



VECTORS of Change in Oceans and Seas Marine Life, Impact on Economic Sectors

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VECTORS Overview

'VECTORS seeks to develop integrated, multidisciplinary research-based understanding that will contribute the information and knowledge required for addressing forthcoming requirements, policies and regulations across multiple sectors.'

Marine life makes a substantial contribution to the economy and society of Europe. In reflection of this VECTORS is a substantial integrated EU funded project of 38 partner institutes and a budget of €16.33 million. It aims to elucidate the drivers, pressures and vectors that cause change in marine life, the mechanisms by which they do so, the impacts that they have on ecosystem structures and functioning, and on the economics of associated marine sectors and society. VECTORS will particularly focus on causes and consequences of invasive alien species, outbreak forming species, and changes in fish distribution and productivity. New and existing knowledge and insight will be synthesized and integrated to project changes in marine life, ecosystems and economies under future scenarios for adaptation and mitigation in the light of new technologies, fishing strategies and policy needs. VECTORS will evaluate current forms and mechanisms of marine governance in relation to the vectors of change. Based on its findings, VECTORS will provide solutions and tools for relevant stakeholders and policymakers, to be available for use during the lifetime of the project.

The project will address a complex array of interests comprising areas of concern for marine life, biodiversity, sectoral interests, regional seas, and academic disciplines and especially the interests of stakeholders. VECTORS will ensure that the links and interactions between all these areas of interest are explored, explained, modeled and communicated effectively to the relevant stakeholders. The VECTORS consortium is extremely experienced and genuinely multidisciplinary. It includes a mixture of natural scientists with knowledge of socio-economic aspects, and social scientists (environmental economists, policy and governance analysts and environmental law specialists) with interests in natural system functioning. VECTORS is therefore fully equipped to deliver the integrated interdisciplinary research required to achieve its objectives with maximal impact in the arenas of science, policy, management and society.

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Executive Summary

This deliverable report discusses the current status of various modelling approaches used to examine changes in the distribution and productivity of fish and other living marine resources. This report dovetails closely with deliverable report 2.2.3, where the results of various VECTORS modelling applications are discussed.

This report reviews and compares five, broad categories of approaches used to model changes in the distribution and productivity of living marine resources including: 1) statistical techniques used to analyse temporal (time only) changes in field data, 2) statistical models which can describe both temporal and spatial changes in field data, 3) physiological-based models that merge ocean physics and the biology of single and/or all life stages, 4) spatially-explicit food web models, and 5) end-to-end models that combine models of water physics, habitat biogeochemistry, food web interactions, and human pressures such as fishing fleet dynamics. These broad categories differ in their ability to assess the effects of interactions in key pressures affecting living marine resources including i) climate-driven changes in temperature regimes and acidification combined with ii) reductions in water quality due to eutrophication (decreased dissolved O₂ concentrations and increased turbidity), and/or iii) the introduction of alien invasive species, and/or iv) reductions in biomass of stocks / populations due to commercial exploitation (fisheries).

Exploring field data using statistical approaches is an important first step in detecting patterns and strengths of associations between physical and biological components of ecosystems. These analyses can help generate hypotheses regarding processes acting to generate complex patterns observed in field time series data. These complex patterns include large-scale, ecosystem reorganizations such as regime shifts (from one stable state to another) and complex predator-prey dynamics such as trophic cascades (reciprocal shifts in adjacent trophic levels).

A consensus opinion emerging from our review of mechanistic models (those beyond mere statistical, correlative approaches), is that advancing our predictive capacity requires adding biological and physical mechanism into models to provide a cause-and-effect understanding of the impacts of multiple pressures. Continuing to add key physiological mechanisms that shape individual behaviour and species life history strategies (such as the seasonal migration patterns observed in many fishes) is a priority as is increasing the realism of food web interactions occurring at different spatial scales.

Many of the models reviewed here are fairly mature (having been used for many years to decades) and a coupled model approach is now recommended that can thoroughly examine key processes. These processes include those emerging from changes in physical controls on the availability of prey or suitable (physical) habitat characteristics for fish (bottom-up processes) or changes in the number (and/or efficiency of prey capture) of predators (top-down processes). An important consideration driving the development of full life cycle models is that different processes can act on different life stages of key species, their predators and their prey. Models that only examine single life stages (e.g., adult distribution) may not capture the relevant drivers of changes in populations. Finally, End-to-end models (e.g., physics to fish to human pressures such as fisheries) offer one of the few opportunities to assess how multiple pressures may interact to cause changes in living marine resources. At the present time, these models are most useful for strategic decisions based upon relative differences (cost and trade-offs) arising from different spatial management actions but are less suited for quantitative (absolute) projections.

Introduction

Marine habitats provide resources critical for the wellbeing of society including providing food security and energy. For the effective stewardship of living marine resources, it is critical to understand the factors and processes that have interacted to cause historical changes in the distribution and productivity of living marine resources. Furthermore, it is important to develop tools and approaches that provide robust projections of future changes. Advancing our predictive capacity of future changes is particularly important within regional seas and their coastal habitats. Nearly one third of our burgeoning human population inhabits areas surrounding regional seas and multiple drivers (e.g., the need to maintain food security, requirements to increase renewable energy sources, maintaining viable shipping routes) have made these areas hotspots of pressures (e.g., the potential for over-fishing, increased land-based pollution causing eutrophication, physical alteration of marine habitats, continued risk of introduction of alien invasive species) acting to alter the abiotic and biotic attributes of marine ecosystems (Doney, 2010). Given the diversity of anthropogenic activities and effects, the development of tools that can examine the interaction of various pressures (e.g., climate x fishing (Perry et al., 2009; Griffith et al., 2012)), will be important to projecting impacts and providing effective management advice for living marine resources.

