

## Coupled and end-to-end models

As each modelling approach has characteristic strengths and simplifications, coupling of different ecological models increases the potential for explicit process integration (cf. Reuter et al., 2010). A range of coupled models is available, and some consist of a complex array of submodels, connecting ecosystem levels and scientific disciplines (Moloney et al., 2011) to achieve an 'end-to-end' representation of climate change impacts, i.e. from physical oceanographic changes via nutrient dynamics and planktonic lower trophic levels, to fish stocks, other higher trophic levels and links to socio-economic dynamics (Travers et al., 2007,

Fulton, 2010, Rose et al., 2010). To link across these levels, models can profit from detailing processes, e.g. related to energy allocation, feeding and behaviour (Nisbet et al., 2000, Brown et al., 2004, Kearney et al., 2010, Persson et al., 2014). Note that recent extensions and advances in end-to-end modelling are not all covered in the peer-reviewed literature, and it is beyond the scope of this paper to provide more than a short overview of these models.

Three conceptually related models integrate oceanographic models, simplified nutrient and lower trophic level dynamics and bioenergetic models for certain pelagic fish species. APECOSM (Apex Predators ECOSystem Model; Maury, 2010) and SEAPODYM (Spatial Ecosystem And POpulations DYnamics Model; Lehodey et al., 2008) represent size-structured predation and movement in different tuna and related species, and have been used to investigate worldwide distribution shifts under climate change (Lefort et al., 2015, Lehodey et al., 2015). NEMURO.FISH (North Pacific Ecosystem Model for Understanding Regional Oceanography - For Including Saury and Herring) has been developed to investigate climate regime effects on Pacific herring (*Clupea pallasii pallasii*, Clupeidae; Megrey et al., 2007, Rose et al., 2008) and Pacific saury (Ito et al., 2004).

OSMOSE (Object-oriented Simulator of Marine ecOSystems Exploitation) is an IBM representing multiple size classes and size-based interactions (Shin and Cury, 2004). Recent OSMOSE versions have been used to investigate combined effects of climate change and fisheries by coupling energy-dependent growth of early life stages to simple models of lower trophic levels (Travers-Trolet et al., 2014). Based on environmental driving from the NEMURO model, a recent multi-species IBM development for the California Current simulates dynamics of Californian anchovy (*Engraulis mordax*, Engraulidae) and Pacific sardine (*Sardinops sagax caerulea*, Clupeidae), linking to an agent-based fisheries model (Fiechter et al., 2015, Rose et al., 2015).

Atlantis is a modular end-to-end model aimed at the evaluation of management strategies (Fulton et al., 2004, Fulton et al., 2011). Fish stocks are age-structured, with average size and condition tracked, and different types of functional responses can be used to describe trophic interactions (Fulton, 2010, Kaplan et al., 2012). Effects of warming, acidification and salinity changes have been integrated on represented processes such as growth, reproduction, and movement (Griffith et al., 2012, Fulton and Gorton).

In principle, these comprehensive models possess a high potential for consideration of multiple drivers for different species and at various levels of description. However, the complexity of model structures causes a high work effort for estimating and analysing empirical parameters, the consideration of scaling issues and the coupling of modules may be limited by calibration issues and the propagation of uncertainties (Fulton et al., 2003, Rose, 2012, Voinov and Shugart, 2013, Evans et al., 2015).

As an alternative to the use of increasingly complex model structures, purposefully simplified end-to-end models can quantify climate change impacts and provide management advice. These have been termed 'models of intermediate complexity' (Hannah et al., 2010) and can be related to or based on multi-species population dynamic models (Plaganyi et al., 2014b). Recent examples have linked nutrient dynamics to fisheries management for the North Sea and Baltic Sea (e.g. Heath, 2012, Radtke et al., 2013). Also, Ecospace models (see 'Trophodynamic & mass-balance models') can be driven with spatial-temporal input from oceanographic models (Steenbeek et al., 2013) to investigate e.g.

interactions of hypoxia and fishing (de Mutsert et al., 2015). Lastly, in system dynamics modeling, which aims at a simplified representation of social-ecological systems (Costanza and Ruth, 1998), some examples for fish stocks in the Northwest Atlantic have incorporated habitat conditions and management elements (Ruth and Lindholm, 1996, Gottlieb, 1998).

