FISH and FISHERIES

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

Journal:	*Fish and Fisheries*
Manuscript ID	FaF-15-May-OA-080.R2
Wiley - Manuscript type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Koenigstein, Stefan; University of Bremen, Sustainabilty Research Center (artec); Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Integrative Ecophysiology Section Mark, Felix; Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Integrative Ecophysiology Section Gößling-Reisemann, Stefan; University of Bremen, Sustainability Research Center (artec); University of Bremen, Department of Resilient Energy Systems Reuter, Hauke; Leibniz Center for Tropical Marine Ecology, Dept. of Theoretical Ecology and Modelling; University of Bremen, Faculty of Biology and Chemistry Pörtner, Hans-Otto; Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Integrative Ecophysiology Section; University of Bremen, Faculty of Biology and Chemistry
Key terms:	ecosystem modeling , environmental drivers, climate change, ocean acidification, fish ecophysiology, process understanding
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.

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

Alternative 1: Modelling climate change impacts on marine fish populations: Process-based integration of environmental drivers

Alternative 2: Integration of process-based understanding into ecological models for marine fish

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

Tel. +49-421-64894, E-mail: koenigstein@uni-bremen.de

running title: Modelling environmental drivers for fish

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

Table of content:

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.

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; 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 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 stocks. 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.

Acknowledgements

SK and FCM are currently funded through the research program BIOACID (Biological Impacts of Ocean Acidification, phase II), by the German Federal Ministry of Education and Research (BMBF, FKZ 03F0655B and 03F0655J). SK gratefully acknowledges additional support through travel grants to relevant international conferences, from ICES (International Council for the Exploration of the Sea), SCOR (Scientific Committee on Ocean Research), the University of Bremen Central Research Development Fund, the German Academic Exchange Service (DAAD) and LabexMer. HOP acknowledges funding through BIOACID and the PACES program of AWI. The authors would like to thank Marta Coll (IRD/IFREMER/CSIC), Øyvind Fiksen (University of Bergen), Bjarte Bogstad (IMR Bergen) and three anonymous reviewers for valuable comments and suggestions that helped to improve the final manuscript.

References

Ahrens, R.N.M., Walters, C.J., Christensen, V. (2012) Foraging arena theory. *Fish and Fisheries* **13,** 41-59.

Ainsworth, C.H., Samhouri, J.F., Busch, D.S., Cheung, W.W.L., Dunne, J., Okey, T.A. (2011) Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES Journal of Marine Science* **68,** 1217-1229.

Albouy, C., Velez, L., Coll, M., *et al.* (2014) From projected species distribution to food-web structure under climate change. *Global Change Biology* **20,** 730-741.

Alvarez, M., Schrey, A.W., Richards, C.L. (2015) Ten years of transcriptomics in wild populations: what have we learned about their ecology and evolution? *Molecular ecology* **24,** 710-725.

Andersen, K.H., Beyer, J.E. (2006) Asymptotic size determines species abundance in the marine size spectrum. *American Naturalist* **168,** 54-61.

Andersen, K.H., Beyer, J.E. (2013) Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish and Fisheries* **16,** 1-22.

Andersen, K.H., Brander, K. (2009) Expected rate of fisheries-induced evolution is slow. *Proceedings of the National Academy of Sciences of the United States of America* **106,** 11657-11660.

Anderson, J.J., Gurarie, E., Bracis, C., Burke, B.J., Laidre, K.L. (2013) Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecological Modelling* **264,** 83-97.

Andrews, J.M., Gurney, W.S.C., Heath, M.R., *et al.* (2006) Modelling the spatial demography of Atlantic cod (Gadus morhua) on the European continental shelf. *Canadian Journal of Fisheries and Aquatic Sciences* **63,** 1027-1048.

Araújo, J.N., Bundy, A. (2012) Effects of environmental change, fisheries and trophodynamics on the ecosystem of the western Scotian Shelf, Canada. *Marine Ecology Progress Series* **464,** 51-67.

Araújo, M.B., Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography* **33,** 1677-1688.

Araújo, M.B., Rozenfeld, A. (2014) The geographic scaling of biotic interactions. *Ecography* **37,** 406-415.

Arunachalam, S., Zalila-Wenkstern, R., Steiner, R. (2008) Environment mediated Multi Agent Simulation Tools-A Comparison. *Sasow 2008: Second Ieee International Conference on Self-Adaptive and Self-Organizing Systems Workshops, Proceedings***,** 43-48.

Asch, R.G. (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences* **112,** E4065-E4074.

Austin, M. (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* **200,** 1-19.

Barange, M., Cheung, W.W.L., Merino, G., Perry, R.I. (2010) Modelling the potential impacts of climate change and human activities on the sustainability of marine resources. *Current Opinion in Environmental Sustainability* **2,** 326-333.

Barange, M., Merino, G., Blanchard, J.L., *et al.* (2014) Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Clim. Change* **4,** 211-216.

Baskett, M.L. (2012) Integrating mechanistic organism-environment interactions into the basic theory of community and evolutionary ecology. *Journal of Experimental Biology* **215,** 948-961.

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D., Marshall, C.T. (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology* **20,** 1023-1031.

Baumann, H., Talmage, S.C., Gobler, C.J. (2012) Reduced early life growth and survival in a fish in direct response to increased carbon dioxide. *Nature Climate Change* **2,** 38-41.

Beauchamp, D.A., Cross, A.D., Armstrong, J.L., *et al.* (2007) Bioenergetic Responses by Pacific Salmon to Climate and Ecosystem Variation. *North Pacific Anadromous Fish Commission Bulletin* **4,** 257–269.

Beaugrand, G., Brander, K.M., Alistair Lindley, J., Souissi, S., Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature* **426,** 661-664.

Beaugrand, G., Kirby, R.R. (2010) Climate, plankton and cod. *Global Change Biology* **16,** 1268-1280.

Beaumont, N.J., Austen, M.C., Atkins, J.P., *et al.* (2007) Identification, definition and quantification of goods and services provided by marine biodiversity: implications for the ecosystem approach. *Marine pollution bulletin* **54,** 253-265.

Benoit, E., Rochet, M.J. (2004) A continuous model of biomass size spectra governed by predation and the effects of fishing on them. *Journal of Theoretical Biology* **226,** 9-21.

Beverton, R., Holt, S.J. (1957) On the Dynamics of Exploited Fish Populations. *Fisheries Investigation Series 2.*

Blanchard, J.L., Jennings, S., Holmes, R., *et al.* (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **367,** 2979-2989.

Blanchard, J.L., Jennings, S., Law, R., *et al.* (2009) How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology* **78,** 270-280.

Blanchard, J.L., Law, R., Castle, M.D., Jennings, S. (2010) Coupled energy pathways and the resilience of size-structured food webs. *Theoretical Ecology* **4,** 289-300.

Bogstad, B., Gjøsæter, H., Haug, T., Lindstrøm, U. (2015) A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Frontiers in Ecology and Evolution* **3,** 29.

Bogstad, B., Hauge, K.H., Ulltang, Ø. (1997) MULTSPEC–a multi-species model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fishery Science* **22**, *317-341.*

Brander, K. (2010) Impacts of climate change on fisheries. *Journal of Marine Systems* **79,** 389-402.

Brander, K., Mohn, R. (2004) Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (Gadus morhua). *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 1558-1564.

Brander, K., Neuheimer, A., Andersen, K.H., Hartvig, M. (2013) Overconfidence in model projections. *ICES Journal of Marine Science* **70,** 1069-1074.

Brander, K.M. (1995) The Effect of Temperature on Growth of Atlantic Cod (Gadus-Morhua L). *ICES Journal of Marine Science* **52,** 1-10.

Brauner, C.J., Baker, D.W. (2009) Patterns of acid-base regulation during exposure to hypercarbia in fishes. In: *Cardio-Respiratory Control in Vertebrates.* (Eds. M.L. Glass, S.C. Wood), Berlin, pp. 43-63.

Bremner, J. (2008) Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology* **366,** 37-47.

Briffa, M., de la Haye, K., Munday, P.L. (2012) High CO□ and marine animal behaviour: potential mechanisms and ecological consequences. *Marine pollution bulletin* **64,** 1519-1528.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B. (2004) Toward a Metabolic Theory of Ecology. *Ecology* **85,** 1771-1789.

Büssenschütt, M., Pahl-Wostl, C. (2000) A discrete, allometric approach to the modeling of ecosystem dynamics. *Ecological Modelling* **126,** 33-48.

Cabral, R.B., Aliño, P.M., Lim, M.T. (2013) A coupled stock-recruitment-age-structured model of the North Sea cod under the influence of depensation. *Ecological Modelling* **253,** 1-8.

Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation*, 2nd ed., Sinauer Associates, Sunderland, MA.

Catullo, R.A., Ferrier, S., Hoffmann, A.A. (2015) Extending spatial modelling of climate change responses beyond the realized niche: estimating, and accommodating, physiological limits and adaptive evolution. *Global Ecology and Biogeography* **24,** 1192-1202.

Chapman, E.W., Jorgensen, C., Lutcavage, M.E. (2011) Atlantic bluefin tuna (Thunnus thynnus): a state-dependent energy allocation model for growth, maturation, and reproductive investment. *Canadian Journal of Fisheries and Aquatic Sciences* **68,** 1934-1951.

Cheung, W., Lam, V., Sarmiento, J.L. (2009) Projecting global marine biodiversity impacts under climate change scenarios - Cheung. *Fish and Fisheries* **10**.

Cheung, W.W.L., Dunne, J., Sarmiento, J.L., Pauly, D. (2011) Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* **68,** 1008-1018.

Cheung, W.W.L., Lam, V.W.Y., Pauly, D. (2008) Dynamic Bioclimate Envelope Model to Predict Climate-Induced Changes in Distribution of Marine Fishes and Invertebrates. Fisheries Centre Research Reports, 5-50.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., *et al.* (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology* **16,** 24-35.

Chown, S.L. (2012) Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **367,** 1615-1627.

Chown, S.L., Hoffmann, A.A., Kristensen, T.N., Angilletta, M.J., Stenseth, N.C., Pertoldi, C. (2010) Adapting to climate change: a perspective from evolutionary physiology. *Climate Research* **43,** 3-15.

Christensen, V., Coll, M., Buszowski, J., *et al.* (2015) The global ocean is an ecosystem: simulating marine life and fisheries. *Global Ecology and Biogeography* **24,** 507-517.

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., Walters, C.J. (2014a) Representing Variable Habitat Quality in a Spatial Food Web Model. *Ecosystems.*

Christensen, V., de la Puente, S., Sueiro, J.C., Steenbeek, J., Majluf, P. (2014b) Valuing seafood: The Peruvian fisheries sector. *Marine Policy* **44,** 302-311.

Christensen, V., Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172,** 109-139.

Chung, W.S., Marshall, N.J., Watson, S.A., Munday, P.L., Nilsson, G.E. (2014) Ocean acidification slows retinal function in a damselfish through interference with GABA(A) receptors. *Journal of Experimental Biology* **217,** 323-326.

Ciannelli, L., Fauchald, P., Chan, K.S., Agostini, V.N., Dingsor, G.E. (2008) Spatial fisheries ecology: Recent progress and future prospects. *Journal of Marine Systems* **71,** 223-236.

Ciannelli, L., Fisher, J.A.D., Skern-Mauritzen, M., *et al.* (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. *Marine Ecology Progress Series* **480,** 227-243.

Claireaux, G., Lefrancois, C. (2007) Linking environmental variability and fish performance: integration through the concept of scope for activity. *Philosophical Transactions of the Royal Society B-Biological Sciences* **362,** 2031-2041.

Clark, R.A., Fox, C.J., Viner, D., Livermore, M. (2003) North Sea cod and climate change - modelling the effects of temperature on population dynamics. *Global Change Biology* **9,** 1669-1680.

Clarke, A., Johnston, N.M. (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* **68,** 893-905.

Cochrane, K.L., Perry, R.I., Daw, T.M., Soto, D., Barange, M., De Silva, S.S. (2009) *Climate change implications for fisheries and aquaculture: overview of current scientific knowledge.* FAO fisheries and aquaculture technical paper Vol. 530, Food and Agriculture Organization of the United Nations, Rome.

Cooley, S.R., Kite-Powell, H.L., Doney, S.C., Act, A. (2009) Ocean acidification's potential to alter global marine ecosystem services. **22,** 172-181.

Cooley, S.R., Rheuban, J.E., Hart, D.R., *et al.* (2015) An Integrated Assessment Model for Helping the United States Sea Scallop (Placopecten magellanicus) Fishery Plan Ahead for Ocean Acidification and Warming. *PloS one* **10**.

Cornwall, C.E., Eddy, T.D. (2015) Effects of near-future ocean acidification, fishing, and marine protection on a temperate coastal ecosystem. *Conservation Biology* **29,** 207-215.

Costanza, R., Ruth, M. (1998) Using dynamic modeling to scope environmental problems and build consensus. *Environmental Management* **22,** 183-195.

Couturier, C.S., Stecyk, J.A.W., Rummer, J.L., Munday, P.L., Nilsson, G.E. (2013) Species-specific effects of near-future CO2 on the respiratory performance of two tropical prey fish and their predator. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **166,** 482-489.

Crozier, L.G., Hutchings, J.A. (2014) Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* **7,** 68-87.

Cucco, A., Sinerchia, M., Lefrançois, C., *et al.* (2012) A metabolic scope based model of fish response to environmental changes. *Ecological Modelling* **237,** 132-141.

Cury, P.M., Shin, Y.J., Planque, B., *et al.* (2008) Ecosystem oceanography for global change in fisheries. *Trends in Ecology & Evolution* **23,** 338-346.

Daewel, U., Hjollo, S.S., Huret, M., *et al.* (2014) Predation control of zooplankton dynamics: a review of observations and models. *ICES Journal of Marine Science* **71,** 254-271.

Daewel, U., Peck, M.A., Schrum, C., St John, M.A. (2008) How best to include the effects of climate-driven forcing on prey fields in larval fish individual-based models. *Journal of Plankton Research* **30,** 1-5.

Dalpadado, P., Ingvaldsen, R.B., Stige, L.C., *et al.* (2012) Climate effects on Barents Sea ecosystem dynamics. *ICES Journal of Marine Science* **69,** 1303-1316.

Dawes, J.H.P., Souza, M.O. (2013) A derivation of Holling's type I, II and III functional responses in predator–prey systems. *Journal of Theoretical Biology* **327,** 11-22.

de Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J. (2015) Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecological Modelling (2015).*

Deigweiher, K., Koschnick, N., Portner, H.O., Lucassen, M. (2008) Acclimation of ion regulatory capacities in gills of marine fish under environmental hypercapnia. *American Journal of Physiology- Regulatory, Integrative and Comparative Physiology* **295,** R1660-R1670.

Denman, K., Christian, J.R., Steiner, N., Portner, H.O., Nojiri, Y. (2011) Potential impacts of future ocean acidification on marine ecosystems and fisheries: current knowledge and recommendations for future research. *ICES Journal of Marine Science* **68,** 1019-1029.

Denny, M., Helmuth, B. (2009) Confronting the physiological bottleneck: A challenge from ecomechanics. *Integrative and comparative biology* **49,** 197-201.

Deriso, R.B., Quinn, I., T J, Neal, P.R. (1985) Catch-Age Analysis with Auxiliary Information. *Canadian Journal of Fisheries and Aquatic Sciences* **42,** 815-824.

Devine, B.M., Munday, P.L., Jones, G.P. (2012) Homing ability of adult cardinalfish is affected by elevated carbon dioxide. *Oecologia* **168,** 269-276.

deYoung, B., Barange, M., Beaugrand, G., *et al.* (2008) Regime shifts in marine ecosystems: detection, prediction and management. *Trends in Ecology & Evolution* **23,** 402-409.

Diamond, S.L., Murphy, C.A., Rose, K.A. (2013) Simulating the effects of global climate change on Atlantic croaker population dynamics in the mid-Atlantic Region. *Ecological Modelling* **264,** 98-114.

Donelson, J.M., Munday, P.L. (2012) Thermal sensitivity does not determine acclimation capacity for a tropical reef fish. *Journal of Animal Ecology* **81,** 1126-1131.

Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., *et al.* (2012) Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science* **4,** 11-37.

Dormann, C.F. (2007) Promising the future? Global change projections of species distributions. *Basic and Applied Ecology* **8,** 387-397.

Dunlop, E.S., Heino, M., Dieckmann, U. (2009) Eco-genetic modeling of contemporary life-history evolution. *Ecological Applications* **19,** 1815-1834.

Dupont, S., Pörtner, H.O. (2013) A snapshot of ocean acidification research. *Marine Biology* **160,** 1765-1771.

Ekau, W., Auel, H., Pörtner, H.O., Gilbert, D. (2010) Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* **7,** 1669-1699.

Elith, J., Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* **40,** 677-697.

Engelhard, G.H., Ellis, J.R., Payne, M.R., ter Hofstede, R., Pinnegar, J.K. (2010) Ecotypes as a concept for exploring responses to climate change in fish assemblages. *ICES Journal of Marine Science***,** 1-12.

Engelhard, G.H., Peck, M.A., Rindorf, A., *et al.* (2014) Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science* **71,** 90-104.

Enzor, L.A., Zippay, M.L., Place, S.P. (2013) High latitude fish in a high CO2 world: Synergistic effects of elevated temperature and carbon dioxide on the metabolic rates of Antarctic notothenioids. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **164,** 154-161.

Evans, K., Brown, J.N., Sen Gupta, A., *et al.* (2015) When 1+1 can be > 2: Uncertainties compound when simulating climate, fisheries and marine ecosystems. *Deep-Sea Research Part II-Topical Studies in Oceanography* **113,** 312-322.

Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C. (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* **65,** 414-432.

Fernandes, J.A., Cheung, W.W.L., Jennings, S., *et al.* (2013) Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. *Global Change Biology* **19,** 2596-2607.

Ferrari, M.C., Manassa, R.P., Dixson, D.L., *et al.* (2012) Effects of ocean acidification on learning in coral reef fishes. *PloS one* **7**.