## From models to understanding and projections: Model choices and challenges for addressing questions of environmental change

Our compilation illustrates that modelling approaches have strongly diverging capacities to incorporate physiological and ecological processes under scenarios of climate change (Table 1). Most approaches concentrate on specific levels of organization and neglect others, although in many cases recently added features have improved capacities. The best choice of model thus depends on the primary question of interest, the relevant processes and the available data.

To exemplify relevant considerations when choosing or constructing a model, we consider five basic research questions asked by the scientific community. Questions 1 to 3 relate to advancing the fundamental understanding of biological responses of fishes to environmental changes (individual tolerance, population adaptation and ecological regime shifts). Questions 4 and 5 focus on projections of the future states of fish stocks (spatial distribution and links to socio-economic developments). We evaluate the capabilities of the presented model classes to treat these questions and suggest how these models may profit from integrating more experimental results and empirical data.

### Question 1: What is the individual response and tolerance of fish to multiple changing environmental drivers?

Laboratory experiments contribute primarily to this research question by investigating organism level processes that determine the effect of multiple and combined environmental drivers (increasing temperature, acidification, hypoxia) on individual performance. Research on the cumulative effects of stressors, life stage-specific sensitivities and trade-offs between physiological processes can build the foundation for explaining the capacity for and the limitations of individual plasticity.

Bioenergetic models can represent individual processes in greatest detail. To project effects on higher-level processes, energy budgets have been successfully integrated in individual-based, trait-based, size-spectrum, species distribution and end-to-end models. Individual-based and trait-based models on the individual level are most directly parameterized with results from experiments, can consider inter-individual heterogeneity, and facilitate a mechanistic understanding of the effects of different constraining or enhancing factors on the performance of individuals. Due to detail richness and specificity of model formulations, these models are often not easily transferable to other species. When applied to multiple species and in a spatial ecosystem context, computational demands can be high.

Species distribution models and Ecospace offer comparatively straightforward integration of physiological performance curves into response functions to single and multiplicative drivers. Due to the implicit assumptions regarding upscaling to higher levels of organization, robustness and uncertainty of the applied response functions can be assessed e.g. by using results on sub-lethal physiological responses, which can be provided by laboratory experiments (Woodin et al., 2013). In single or

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Table *1*: Overview on model classes for marine fish and their potential for representation of processes on various levels of biological organisation. Processes marked by an asterisk* are incorporated on an aggregate level or non-dynamically (state-independent). Processes in brackets ( ) can only be incorporated in a subset of models of the class or by using additional software features (see text for details). Coupled and end-to-end models can in principle incorporate all processes, and their specific capabilities depend on the model classes they are based on.

| model class | incorporated processes on level of description | | | | main use in climate change context |
|---|---|---|---|---|---|
| | **Organism** | **Population** | **Community** | **Ecosystem** | |
| 1. Single-species population dynamic | growth*<br>mortality*<br>(development*) | recruitment<br>(reproduction) | -- | migration*<br>dispersal* | stock management (no relevant stock interactions) |
| 2. Multi-species population dynamic | growth*<br>mortality*<br>(development*)<br>(foraging*) | recruitment<br>(reproduction) | predation*<br>competition* | migration*<br>dispersal* | stock management (interactions important), community dynamics |
| 3. tropho-dynamic & mass-balance | growth*<br>mortality*<br>(development*)<br>foraging* | (recruitment)<br>(reproduction*) | predation*<br>competition*<br>mutualism* | migration<br>(dispersal)<br>habitat<br><br>*(all in Ecospace)* | community and ecosystem resilience, ecosystem-based management |
| 4. species distribution (SDM) | growth*<br>mortality*<br>foraging*<br>limitations* | recruitment* | (predation*)<br>(competition)<br><br>*(with size spectrum or trophic models)* | migration*<br>(dispersal*)<br>habitat | distribution range shifts, local fish catch potential |