Ferrari, M.C.O., McCormick, M.I., Munday, P.L., *et al.* (2011) Putting prey and predator into the CO2 equation - qualitative and quantitative effects of ocean acidification on predator-prey interactions. *Ecology letters* **14,** 1143-1148.

Fiechter, J., Rose, K.A., Curchitser, E.N., Hedstrom, K.S. (2015) The role of environmental controls in determining sardine and anchovy population cycles in the California Current: Analysis of an end-to-end model. *Progress in Oceanography* **138,** 381-398.

Field, J.C., Francis, R.C., Aydin, K. (2006) Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography* **68,** 238-270.

Fiksen, O., Jørgensen, C. (2011) Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. *Marine Ecology Progress Series* **432,** 207-219.

Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., Huse, G. (2007) Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Marine Ecology Progress Series* **347,** 195-205.

Folke, C. (2006) Resilience: The emergence of a perspective for social–ecological systems analyses. *Global Environmental Change* **16,** 253-267.

Fordham, D.A., Akcakaya, H.R., Araujo, M.B., Keith, D.A., Brook, B.W. (2013) Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography* **36,** 956-964.

Fournier, D.A., Hampton, J., Sibert, J.R. (1998) MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, Thunnus alalunga. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 2105-2116.

Fournier, D.A., Sibert, J.R., Majkowski, J., Hampton, J. (1990) Multifan a Likelihood-Based Method for Estimating Growth-Parameters and Age Composition from Multiple Length Frequency Data Sets Illustrated Using Data for Southern Bluefin Tuna (Thunnus-Maccoyii). *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 301-317.

Fouzai, N., Coll, M., Palomera, I., Santojanni, A., Arneri, E., Christensen, V. (2012) Fishing management scenarios to rebuild exploited resources and ecosystems of the Northern-Central Adriatic (Mediterranean Sea). *Journal of Marine Systems* **102,** 39-51.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C. (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308,** 1621-1623.

Frank, K.T., Petrie, B., Shackell, N.L., Choi, J.S. (2006) Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology letters* **9,** 1096-1105.

Franke, A., Clemmesen, C. (2011) Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences Discussions* **8,** 7097-7126.

Freitas, V., Cardoso, J.F.M.F., Lika, K., *et al.* (2010) Temperature tolerance and energetics: a dynamic energy budget-based comparison of North Atlantic marine species. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365,** 3553-3565.

Frommel, A., Maneja, R., Lowe, D., *et al.* (2012) Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nature Climate Change* **2,** 42–46.

Frommel, A., Stiebens, V., Clemmesen, C., Havenhand, J. (2010) Effect of ocean acidification on marine fish sperm (Baltic cod: *Gadus morhua*). *Biogeosciences Discussions* **7,** 5859-5872.

Frøysa, K.G., Bogstad, B., Skagen, D.W. (2002) Fleksibest - an age-length structured fish stock assessment model. *Fisheries Research* **55,** 87-101.

Fulton, E.A. (2010) Approaches to end-to-end ecosystem models. *Journal of Marine Systems* **81,** 171-183.

Fulton, E.A., Gorton, R. (2014) Adaptive futures for SE Australian Fisheries & Aquaculture: Climate Adaptation Simulations. CSIRO, Australia.

Fulton, E.A., Link, J.S., Kaplan, I.C., *et al.* (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* **12,** 171-188.

Fulton, E.A., Parslow, J.S., Smith, A.D.M., Johnson, C.R. (2004) Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. *Ecological Modelling* **173,** 371-406.

Fulton, E.A., Smith, A.D.M., Johnson, C.R. (2003) Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series* **253,** 1-16.

Gallego, A., North, E.W., Petitgas, P. (2007) Introduction: status and future of modelling physical-biological interactions during the early life of fishes. *Marine Ecology Progress Series* **347,** 121-126.

Garrison, L.P., Link, J.S., Kilduff, D.P., *et al.* (2010) An expansion of the MSVPA approach for quantifying predator-prey interactions in exploited fish communities. *ICES Journal of Marine Science* **67,** 856-870.

Gascuel, D., Guenette, S., Pauly, D. (2011) The trophic-level-based ecosystem modelling approach: theoretical overview and practical uses. *ICES Journal of Marine Science* **68,** 1403-1416.

Gascuel, D., Pauly, D. (2009) EcoTroph: Modelling marine ecosystem functioning and impact of fishing. *Ecological Modelling* **220,** 2885-2898.

Gaylord, B., Kroeker, K.J., Sunday, J.M., *et al.* (2015) Ocean acidification through the lens of ecological theory. *Ecology* **96,** 3-15.

Gilbert, N., Terna, P. (2000) How to build and use agent-based models in social science. *Mind & Society* **1,** 57-72.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution* **25,** 325-331.

Giske, J., Eliassen, S., Fiksen, Ø., *et al.* (2014) The emotion system promotes diversity and evolvability. *Proceedings of the Royal Society B-Biological Sciences* **281**.

Gislason, H. (1999) Single and multispecies reference points for Baltic fish stocks. *ICES Journal of Marine Science* **56,** 571-583.

Goethel, D.R., Quinn, I., Terrance J, Cadrin, S.X. (2011) Incorporating Spatial Structure in Stock Assessment: Movement Modeling in Marine Fish Population Dynamics. *Reviews in Fisheries Science* **19,** 119-136.

Gottlieb, S.J. (1998) Nutrient removal by age-0 Atlantic menhaden (Brevoortia tyrranus) in Chesapeake Bay and implications for seasonal management of the fishery. *Ecological Modelling* **112,** 111-130.

Griffith, G.P., Fulton, E.A. (2014) New approaches to simulating the complex interaction effects of multiple human impacts on the marine environment. *ICES Journal of Marine Science* **71,** 764-774.

Griffith, G.P., Fulton, E.A., Gorton, R., Richardson, A.J. (2012) Predicting Interactions among Fishing, Ocean Warming, and Ocean Acidification in a Marine System with Whole-Ecosystem Models. *Conservation Biology* **26,** 1145-1152.

Grimm, V. (1999) Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* **115,** 129-148.

Guisan, A., Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology letters* **8,** 993-1009.

Guisan, A., Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135,** 147-186.

Hamilton, T.J., Holcombe, A., Tresguerres, M. (2014) CO2-induced ocean acidification increases anxiety in Rockfish via alteration of GABA(A) receptor functioning. *Proceedings of the Royal Society B-Biological Sciences* **281**.

Hannah, C., Vezina, A., John, M.S. (2010) The case for marine ecosystem models of intermediate complexity. *Progress in Oceanography* **84,** 121-128.

Hansen, M.J., Boisclair, D., Brandt, S.B., *et al.* (1993) Applications of Bioenergetics Models to Fish Ecology and Management: Where Do We Go from Here? *Transactions of the American Fisheries Society* **122,** 1019-1030.

Hare, J.A. (2014) The future of fisheries oceanography lies in the pursuit of multiple hypotheses. *ICES Journal of Marine Science* **71,** 2343-2356.

Hartman, K.J., Kitchell, J.F. (2008) Bioenergetics Modeling: Progress since the 1992 Symposium. *Transactions of the American Fisheries Society* **137,** 216-223.

Hartog, J.R., Hobday, A.J., Matear, R., Feng, M. (2011) Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery – implications for present and future spatial management. *Deep Sea Research Part II: Topical Studies in Oceanography* **58,** 746-752.

Hartvig, M., Andersen, K.H., Beyer, J.E. (2011) Food web framework for size-structured populations. *Journal of Theoretical Biology* **272,** 113-122.

Heath, M.R. (2012) Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model. *Progress in Oceanography* **102,** 42-66.

Heath, M.R., Kunzlik, P.A., Gallego, A., Holmes, S., Wright, P.J. (2008) A model of meta-population dynamics for North Sea and West of Scotland cod - The dynamic consequences of natal fidelity. *Fisheries Research* **93,** 92-116.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T. (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography* **30,** 751-777.

Heisler, N. (1984) Acid-Base Regulation in Fishes. *Fish Physiology* **10,** 315-401.

Hemmer-Hansen, J., Nielsen, E.E., Therkildsen, N.O., *et al.* (2013) A genomic island linked to ecotype divergence in Atlantic cod. *Molecular ecology* **22,** 2653-2667.

Hemmer-Hansen, J., Therkildsen, N.O., Pujolar, J.M. (2014) Population Genomics of Marine Fishes: Next-Generation Prospects and Challenges. *Biological Bulletin* **227,** 117-132.

Hermann, A.J., Hinckley, S., Megrey, B.A., Napp, J.M. (2001) Applied and theoretical considerations for constructing spatially explicit individual-based models of marine larval fish that include multiple trophic levels. *ICES Journal of Marine Science.*

Heymans, J.J., Coll, M., Libralato, S., Morissette, L., Christensen, V. (2014) Global Patterns in Ecological Indicators of Marine Food Webs: A Modelling Approach. *PloS one* **9**.

Hidalgo, M., Gusdal, Y., Dingsor, G.E., *et al.* (2012) A combination of hydrodynamical and statistical modelling reveals non-stationary climate effects on fish larvae distributions. *Proceedings of the Royal Society B-Biological Sciences* **279,** 275-283.

Hilborn, R. (2012) The Evolution of Quantitative Marine Fisheries Management 1985-2010. *Natural Resource Modeling* **25,** 122-144.

Hildebrandt, N., Niehoff, B., Sartoris, F.J. (2014) Long-term effects of elevated CO2 and temperature on the Arctic calanoid copepods Calanus glacialis and C. hyperboreus. *Marine pollution bulletin* **80,** 59-70.

Hilmi, N., Allemand, D., Dupont, S., *et al.* (2013) Towards improved socio-economic assessments of ocean acidification's impacts. *Marine Biology* **160,** 1773-1787.

Hinckley, S., Hermann, A.J., Megrey, B.A. (1996) Development of a spatially explicit, individual-based model of marine fish early life history. *Marine Ecology Progress Series* **139,** 47-68.

Hinrichsen, H.H., Dickey-Collas, M., Huret, M., Peck, M.A., Vikebo, F.B. (2011) Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science* **68,** 1478-1487.

Hölker, F., Breckling, B. (2005) A spatiotemporal individual-based fish model to investigate emergent properties at the organismal and the population level. *Ecological Modelling* **186,** 406-426.

Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist.*

Hollowed, A.B. (2000) Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES Journal of Marine Science* **57,** 707-719.

Hollowed, A.B., Barange, M., Beamish, R.J., *et al.* (2013) Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science* **70,** 1023-1037.

Hollowed, A.B., Bond, N.A., Wilderbuer, T.K., *et al.* (2009) A framework for modelling fish and shellfish responses to future climate change. *ICES Journal of Marine Science* **66,** 1584-1594.

Hollowed, A.B., Curchitser, E.N., Stock, C.A., Zhang, C.I. (2012) Trade-offs associated with different modeling approaches for assessment of fish and shellfish responses to climate change. *Climatic Change* **119,** 111-129.

Holsman, K.K., Essington, T., Miller, T.J., Koen-Alonso, M., Stockhausen, W.J. (2012) Comparative analysis of cod and herring production dynamics across 13 northern hemisphere marine ecosystems. *Marine Ecology Progress Series* **459,** 231-246.

Holt, R.E., Jørgensen, C. (2014) Climate warming causes life-history evolution in a model for Atlantic cod (Gadus morhua). *Conservation Physiology* **2,** 1-16.

Holt, R.E., Jørgensen, C. (2015) Climate change in fish: effects of respiratory constraints on optimal life history and behaviour. *Biology letters* **11**.

Howell, D., Filin, A.A., Bogstad, B., Stiansen, J.E. (2013) Unquantifiable uncertainty in projecting stock response to climate change: Example from North East Arctic cod. *Marine Biology Research* **9,** 920-931.

Huebert, K.B., Peck, M.A. (2014) A Day in the Life of Fish Larvae: Modeling Foraging and Growth Using Quirks. *PloS one* **9**.

Hunsicker, M.E., Ciannelli, L., Bailey, K.M., *et al.* (2011) Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts. *Ecology letters* **14,** 1288-1299.

Huse, G., Fiksen, Ø. (2010) Modelling encounter rates and distribution of mobile predators and prey. *Progress in Oceanography* **84,** 93-104.

Huston, M., DeAngelis, D., Post, W. (1988) New Computer Models Unify Ecological Theory. *BioScience* **38,** 682-691.

Inaba, K., Dreanno, C., Cosson, J. (2003) Control of flatfish sperm motility by CO2 and carbonic anhydrase. *Cell Motility and the Cytoskeleton* **55,** 174-187.

Ito, S., Kishi, M.J., Kurita, Y., *et al.* (2004) Initial design for a fish bioenergetics model of Pacific saury coupled to a lower trophic ecosystem model. *Fisheries Oceanography* **13,** 111-124.

Jacobsen, N.S., Gislason, H., Andersen, K.H. (2014) The consequences of balanced harvesting of fish communities. *Proceedings of the Royal Society B-Biological Sciences* **281**.

Janssen, M.A., Bodin, O., Anderies, J.M., *et al.* (2006) Toward a network perspective of the study of resilience in social-ecological systems. *Ecology and Society* **11**.

Jennings, S., Brander, K. (2010) Predicting the effects of climate change on marine communities and the consequences for fisheries. *Journal of Marine Systems* **79,** 418-426.

Jones, M.C., Dye, S.R., Pinnegar, J.K., Warren, R., Cheung, W.W. (2014) Using scenarios to project the changing profitability of fisheries under climate change. *Fish and Fisheries.*

Jørgensen, C., Enberg, K., Dunlop, E.S., *et al.* (2007) Managing evolving fish stocks. *Science.*

Jørgensen, C., Fiksen, Ø. (2006) State-dependent energy allocation in cod (Gadus morhua). *Canadian Journal of Fisheries and Aquatic Sciences* **63,** 186-199.

Jørgensen, C., Peck, M.A., Antognarelli, F., *et al.* (2012) Conservation physiology of marine fishes: advancing the predictive capacity of models. *Biology letters* **8,** 900-903.

Judson, O.P. (1994) The Rise of the Individual-Based Model in Ecology. *Trends in Ecology & Evolution* **9,** 9-14.

Jutfelt, F., Bresolin de Souza, K., Vuylsteke, A., Sturve, J. (2013) Behavioural Disturbances in a Temperate Fish Exposed to Sustained High-CO_2 Levels. *PloS one* **8**.

Jutfelt, F., Hedgarde, M. (2013) Atlantic cod actively avoid CO2 and predator odour, even after long-term CO2 exposure. *Frontiers in Zoology* **10**.

Kaplan, I.C., Horne, P.J., Levin, P.S. (2012) Screening California Current fishery management scenarios using the Atlantis end-to-end ecosystem model. *Progress in Oceanography* **102,** 5-18.

Kaschner, K., Watson, R., Trites, A.W., Pauly, D. (2006) Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series* **316,** 285-310.

Kearney, M., Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology letters* **12,** 334-350.

Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B. (2010) Modelling the ecological niche from functional traits. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365,** 3469-3483.

Keith, D.A., Akcakaya, H.R., Thuiller, W., *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology letters* **4,** 560-563.

Kempf, A., Dingsor, G.E., Huse, G., Vinther, M., Floeter, J., Temming, A. (2010) The importance of predator-prey overlap: predicting North Sea cod recovery with a multispecies assessment model. *ICES Journal of Marine Science* **67,** 1989-1997.

Keyl, F., Wolff, M. (2007) Environmental variability and fisheries: what can models do? *Reviews in Fish Biology and Fisheries* **18,** 273-299.

Kitagawa, T., Nakata, H., Kimura, S., Itoh, T., Tsuji, S., Nitta, A. (2000) Effect of ambient temperature on the vertical distribution and movement of Pacific bluefin tuna Thunnus thynnus orientalis. *Marine Ecology Progress Series* **206,** 251-260.

Kjesbu, O.S., Bogstad, B., Devine, J.A., *et al.* (2014) Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences of the United States of America* **111,** 3478-3483.

Klanjscek, T., Caswell, H., Neubert, M.G., Nisbet, R.M. (2006) Integrating dynamic energy budgets into matrix population models. *Ecological Modelling* **196,** 407-420.

Knudby, A., Brenning, A., LeDrew, E. (2010) New approaches to modelling fish–habitat relationships. *Ecological Modelling* **221,** 503-511.

Knutsen, H., Moland Olsen, E., Ciannelli, L., *et al.* (2007) Egg distribution, bottom topography and small-scale cod population structure in a coastal marine system. *Marine Ecology Progress Series* **333,** 249-255.

Kooijman, S.A.L.M. (2000) *Dynamic energy and mass budgets in biological systems*, 2nd edn Vol., Cambridge University Press, Cambridge, UK ; New York, NY, USA.

Köster, F.W., Hinrichsen, H.-H., St John, M.A., *et al.* (2001) Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. *Canadian Journal of Fisheries and Aquatic Sciences* **58,** 1534-1556.

Kristiansen, T., Drinkwater, K.F., Lough, R.G., Sundby, S. (2011) Recruitment Variability in North Atlantic Cod and Match-Mismatch Dynamics. *PloS one* **6,** e17456.

Kristiansen, T., Jorgensen, C., Lough, R.G., Vikebo, F., Fiksen, Ø. (2009) Modeling rule-based behavior: habitat selection and the growth-survival trade-off in larval cod. *Behavioral Ecology* **20,** 490-500.

Lassalle, G., Bourdaud, P., Saint-Béat, B., Rochette, S., Niquil, N. (2014) A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model. *Ecological Modelling* **285,** 13-21.

Law, R. (2000) Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* **57,** 659-668.

Le Quesne, W.J.F., Pinnegar, J.K. (2012) The potential impacts of ocean acidification: scaling from physiology to fisheries. *Fish and Fisheries* **13,** 333-344.

Leduc, A.O.H.C., Munday, P.L., Brown, G.E., Ferrari, M.C.O. (2013) Effects of acidification on olfactory-mediated behaviour in freshwater and marine ecosystems: a synthesis. *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**.

Lefort, S., Aumont, O., Bopp, L., Arsouze, T., Gehlen, M., Maury, O. (2015) Spatial and body-size dependent response of marine pelagic communities to projected global climate change. *Global Change Biology* **21,** 154-164.