| 5. trait-based & size-spectrum | (plasticity) behaviour growth mortality development foraging (metabolism) energy allocation limitations | recruitment* reproduction adaptation | predation* competition* | habitat* | trade-offs in organismal processes, adaptation and community structure |
|---|---|---|---|---|---|
| 6. individual-based (IBM) | (plasticity) behaviour growth mortality development foraging (metabolism) energy allocation limitations | recruitment* reproduction adaptation | predation competition mutualism* | migration dispersal habitat | larval dispersal, behavioural and population adaptation |
| 7. bio-energetic | growth mortality (development) foraging metabolism energy allocation (limitations) | (recruitment) (reproduction)  *(in IBMs)* | (predation) (competition)  *(in size-spectrum models)* | (migration) (habitat)  *(in IBMs or SDMs)* | trade-offs in organismal processes, linking of individual effects to community dynamics |
| 8. coupled & end-to-end | [based on multi-species, size-spectrum, IBM, or bioenergetic] | recruitment* reproduction adaptation | predation competition mutualism* | migration dispersal habitat | ecosystem-based management, distribution and regime shifts |

multi-species population dynamic and mass-balance models, experimental results can be used to adjust growth, consumption and mortality of (age/size) stages or cohorts. As this kind of aggregated integration of results does not account for individual variation in responses, robustness of these representations should be assessed over the range of responses in regard to interactions with other drivers and with processes on higher levels (such as predation and selection). This can be conducted e.g. by sensitivity analyses informed by physiological and ecological results, and by including multiple aggregate parameterisations to reflect some level of variation.

Advancements are necessary in the individual-level integration of multiple drivers, which can be informed by results from specifically designed experiments. Models will benefit from the integration of data on energy allocation and well-established physiological performance measures, such as aerobic scope, to define habitat suitability under driver combinations (Teal et al., 2015). These can be used to integrate experimental results directly into hydrodynamic and biogeochemical models (e.g. Cucco et al., 2012). Integrative concepts such as scope for activity (Claireaux and Lefrancois, 2007) and oxygen- and capacity-limited thermal tolerance (OCLTT; Pörtner, 2010) can be used to reduce complexity of representation and serve as a matrix for integration of multiple driver effects in order to generalize organismal performance and stress sensitivity (Pörtner, 2012).

Models should also increasingly incorporate dynamic responses, to account for acclimation and evolution. Laboratory measurements of organismal acclimation and phenotypic response variation within populations, as well as knowledge of the functional mechanisms underlying organismal responses, can help to estimate organismal adaptive capacity (see also question 2).

## Question 2: How will climate change affect the population dynamics of fish stocks and what is their capacity for adaptation?

To assess fish stock responses to climate change, integration of the population level processes recruitment and reproduction, and of the adaptation capacity of populations is needed. Recent meta-analyses and statistical models show that for many stocks, recruitment may be strongly dependent on the environment (Ottersen et al., 2013, Szuwalski et al., 2014, Pecuchet et al., 2015). Data from different early life stages, the reproduction process and from trans-generational experiments can contribute to create a more mechanistic description of the environmental dependence of population dynamics and to determine the capacity of stocks to undergo adaptation.

Stage-structured single or multi-species population dynamic models can be used to investigate the impacts of environmental change on population size and age structure. The use of generalized stock-recruitment relationships or environmental carrying capacities entails strong assumptions, such as homogeneity of a cohort and of environmental conditions (Metcalfe et al., 2012), and the recruitment function can put considerable uncertainty on projections from these models (e.g. Cabral et al., 2013, Howell et al., 2013). An improved integration of environmental effects could be based on the explicit representation of different early life stages (e.g. eggs, non-feeding and feeding larval stages), as realized in some matrix projection models. To incorporate spatially resolved habitat drivers of population processes, increasing focus should also be put on the development of mechanistic SDMs that incorporate stage-structured population dynamic models, as they have been realized for terrestrial systems (e.g. Keith et al., 2008, Fordham et al., 2013, Lurgi et al., 2014).

For a more detailed investigation of population structure across life stages and to investigate population adaptation based on acclimation and evolution, trait-based models and IBMs making use of heritable, physiology-based traits will play an important role. While next-generation population genomic methods will help to link genotype and phenotype (Hemmer-Hansen et al., 2014), laboratory studies on organismal tolerance ranges and individual adaptation can help to identify plasticity and within-population variation in phenotypic traits. Investigation of adaption will advance further once gene expression can be more precisely linked to physiological functions and environmental performance, making use of transcriptomic data and transgenerational experiments (Munday, 2014, Logan and Buckley, 2015). This approach would improve mechanistic understanding of acclimation and evolution (Whitehead, 2012, Alvarez et al., 2015) and could be informed by data gained from 'common garden' experiments with fish from different environmental conditions (e.g. Oomen and Hutchings, 2015) and from laboratory experiments (Munday et al., 2013b). Investigations for early life stages can be complemented by large-scale manipulations conducted e.g. in mesocosms (cf. Munday et al., 2013b, Stewart et al., 2013).

Thus, using genetic data and physiological knowledge, exploratory studies about detailed scaling of key processes from organism to population level may succeed when using trait-based models or IBMs that integrate key traits for physiological mechanisms (cf. Reuter et al., 2008). Behavioural traits mediate a wide range of organism-organism and organism-habitat interactions in fish (Munday et al., 2013b, Nagelkerken and Munday, 2015), and thus may become valuable in modelling phenotypic variation and adaptive potential in the context of communities and ecosystems (e.g. Giske et al., 2014). Most trait-based models, however, currently include only a low number of different traits. In IBMs, 'super-individuals' can represent a variable number of real individuals (Scheffer et al., 1995). This concept can be used to scale up organismal properties to higher-level dynamics, maintaining self-organised population properties (Reuter et al., 2005) while limiting computational demands. It has been extended into grid-based approaches, for community size-spectra in OSMOSE (Shin and Cury 2004) and for sardine and anchovy in the Californian Current in NEMURO.FISH (Fiechter et al., 2015, Rose et al., 2015).

## Question 3: Will marine food webs be resilient to climate change, or can regime shifts occur?

Regime shifts in marine ecosystems can have strong impacts on fish stocks and are difficult to predict (Frank et al., 2005, deYoung et al., 2008), but community responses to environmental drivers may be crucially determined by characteristics of food web interactions (Mangel and Levin, 2005, Hunsicker et al., 2011, Plaganyi et al., 2014a). Food web topology can be elucidated by analysing biochemical tracers such as stable isotopes and fatty acids (Young et al., 2015). Experimental results on feeding parameters, predation behaviour (e.g. prey switching) and size-dependence can help to detail the interactions and mechanistically describe changes in community-level processes under multiple climate change drivers (Stefansson, 2003, Persson et al., 2014, Nagelkerken and Munday, 2015).

In trophic mass-balance models such as EwE and in end-to-end models, different types of trophic control (bottom-up, top-down, or a mixture) can be integrated through vulnerability parameters (e.g. Ahrens et al., 2012), and network analysis indicators can be used to characterize the resulting food web dynamics and identify key functional groups (Heymans et al., 2014). Yet, aiming for a complete

representation of food webs causes a comparatively high need for field data, especially when analysing dynamics over time.

Multi-species stock models are less data demanding and have been used to compare conditions for regime shifts and thresholds among different systems (e.g. Petrie et al., 2009, Plaganyi et al., 2014a). Their simplified structure should be informed by ecological knowledge, such as identification of major trophic pathways and selection of key components (Gilman et al., 2010, Shin et al., 2010), network analysis of more complex models (e.g. Metcalf et al., 2008, Livi et al., 2011), or 'ecotypes' that represent mixed ecological characteristics (Engelhard et al., 2010).

Size spectrum models can investigate food web dynamics based on size structure (e.g. Blanchard et al., 2010), but representation of other properties that affect interactions is currently limited. To quantitatively characterize the vulnerability of interaction processes to predator/prey or environmental changes, IBMs and trait-based models can use behavioural rules and inter-individual variability to produce emergent feeding interactions, instead of relying on a statistical functional response (Fiksen et al., 2007, Mariani and Visser, 2010). Understanding of marine ecosystem resilience under climate change could be advanced by trait-based models with a focus on ecologically functional traits (Bremner, 2008, Mouillot et al., 2013) and by multi-species IBMs that use empirical results on food uptake, energy allocation and predation behaviour to set parameter values (see 'Coupled and end-to-end models'). Predation and energy allocation are key processes to link fish models to lower trophic level changes (Cury et al., 2008), and a realistic two-way coupling is necessary to describe ecosystem dynamics, especially in top-down controlled systems (Travers et al., 2009, Daewel et al., 2014).