Lehodey, P., Alheit, J., Barange, M., *et al.* (2006) Climate Variability, Fish, and Fisheries. *Journal of Climate* **19,** 5009-5030.

Lehodey, P., Senina, I., Murtugudde, R. (2008) A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations. *Progress in Oceanography* **78,** 304-318.

Lehodey, P., Senina, I., Nicol, S., Hampton, J. (2015) Modelling the impact of climate change on South Pacific albacore tuna. *Deep-Sea Research Part Ii-Topical Studies in Oceanography* **113,** 246-259.

Lenoir, S., Beaugrand, G., Lecuyer, É. (2010) Modelled spatial distribution of marine fish and projected modifications in the North Atlantic Ocean. *Global Change Biology* **17,** 115-129.

Lett, C., Ayata, S.-D., Huret, M., Irisson, J.-O. (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography* **87,** 106-113.

Lett, C., Verley, P., Mullon, C., *et al.* (2008) A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling and Software* **23,** 1210-1214.

Lewy, P., Vinther, M. (2004) A stochastic age-length-structured multispecies model applied to North Sea stocks. ICES CM, 33.

Libralato, S., Solidoro, C. (2009) Bridging biogeochemical and food web models for an End-to-End representation of marine ecosystem dynamics: The Venice lagoon case study. *Ecological Modelling* **220,** 2960-2971.

Lika, K., Kooijman, S.A.L.M. (2011) The comparative topology of energy allocation in budget models. *Journal of Sea Research* **66,** 381-391.

Lindegren, M., Checkley, D.M. (2013) Temperature dependence of Pacific sardine (Sardinops sagax) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Sciences* **70,** 245-252.

Lindstrøm, U., Smout, S., Howell, D., Bogstad, B. (2009) Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. *Deep-Sea Research Part II* **56,** 2068-2079.

Link, J., Overholtz, W., O'Reilly, J., *et al.* (2008) The Northeast US continental shelf Energy Modeling and Analysis exercise (EMAX): Ecological network model development and basic ecosystem metrics. *Journal of Marine Systems* **74,** 453-474.

Link, J.S. (2010) Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL. *Ecological Modelling* **221,** 1580-1591.

Link, J.S., Bogstad, B., Sparholt, H., Lilly, G.R. (2009) Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries* **10,** 58-87.

Liquete, C., Piroddi, C., Drakou, E.G., *et al.* (2013) Current Status and Future Prospects for the Assessment of Marine and Coastal Ecosystem Services: A Systematic Review. *PloS one* **8,** e67737.

Lischka, S., Riebesell, U. (2012) Synergistic effects of ocean acidification and warming on overwintering pteropods in the Arctic. *Global Change Biology* **18,** 3517-3528.

Livi, C.M., Jordán, F., Lecca, P., Okey, T.A. (2011) Identifying key species in ecosystems with stochastic sensitivity analysis. *Ecological Modelling* **222,** 2542-2551.

Livingston, P. (2000) A multispecies virtual population analysis of the eastern Bering Sea. *ICES Journal of Marine Science* **57,** 294-299.

Llopiz, J.K., Cowen, R.K., Hauff, M.J., *et al.* (2014) Early Life History and Fisheries Oceanography New Questions in a Changing World. *Oceanography* **27,** 26-41.

Logan, C.A., Buckley, B.A. (2015) Transcriptomic responses to environmental temperature in eurythermal and stenothermal fishes. *Journal of Experimental Biology* **218,** 1915-1924.

Lurgi, M., Brook, B.W., Saltré, F., Fordham, D.A. (2014) Modelling range dynamics under global change: which framework and why? *Methods in Ecology and Evolution.*

Magnússon, K. (1995) An overview of the multispecies VPA - theory and applications. *Reviews in Fish Biology and Fisheries* **5,** 195-212.

Mangel, M., Levin, P.S. (2005) Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **360,** 95-105.

Mariani, P., Visser, A.W. (2010) Optimization and emergence in marine ecosystem models. *Progress in Oceanography* **84,** 89-92.

Martin, B.T., Jager, T., Nisbet, R.M., Preuss, T.G., Grimm, V. (2013) Predicting Population Dynamics from the Properties of Individuals: A Cross-Level Test of Dynamic Energy Budget Theory. *The American Naturalist* **181,** 506-519.

Martin, B.T., Zimmer, E.I., Grimm, V., Jager, T. (2011) Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation. *Methods in Ecology and Evolution* **3,** 445-449.

Maury, O. (2010) An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. *Progress in Oceanography* **84,** 113-117.

Maury, O., Poggiale, J.-C. (2013) From individuals to populations to communities: A dynamic energy budget model of marine ecosystem size-spectrum including life history diversity. *Journal of Theoretical Biology* **324,** 52-71.

Megrey, B.a., Rose, K.a., Klumb, R.a., *et al.* (2007) A bioenergetics-based population dynamics model of Pacific herring (Clupea harengus pallasi) coupled to a lower trophic level nutrient–phytoplankton–zooplankton model: Description, calibration, and sensitivity analysis. *Ecological Modelling* **202,** 144-164.

Melzner, F., Göbel, S., Langenbuch, M., Gutowska, M.A., Pörtner, H.-O., Lucassen, M. (2009a) Swimming performance in Atlantic Cod (Gadus morhua) following long-term (4–12 months) acclimation to elevated seawater PCO2. *Aquatic Toxicology* **92,** 30-37.

Melzner, F., Gutowska, M.A., Langenbuch, M., *et al.* (2009b) Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny? *Biogeosciences* **6,** 2313-2331.

Merino, G., Barange, M., Mullon, C. (2010) Climate variability and change scenarios for a marine commodity: Modelling small pelagic fish, fisheries and fishmeal in a globalized market. *Journal of Marine Systems* **81,** 196-205.

Metcalf, S., Dambacher, J., Hobday, A., Lyle, J. (2008) Importance of trophic information, simplification and aggregation error in ecosystem models. *Marine Ecology Progress Series* **360,** 25-36.

Metcalfe, J.D., Le Quesne, W.J.F., Cheung, W.W.L., Righton, D.a. (2012) Conservation physiology for applied management of marine fish: an overview with perspectives on the role and value of telemetry. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **367,** 1746-1756.

Michaelidis, B., Spring, A., Pörtner, H.O. (2007) Effects of long-term acclimation to environmental hypercapnia on extracellular acid-base status and metabolic capacity in Mediterranean fish *Sparus aurata. Marine Biology* **150,** 1417-1429.

Miller, G.M., Kroon, F.J., Metcalfe, S., Munday, P.L. (2015) Temperature is the evil twin: effects of increased temperature and ocean acidification on reproduction in a reef fish. *Ecological Applications* **25,** 603-620.

Miller, G.M., Watson, S.A., Donelson, J.M., McCormick, M.I., Munday, P.L. (2012) Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. *Nature Climate Change* **2,** 858-861.

Miller, K., Charles, A., Barange, M., *et al.* (2010) Climate change, uncertainty, and resilient fisheries: Institutional responses through integrative science. *Progress in Oceanography* **87,** 338-346.

Miller, T.J. (2007) Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. *Marine Ecology Progress Series* **347,** 127-138.

Mittelbach, G.G., Ballew, N.G., Kjelvik, M.K. (2014) Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* **71,** 927-944.

Moloney, C.L., St John, M.A., Denman, K.L., *et al.* (2011) Weaving marine food webs from end to end under global change. *Journal of Marine Systems* **84,** 106-116.

Monaco, C.J., Helmuth, B. (2011) Tipping points, thresholds and the keystone role of physiology in marine climate change research. Vol. 60. Elsevier, pp. 123-160.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* **28,** 167-177.

Mullon, C., Cury, P., Penven, P. (2002) Evolutionary individual-based model for the recruitment of anchovy (Engraulis capensis) in the southern Benguela. *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 910-922.

Munday, P.L. (2014) Transgenerational acclimation of fishes to climate change and ocean acidification. *F1000Prime Rep* **6,** 99.

Munday, P.L., Dixson, D.L., Mccormick, M.I., Meekan, M., Ferrari, M.C.O., Chivers, D.P. (2010) Replenishment of fish populations is threatened by ocean acidification. *Proceedings of the National Academy of Sciences of the United States of America* **107,** 12930-12934.

Munday, P.L., Pratchett, M.S., Dixson, D.L., *et al.* (2013a) Elevated CO2 affects the behavior of an ecologically and economically important coral reef fish. *Marine Biology* **160,** 2137-2144.

Munday, P.L., Warner, R.R., Monro, K., Pandolfi, J.M., Marshall, D.J. (2013b) Predicting evolutionary responses to climate change in the sea. *Ecology letters* **16,** 1488-1500.

Myers, R.A. (1998) When do environment-recruitment correlations work? *Reviews in Fish Biology and Fisheries* **8,** 285-305.

Nagelkerken, I., Munday, P.L. (2015) Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community□level responses. *Global Change Biology***,** n/a-n/a.

Nagelkerken, I., Russell, B.D., Gillanders, B.M., Connell, S.D. (2015) Ocean acidification alters fish populations indirectly through habitat modification. *Nature Clim. Change* **6,** 89-93.

Needle, C.L. (2001) Recruitment models: diagnosis and prognosis. *Reviews in Fish Biology and Fisheries* **11,** 95-111.

Nielsen, E.E., Hemmer-Hansen, J., Larsen, P.F., Bekkevold, D. (2009) Population genomics of marine fishes: identifying adaptive variation in space and time. *Molecular ecology* **18,** 3128-3150.

Nikinmaa, M. (2013) Climate change and ocean acidification Interactions with aquatic toxicology. *Aquatic Toxicology* **126,** 365-372.

Nilsson, G.E., Dixson, D.L., Domenici, P., *et al.* (2012) Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nature Climate Change* **2,** 201-204.

Nisbet, R.M., Jusup, M., Klanjscek, T., Pecquerie, L. (2012) Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *Journal of Experimental Biology* **215,** 1246-1246.

Nisbet, R.M., Muller, E.B., Lika, K., Kooijman, S.A.L.M. (2000) From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology* **69,** 913-926.

Norman-Lopez, A., Plaganyi, E., Skewes, T., *et al.* (2013) Linking physiological, population and socio-economic assessments of climate-change impacts on fisheries. *Fisheries Research* **148,** 18-26.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., *et al.* (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* **104,** 1266-1271.

Oomen, R.A., Hutchings, J.a. (2015) Variation in spawning time promotes genetic variability in population responses to environmental change in a marine fish. *Conservation Physiology* **3,** cov027.

Österblom, H., Merrie, A., Metian, M., *et al.* (2013) Modeling Social-Ecological Scenarios in Marine Systems. *BioScience* **63,** 735-744.

Ottersen, G., Hjermann, D.O., Stenseth, N.C. (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (Gadus morhua) stock. *Fisheries Oceanography* **15,** 230-243.

Ottersen, G., Stige, L.C., Durant, J.M., *et al.* (2013) Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Marine Ecology Progress Series* **480,** 205-225.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* **37,** 637-669.

Pauly, D. (2010) *Gasping fish and panting squids: oxygen, temperature and the growth of water-breathing animals.* Excellence in ecology, Vol. 22, International Ecology Institute, Oldendorf/Luhe, Germany.

Peck, M.A., Hufnagl, M. (2012) Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. *Journal of Marine Systems* **93,** 77-93.

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. *Journal of Sea Research* **62,** 93-105.

Pecuchet, L., Nielsen, J.R., Christensen, A. (2015) Impacts of the local environment on recruitment: a comparative study of North Sea and Baltic Sea fish stocks. *ICES Journal of Marine Science* **72,** 1323-1335.

Perez-Rodriguez, A., Saborido-Rey, F. (2012) Food consumption of Flemish Cap cod Gadus morhua and redfish Sebastes sp. using generic bioenergetic models. 1-15.

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.

Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmann, C., Planque, B. (2010) Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *Journal of Marine Systems* **79,** 427-435.

Perry, R.I., Ommer, R.E. (2003) Scale issues in marine ecosystems and human interactions. *Fisheries Oceanography* **12,** 513-522.

Perry, R.I., Ommer, R.E., Barange, M., Jentoft, S., Neis, B., Sumaila, U.R. (2011) Marine social-ecological responses to environmental change and the impacts of globalization. *Fish and Fisheries* **12,** 427-450.

Persson, L., Van Leeuwen, A., De Roos, A.M. (2014) The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics. *ICES Journal of Marine Science* **71,** 2268-2280.

Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., *et al.* (2012) Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography* **22,** 1-19.

Petrie, B., Frank, K.T., Shackell, N.L., Leggett, W.C. (2009) Structure and stability in exploited marine fish communities: quantifying critical transitions. *Fisheries Oceanography* **18,** 83-101.

Piou, C., Prévost, E. (2012) A demo-genetic individual-based model for Atlantic salmon populations: Model structure, parameterization and sensitivity. *Ecological Modelling* **231,** 37-52.

Pistevos, J.C.A., Nagelkerken, I., Rossi, T., Olmos, M., Connell, S.D. (2015) Ocean acidification and global warming impair shark hunting behaviour and growth. *Scientific Reports* **5**.

Plagányi, É.E. (2007) Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper, 1-124.

Plagányi, E.E., Bell, J.D., Bustamante, R.H., *et al.* (2011) Modelling climate-change effects on Australian and Pacific aquatic ecosystems: a review of analytical tools and management implications. *Marine and Freshwater Research* **62,** 1132.

Plagányi, E.E., Ellis, N., Blamey, L.K., *et al.* (2014a) Ecosystem modelling provides clues to understanding ecological tipping points. *Marine Ecology Progress Series* **512,** 99-113.

Plagányi, E.E., Punt, A.E., Hillary, R., *et al.* (2014b) Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish and Fisheries* **15,** 1-22.

Polovina, J.J. (1984) Model of a Coral-Reef Ecosystem. 1. The Ecopath Model and Its Application to French Frigate Shoals. *Coral Reefs* **3,** 1-11.

Pope, J.G. (1979) A modified cohort analysis in which constant natural mortality is replaced by estimates of predation levels.

Pope, J.G. (1991) The ICES multispecies assessment working group: evolution, insights, and future problems. *ICES Marine Science Symposium.*

Pope, J.G., Falk-Pedersen, J., Jennings, S., Rice, J.C., Gislason, H., Daan, N. (2009) Honey, I cooled the cods: Modelling the effect of temperature on the structure of Boreal/Arctic fish ecosystems. *Deep-Sea Research Part Ii-Topical Studies in Oceanography* **56,** 2097-2107.

Pope, J.G., Rice, J.C., Daan, N., Jennings, S., Gislason, H. (2006) Modelling an exploited marine fish community with 15 parameters – results from a simple size-based model. *ICES Journal of Marine Science* **63,** 1029-1044.

Pörtner, H.-O. (2010) Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *The Journal of experimental biology* **213,** 881-893.

Pörtner, H.O. (2012) Integrating climate-related stressor effects on marine organisms: unifying principles linking molecule to ecosystem-level changes. *Marine Ecology Progress Series* **470,** 273-290.

Pörtner, H.O., Farrell, A.P. (2008) Physiology and Climate Change. *Science* **322,** 690-692.

Pörtner, H.O., Karl, D.M., Boyd, P.W., *et al.* (2014) Ocean Systems. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (Eds. C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, L.L. White), Cambridge University Press, Cambridge, UK & New York, USA, pp. 411-484.

Pörtner, H.O., Mark, F.C., Bock, C. (2004) Oxygen limited thermal tolerance in fish?--Answers obtained by nuclear magnetic resonance techniques. *Respiratory Physiology & Neurobiology* **141,** 243-260.

Pörtner, H.O., Peck, M.A. (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of fish biology* **77,** 1745-1779.

Prato, G., Gascuel, D., Valls, A., Francour, P. (2014) Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints. *Marine Ecology Progress Series* **512,** 71-88.

Queirós, A.M., Fernandes, J.A., Faulwetter, S., *et al.* (2015) Scaling up experimental ocean acidification and warming research: from individuals to the ecosystem. *Global Change Biology* **21,** 130-143.

Radtke, H., Neumann, T., Fennel, W. (2013) A Eulerian nutrient to fish model of the Baltic Sea — A feasibility-study. *Journal of Marine Systems* **125,** 61-76.

Railsback, S.F., Lytinen, S.L., Jackson, S.K. (2006) Agent-based simulation platforms: Review and development recommendations. *Simulation-Transactions of the Society for Modeling and Simulation International* **82,** 609-623.

Reusch, T.B.H. (2014) Climate change in the oceans: evolutionary versus phenotypically plastic responses of marine animals and plants. *Evolutionary Applications* **7,** 104-122.

Reuter, H., Hölker, F., Middelhoff, U., Jopp, F., Eschenbach, C., Breckling, B. (2005) The concepts of emergent and collective properties in individual-based models - Summary and outlook of the Bornhoved case studies. *Ecological Modelling* **186,** 489-501.

Reuter, H., Jopp, F., Blanco-Moreno, J.M., Damgaard, C., Matsinos, Y., DeAngelis, D.L. (2010) Ecological hierarchies and self-organisation - Pattern analysis, modelling and process integration across scales. *Basic and Applied Ecology* **11,** 572-581.

Reuter, H., Jopp, F., Holker, F., Eschenbach, C., Middelhoff, U., Breckling, B. (2008) The ecological effect of phenotypic plasticity - Analyzing complex interaction networks (COIN) with agent-based models. *Ecological Informatics* **3,** 35-45.

Ricker, W.E. (1954) Stock and Recruitment. *Journal of the Fisheries Research Board of Canada* **11,** 559-623.

Riebesell, U., Gattuso, J.-p. (2015) Lessons learned from ocean acidification research. *Nature Climate Change* **5,** 12-14.

Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Mollmann, C., Pinnegar, J.K. (2009) Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* **66,** 1570-1583.

Rindorf, A., Lewy, P. (2006) Warm, windy winters drive cod north and homing of spawners keeps them there. *Journal of Applied Ecology* **43,** 445-453.

Rindorf, A., Schmidt, J., Bogstad, B., Reeves, S., Walther, Y. (2013) A Framework for Multispecies Assessment and Management. An ICES/NCM Background Document.