To provide data for parameterization of these models, more systematic experimental investigation of environmental influences on foraging and assimilation processes is necessary. The effects of different functional response formulations on model behaviour should be tested more routinely, and whenever feasible, relevant behavioural and habitat aspects be represented dynamically. Options include using integrative suitability or vulnerability settings (e.g. Kempf et al., 2010, Ahrens et al., 2012) and multi-dimensional functional responses (e.g. Büssenschütt and Pahl-Wostl, 2000, Dawes and Souza, 2013). These community models can then inform spatially resolved models to explore how local food web dynamics respond to changes in spatial distribution of species abundance.

## Question 4: How will the spatial distribution and range of stocks change?

This research question combines data on different levels of biological organization (cf. Fig. 1), as individual responses to local environmental factors (e.g. temperatures, oxygen levels), adaptation and changes in recruitment, food web interactions, and dispersal and habitat availability all influence the distribution of fish stocks (Roessig et al., 2005, Rose, 2005, Hollowed et al., 2013).

Spatial variability is well represented in Species Distribution Models. SDMs have advanced considerably in incorporating details on organism-level processes, population dynamics, competition and spatial-temporal processes, and can be based upon experimental results on different levels, as exemplified for acidification and warming effects on a marine invertebrate species (Queirós et al., 2015). Underlying assumptions of steady-state relations in SDMs should always be critically examined (e.g. Guisan and Thuiller, 2005, Knudby et al., 2010). Additional empirical results should be used to consider potentially critical effects in processes not explicitly represented, e.g.

recruitment, population adaptation, migration and dispersal, and changes in species interactions (cf. Brander et al., 2013).

Further development of SDMs in the marine realm should also be inspired from extensive experience with related models in terrestrial applications, especially with respect to dynamic (state-dependent) integration of population and community level processes (Robinson et al., 2011, Fordham et al., 2013) and to physiological limits and adaptive evolution (Catullo et al., 2015), although not all concepts may be transferable to marine systems. The trophodynamic model Ecospace offers functionality similar to SDMs in its 'habitat capacity' response functions, with dynamic integration of spatial processes into the food web context and the option to link to spatial-temporal input (Steenbeek et al., 2013, Christensen et al., 2014a). As end-to-end models usually resolve spatial and community processes, they possess high capacity for more integrative projections of distribution changes (e.g. Rose et al., 2015).

IBMs have been used to describe larval growth and dispersal in high spatial resolution and integrate sampling data (Lett et al., 2010, Hidalgo et al., 2012). Energy allocation principles may be able to trace recruitment success and the evolution of spawning migrations, but need to be informed by more experimental research and coupled between all life stages (cf. Fiksen et al., 2007, Peck and Hufnagl, 2012). Integrative physiological concepts may be used to generalize changes in relative performance of interacting or competing species (Pörtner and Farrell, 2008, Pörtner, 2012). Additionally, more observational, telemetric and demographic data will be needed to improve incorporation of spatial structure and processes (Runge et al., 2010, Metcalfe et al., 2012).

The incorporation of active migration of later life stages and of spatially resolved and potentially patchy distribution of spawning habitat, and in general the integration of lower and higher level processes represent significant challenges in achieving reliable projections about spatial shifts of fish stocks under climate change. In the near future, these challenges will probably be handled using coupling of different modelling approaches and end-to-end models along with case-dependent strategies for reduction of complexity. In the meantime, adequate use of simpler representations will remain valuable for management and policy advice.

## Question 5: What will be the socio-economic impacts and the implications for management of changing marine ecosystems?

Climate-mediated changes in marine ecosystems and fish stocks can have different socio-economic effects in different regions and affect a range of ecosystem services used by human societies (Cooley et al., 2009, Sumaila et al., 2011, Pörtner et al., 2014). Climate change effects can interact with human uses, e.g. by fishing, and can be modified by other short-term anthropogenic drivers such as eutrophication or pollution and amplified or even overridden by general socio-economic developments (Perry et al., 2010). Therefore, an analysis of ecosystem impacts of climate change in exploited marine systems, and especially the assessment of their socio-economic consequences, need to link biological and socio-economic research approaches, building on an identification of involved ecological processes and incorporating interactions with human societies (Le Quesne and Pinnegar, 2012, Hilmi et al., 2013).