Robinson, L.M., Elith, J., Hobday, A.J., *et al.* (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* **20,** 789-802.

Roessig, J.M., Woodley, C.M., Cech, J., Joseph J, Hansen, L.J. (2005) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries* **14,** 251-275.

Rose, G.A. (2004) Reconciling overfishing and climate change with stock dynamics of Atlantic cod (Gadus morhua) over 500 years. *Can. J. Fish. Aquat. Sci.* **61,** 1553-1557.

Rose, G.A. (2005) On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science* **62,** 1360-1374.

Rose, K.A. (2012) End-to-end models for marine ecosystems: Are we on the precipice of a significant advance or just putting lipstick on a pig? *Scientia Marina* **76,** 195-201.

Rose, K.A., Allen, J.I., Artioli, Y., *et al.* (2010) End-To-End Models for the Analysis of Marine Ecosystems: Challenges, Issues, and Next Steps. *Marine and Coastal Fisheries* **2,** 115-130.

Rose, K.A., Cowan, J., James H, Winemiller, K.O., Myers, R.A., Hilborn, R. (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* **2,** 293-327.

Rose, K.A., Fiechter, J., Curchitser, E.N., *et al.* (2015) Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Progress in Oceanography* **138,** 348-380.

Rose, K.A., Megrey, B.A., Hay, D., Werner, F., Schweigert, J. (2008) Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. *Transactions of the American Fisheries Society* **137,** 278-297.

Rose, K.A., Sable, S.E. (2009) Multispecies modeling of fish populations. In: *Computers in fisheries research.* Springer, pp. 373-397.

Rossoll, D., Bermudez, R., Hauss, H., *et al.* (2012) Ocean Acidification-Induced Food Quality Deterioration Constrains Trophic Transfer. *PloS one* **7**.

Rothschild, B.J., Osborn, T.R., Dickey, T.D., Farmer, D.M. (1989) The Physical Basis for Recruitment Variability in Fish Populations. *Journal Du Conseil* **45,** 136-145.

Rummer, J.L., Stecyk, J.A.W., Couturier, C.S., Watson, S.-A., Nilsson, G.E., Munday, P.L. (2013) Elevated CO2 enhances aerobic scope of a coral reef fish. *Conservation Physiology* **1,** 1-7.

Runge, J.A., Kovach, A.I., Churchill, J.H., *et al.* (2010) Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. *Progress in Oceanography* **87,** 251-263.

Russell, B.D., Harley, C.D.G., Wernberg, T., *et al.* (2012) Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. *Biology letters* **8,** 164-166.

Ruth, M., Lindholm, J. (1996) Dynamic modelling of multispecies fisheries for consensus building and management. *Environmental Conservation* **23,** 332-342.

Scheffer, M., Baveco, J.M., DeAngelis, D.L., Rose, K.A., van Nes, E.H. (1995) Super-individuals a simple solution for modelling large populations on an individual basis. *Ecological Modelling* **80,** 161-170.

Schlüter, M., Mcallister, R.R.J., Arlinghaus, R., *et al.* (2012) New Horizons for Managing the Environment: A Review of Coupled Social-Ecological Systems Modeling. *Natural Resource Modeling* **25,** 219-272.

Scott, F., Blanchard, J.L., Andersen, K.H. (2014) mizer: an R package for multispecies, trait-based and community size spectrum ecological modelling. *Methods in Ecology and Evolution* **5,** 1121-1125.

Shama, L.N.S., Strobel, A., Mark, F.C., Wegner, K.M. (2014) Transgenerational plasticity in marine sticklebacks: maternal effects mediate impacts of a warming ocean. *Functional Ecology* **28,** 1482–1493.

Shannon, L., Coll, M., Bundy, A., *et al.* (2014) Trophic level-based indicators to track fishing impacts across marine ecosystems. *Marine Ecology Progress Series* **512,** 115-140.

Shannon, L.J., Christensen, V., Walters, C.J. (2004) Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. *African Journal of Marine Science* **26,** 179-196.

Shin, Y.-J., Travers, M., Maury, O. (2010) Coupling low and high trophic levels models: Towards a pathways-orientated approach for end-to-end models. *Progress in Oceanography* **84,** 105-112.

Shin, Y.J., Cury, P. (2001) Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquatic Living Resources* **14,** 65-80.

Shin, Y.J., Cury, P. (2004) Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 414-431.

Sibly, R.M., Grimm, V., Martin, B.T., *et al.* (2013) Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods in Ecology and Evolution* **4,** 151-161.

Simpson, S.D., Munday, P.L., Wittenrich, M.L., *et al.* (2011) Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biology letters* **7,** 917-920.

Somero, G.N. (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *The Journal of experimental biology* **213,** 912-920.

Sousa, T., Domingos, T., Kooijman, S.A.L.M. (2008) From empirical patterns to theory: a formal metabolic theory of life. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **363,** 2453-2464.

Speirs, D.C., Guirey, E.J., Gurney, W.S.C., Heath, M.R. (2010) A length-structured partial ecosystem model for cod in the North Sea. *Fisheries Research* **106,** 474-494.

Steenbeek, J., Coll, M., Gurney, L., *et al.* (2013) Bridging the gap between ecosystem modeling tools and geographic information systems: Driving a food web model with external spatial-temporal data. *Ecological Modelling* **263,** 139-151.

Stefansson, G. (2003) Issues in Multispecies Models. *Natural Resource Modeling* **16,** 1-23.

Stensholt, B. (2001) Cod migration patterns in relation to temperature: analysis of storage tag data. *ICES Journal of Marine Science* **58,** 770-793.

Stewart, R.I.A., Dossena, M., Bohan, D.A., *et al.* (2013) Mesocosm Experiments as a Tool for Ecological Climate-Change Research. *Advances in Ecological Research, Vol 48: Global Change in Multispecies Systems, Pt 3* **48,** 71-181.

Stock, C.A., Alexander, M.A., Bond, N.A., *et al.* (2011) On the use of IPCC-class models to assess the impact of climate on Living Marine Resources. *Progress in Oceanography* **88,** 1-27.

Stramma, L., Schmidtko, S., Levin, L.A., Johnson, G.C. (2010) Ocean oxygen minima expansions and their biological impacts. *Deep-Sea Research Part I-Oceanographic Research Papers* **57,** 587-595.

Strobel, A., Bennecke, S., Leo, E., Mintenbeck, K., Portner, H.O., Mark, F.C. (2012) Metabolic shifts in the Antarctic fish Notothenia rossii in response to rising temperature and PCO2. *Frontiers in Zoology* **9,** 28.

Strobel, A., Leo, E., Pörtner, H.O., Mark, F.C. (2013) Elevated temperature and PCO2 shift metabolic pathways in differentially oxidative tissues of Notothenia rossii. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* **166,** 48-57.

Sumaila, U.R., Cheung, W.W.L., Lam, V.W.Y., Pauly, D., Herrick, S. (2011) Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change* **1,** 449-456.

Szuwalski, C.S., Vert□Pre, K.A., Punt, A.E., Branch, T.A., Hilborn, R. (2014) Examining common assumptions about recruitment: a meta□analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries* **16,** 633-648.

Takasuka, A., Oozeki, Y., Aoki, I. (2007) Optimal growth temperature hypothesis: Why do anchovy flourish and sardine collapse or vice versa under the same ocean regime? *Canadian Journal of Fisheries and Aquatic Sciences* **64,** 768-776.

Teal, L.R., Marras, S., Peck, M.A., Domenici, P. (2015) Physiology-based modelling approaches to characterize fish habitat suitability: Their usefulness and limitations. *Estuarine, Coastal and Shelf Science 2015.*

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. *Global Change Biology* **18,** 3291-3305.

Thuiller, W., Lafourcade, B., Engler, R., Araujo, M.B. (2009) BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* **32,** 369-373.

Tian, Y., Akamine, T., Suda, M. (2004) Modeling the influence of oceanic-climatic changes on the dynamics of Pacific saury in the northwestern Pacific using a life cycle model. *Fisheries Oceanography* **13,** 125-137.

Tjelmeland, S., Bogstad, B. (1998) MULTSPEC - a review of a multispecies modelling project for the Barents Sea. *Fisheries Research* **37,** 127-142.

Travers, M., Shin, Y.J., Jennings, S., Cury, P. (2007) Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography* **75,** 751-770.

Travers, M., Shin, Y.J., Jennings, S., *et al.* (2009) Two-way coupling versus one-way forcing of plankton and fish models to predict ecosystem changes in the Benguela. *Ecological Modelling* **220,** 3089-3099.

Travers-Trolet, M., Shin, Y.-J., Shannon, L.J., Moloney, C.L., Field, J.G. (2014) Combined Fishing and Climate Forcing in the Southern Benguela Upwelling Ecosystem: An End-to-End Modelling Approach Reveals Dampened Effects. *PloS one* **9,** e94286.

Ulanowicz, R.E. (1985) *Growth and Development: Ecosystems Phenomenology.* Springer.

Ulanowicz, R.E. (2004) Quantitative methods for ecological network analysis. *Computational Biology and Chemistry* **28,** 321-339.

van der Meer, J. (2006) An introduction to Dynamic Energy Budget (DEB) models with special emphasis on parameter estimation. *Journal of Sea Research* **56,** 85-102.

van der Veer, H.W., Kooijman, S.A.L.M., van der Meer, J. (2001) Intra- and interspecies comparison of energy flow in North Atlantic flatfish species by means of dynamic energy budgets. *Journal of Sea Research* **45,** 303-320.

Van Winkle, W., Rose, K.A., Chambers, R.C. (1993) Individual-Based Approach to Fish Population Dynamics: An Overview. *Transactions of the American Fisheries Society* **122,** 397-403.

Vikebo, F., Jorgensen, C., Kristiansen, T., Fiksen, Ø. (2007) Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. *Marine Ecology Progress Series* **347,** 207-219.

Vikebo, F.B., Husebo, A., Slotte, A., Stenevik, E.K., Lien, V.S. (2010) Effect of hatching date, vertical distribution, and interannual variation in physical forcing on northward displacement and temperature conditions of Norwegian spring-spawning herring larvae. *ICES Journal of Marine Science* **67,** 1948-1956.

Voinov, A., Shugart, H.H. (2013) 'Integronsters', integral and integrated modeling. *Environmental Modelling and Software* **39,** 149-158.

Voss, R., Hinrichsen, H.H., Quaas, M.F., Schmidt, J.O., Tahvonen, O. (2011) Temperature change and Baltic sprat: from observations to ecological-economic modelling. *ICES Journal of Marine Science* **68,** 1244-1256.

Walters, C., Christensen, V., Walters, W., Rose, K. (2010) Representation of multistanza life histories in Ecospace models for spatial organization of ecosystem trophic interaction patterns. *Bulletin of Marine Science* **86,** 439-459.

Walters, C., Pauly, D., Christensen, V. (1999) Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2,** 539-554.

Watson, J.R., Stock, C.A., Sarmiento, J.L. (2014) Exploring the role of movement in determining the global distribution of marine biomass using a coupled hydrodynamic–Size-based ecosystem model. *Progress in Oceanography.*

Wayte, S.E. (2013) Management implications of including a climate-induced recruitment shift in the stock assessment for jackass morwong (Nemadactylus macropterus) in south-eastern Australia. *Fisheries Research* **142,** 47-55.

Whitehead, A. (2012) Comparative genomics in ecological physiology: toward a more nuanced understanding of acclimation and adaptation. *The Journal of Experimental Biology* ***215****,* *884-891.*

Wiedmann, M.A., Aschan, M., Certain, G., *et al.* (2014) Functional diversity of the Barents Sea fish community. *Marine Ecology Progress Series* **495,** 205-218.

Woodin, S.A., Hilbish, T.J., Helmuth, B., Jones, S.J., Wethey, D.S. (2013) Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. *Ecology and Evolution* **3,** 3334-3346.

Woodworth-Jefcoats, P.A., Polovina, J.J., Dunne, J.P., Blanchard, J.L. (2013) Ecosystem size structure response to 21st century climate projection: large fish abundance decreases in the central North Pacific and increases in the California Current. *Global Change Biology* **19,** 724-733.

Young, J.W., Hunt, B.P.V., Cook, T.R., *et al.* (2015) The trophodynamics of marine top predators: Current knowledge, recent advances and challenges. *Deep-Sea Research Part Ii-Topical Studies in Oceanography* **113,** 170-187.

Zimmermann, F., Jorgensen, C. (2015) Bioeconomic consequences of fishing-induced evolution: a model predicts limited impact on net present value. *Canadian Journal of Fisheries and Aquatic Sciences* **72,** 612-624.

Table *1*: Overview on model classes for marine fish and their potential for representation of physiological processes and integration of experimental results on various levels of biological organisation. Processes marked by an asterisk* are either 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.

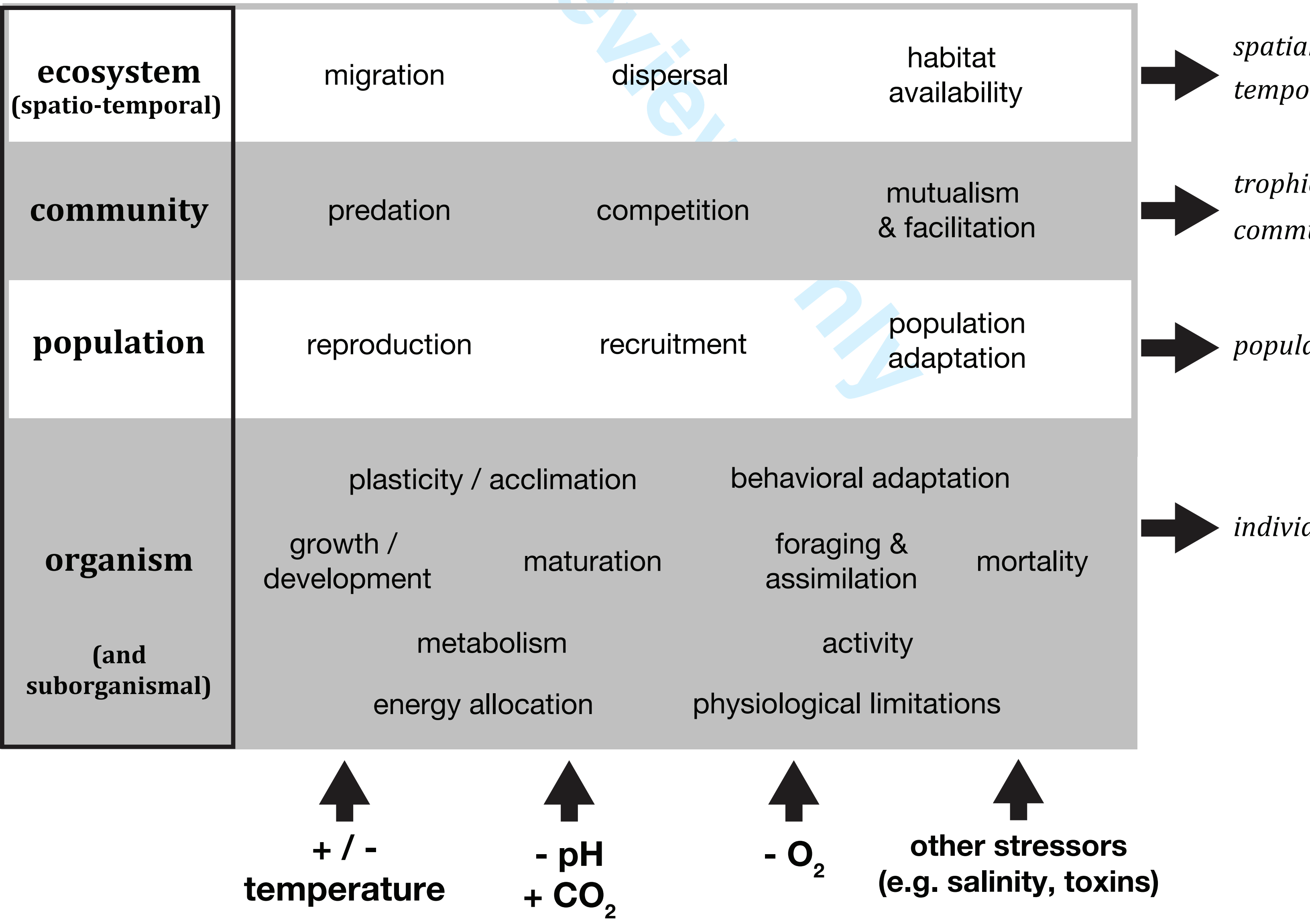
model class	**incorporated processes on level of description**				**main use in climate change context**
	Organism	**Population**	**Community**	**Ecosystem**	
1. Single-species population dynamic	growth* mortality* (development*)	recruitment (reproduction)	--	migration* dispersal*	stock management (no relevant stock interactions)
2. Multi-species population dynamic	growth* mortality* (development*) (foraging*) (assimilation*)	recruitment (reproduction)	predation* competition*	migration* dispersal*	stock management (interactions important), community dynamics

3. tropho-dynamic & mass-balance	growth* mortality* (development*) foraging* assimilation*	(recruitment) (reproduction*)	predation* competition* mutualism*	migration (dispersal) habitat *(all in Ecospace)*	community and ecosystem resilience, ecosystem-based management
4. species distri-bution (SDM)	growth* mortality* foraging* limitations*	recruitment*	(predation*) (competition) (*with size spectrum or trophic models)*	migration* (dispersal*) habitat	distribution range shifts, local fish catch potential
5. trait-based & size-spectrum	(plasticity) behaviour growth mortality development foraging assimilation (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 assimilation (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 assimilation 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

1933

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.


ecosystem
(spatio-temporal)
migration
dispersal
habitat availability
spatia
tempo
community
predation
competition
mutualism & facilitation
trophi
comm
population
reproduction
recruitment
population adaptation
popula
organism
(and suborganismal)
plasticity / acclimation
behavioral adaptation
growth / development
maturation
foraging & assimilation
mortality
metabolism
activity
energy allocation
physiological limitations
indivi
+ / - temperature
- pH
+ CO_2
- O_2
other stressors
(e.g. salinity, toxins)