Different model classes have been used to assess management or adaptation strategies to climate change effects for fish stocks and marine ecosystems, but societal dynamics have until recently received little attention (Barange et al., 2010). Socio-economic dynamics and

background scenarios related to fish markets have been integrated into extended population dynamic or 'bioeconomic' models (e.g. Merino et al., 2010, Norman-Lopez et al., 2013), species distribution models (Cheung et al., 2010, Jones et al., 2014), mass-balance models (Christensen et al., 2015), size spectrum and trait-based models (Woodworth-Jefcoats et al., 2013, Barange et al., 2014, Zimmermann and Jorgensen, 2015) and the end-to-end model Atlantis (Fulton et al., 2011, Griffith et al., 2012).

Societies have a range of adaptation options to climate change-induced changes, e.g. increase of fishing effort, economic diversification, or change of fishing grounds (Perry et al., 2011). Incorporating adaptive societal responses and their social and cultural conditions, based on observations and models, can enable improved governance and increase resilience of marine social-ecological systems (Folke, 2006, Miller et al., 2010, Schlüter et al., 2012). Societal dynamics can be implemented e.g. using network models (Janssen et al., 2006) or arising from individual actor behaviour in 'agent-based' models (Gilbert and Terna, 2000).

The advancement of integrated models is promising to achieve more accurate projections of the future states of social-ecological systems (Österblom et al., 2013, Griffith and Fulton, 2014), and models for informing fisheries management under changing environmental drivers have been developed (e.g. Cooley et al., 2015). Advances are necessary in identifying specific societal adaptive capacities in response to regionally expected impacts of climate change, based on reliable quantitative data. Beyond fisheries, quantification of impacts of other marine industries and on the provision of other marine ecosystem services is needed, such as tourism, carbon sequestration, or coastal protection (cf. Beaumont et al., 2007, Liquete et al., 2013). Conceptual challenges relate to scale differences and the identification of processes which determine adaptive capacities of natural and social systems (Perry and Ommer, 2003, Griffith and Fulton, 2014).

## Conclusions

The integration of physiological and ecological processes has great potential to advance ecological models for fish. Representation of mechanisms mediating climate effects can be increased by 1) identifying key processes for the question of interest across levels of organization, 2) using and coupling models which represent the key processes, and 3) incorporating experimental results from a range of conditions and across life history stages and generations.

For investigating the direct effects of multiple environmental drivers on fish, models should be adapted sensibly to integrate experimental data and investigate organism-level trade-offs and sensitivities, e.g. by making use of energy allocation principles. The investigation of changes in population dynamics can benefit from increased model detail in the representation of effects on early life stages and reproduction. Understanding of acclimation and evolution under climate change can be advanced by assessment of functional traits and specifically designed experiments. Marine community shifts under multiple drivers can be better anticipated by analysis of food web structure and quantification of functional responses. Research on stock distribution shifts and socio-economic impacts of changes in marine living resources should increasingly incorporate results on the co-determination of spatial movement and dispersal by behavioural fish responses and trade-offs in energy allocation and community interactions, and improve the integration of societal dynamics. Coupling of models to address these higher-order questions can be informed e.g. by data on food energy content and transfer, and by behavioural observations of fish and people.

Improvements in projection capacities by integrating these processes, and potential trade-offs e.g. with regard to parameter uncertainties, will have to be verified on a case-to-case basis. Scaling issues will have to be addressed to reduce the complexity of models while maintaining sensitivities across scales: a focus should be put on the identification of mechanisms and techniques that span levels of description and can couple specialized models without levelling out heterogeneity and variability at lower levels that may be decisive for higher level dynamics. Examples include the super-individual concept in individual-based models and physiological concepts for estimating organism sensitivity towards multiple drivers.

To this end, planning of experiments and structuring of models should be coordinated more closely in the research process and based on an improved dialogue between modellers and experimentalists. This will warrant meaningful physiological experiments and an improved integration of both empirical results and mechanistic understanding of effects into existing and future models.

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