The general goal of WP 2.2 was to identify generic mechanisms of change in the productivity and distribution of species within European regional seas examined in VECTORS (Baltic, North, and Mediterranean Seas). Advanced statistical methods for detecting changes in the distribution and productivity of populations of key species were developed according to the specific requirements of the VECTORS case studies and data sets. The relationships within the ecosystem, possible positive and negative feedback loops, as well as directions, strengths and uncertainties in the quantification of the pressures of change, as identified in WP 1, were considered. The ultimate goal was to provide the necessary tools to parameterize region-specific, spatially-resolved ecosystem models in WP4 and WP5, which will be the foundation of any integrated ecosystem assessment and evaluation of ecosystem management strategies. The research reported within WP2 is being integrated with on-going investigations of possible mechanisms of mitigation in WPs 2.3, 3 and 6, where the goal is to identify management options that could support mitigation through human behaviour or technological development.

The current deliverable report is one of three within WP2. The first deliverable report (2.2.1) summarized different methods for estimating primary productivity in marine systems. That work was related to Task 2.2.1 (assessing energy inputs to the systems). Primary production provides the base of the marine food web and is critical to understand if we hope to understand how energy cycles through the food web. Spatial and temporal changes in primary productivity that will drive, to a large extent, spatial and temporal variability in the abundance of primary consumers and the productivity and distribution of members of upper trophic levels of marine food webs. This deliverable report (2.2.2) is a review of models that have been developed and utilized in VECTORS and elsewhere to understand fish distribution and migration. The goal was to provide a generic review to highlight not only advancements and progress but also future avenues of research needed to strengthen various modelling approaches. The third deliverable (2.2.3) is a more detailed report that includes model descriptions and summaries of the results of 25+ models developed to examine changes in the distribution and productivity of fishes and other living marine resources. These two deliverable reports (2.2.2 and 2.2.3) are associated with Task 2.2.2 (Modelling spatiotemporal pathways of energy flow) and Task 2.2.3 (Statistical appraisal).

The present report is a summary of modelling efforts used within VECTORS and elsewhere to describe and, in some cases, predict the distribution and migrations of marine fishes and other living marine resources. After a brief introduction regarding the processes affecting marine fishes, the report reviews of advances made in various modelling approaches. The report highlighting the strengths and weaknesses of various approaches, such an appraisal was deemed necessary to better interpret the models and results provided in deliverable report 2.2.3.

Core Activity

Introduction

Changes in the productivity and changes in the distribution of a species are likely to be strongly coupled, but the processes causing the former and latter may differ. On the one hand, the distribution of living marine resources results from the interaction between physical (ocean currents / inflow, salinity, or substrate type) and biological (e.g. primary and secondary production, predator-prey relationships, competition) processes as influenced by anthropogenic activities. Changes in the distribution of marine organisms are becoming increasingly documented including shifts towards higher latitudes or deeper waters in response to ocean warming (Dulvy et al., 2008; Rijnsdorp et al., 2009; Sunday et al., 2011). Within temperate latitudes, these shifts are associated with the appearance of Lusitanian fauna (organisms traditionally distributed in warmer waters) and reduced extent or loss of boreal species (Sunday et al., 2012). In European waters and elsewhere, these climate-driven shifts (Beaugrand and Reid, 2003, Beare et al., 2004, Perry et al., 2005; Rijnsdorp et al., 2009 as well as the increasing number of alien species introduced via ballast waters or released from aquaculture (Hulme et al., 2008) are creating novel mixtures of species with unforeseen consequences to ecosystem structure and function (i.e. Hobbs et al., 2009).

In contrast to a species' distribution, the productivity of a species can be influenced by both bottom-up and top-down processes. Bottom-up processes can change the reproductive potential of adult fish (Marshall et al., 2000, Kraus et al. 2002) and the rates of survival of their progeny (e.g. Sundby, 2000; O'Brien, 2000). Top-down processes also have the potential to regulate lower trophic levels (Shurin et al., 2002; Mueter et al., 2006). Effects of changes in key abiotic factors such as temperature will act on higher trophic levels both directly and indirectly. Direct effects include mortality due to intolerable levels of key abiotic factors such as temperature, oxygen or pH (Pörtner and Peck, 2010; Pörtner 2012). Indirect pathways include, among others, alteration of the spatiotemporal availability (match-mismatch dynamics) between predators and their prey resources (Clark and Frid, 2001, Hunt et al., 2002, Beaugrand et al., 2003; Kempf et al., 2013) leading to either reduced or increased survival rates. Top-down processes are important drivers of population dynamics within marine ecosystems but it is notoriously difficult to assess the spatial and temporal scales at which mortality occurs (Temming et al., 2007). For example, the mortality rates of marine fish early life stages are extremely high and determine, to a large extent, the strength of recruitment (the number of individuals that will eventually develop into adults and reproduce (Houde, 1997).

A variety of modelling tools has been utilized to examine historical changes in distribution and/or productivity of living marine resources (Figure 1). Often designed for specific objectives, these tools differ markedly in their complexity from statistical descriptions of trends in historical field data to biophysical model simulations of the physical characteristics of areas (water currents, temperature, salinity) that make use of knowledge on the physiological-based habitat

requirements of species, trophic groups or any other kind of assemblage (Jørgensen et al., 2012). The dynamics of various parts or components of marine ecosystems have been explored using another set of modelling tools that provide spatially-explicit representations of trophodynamic structure and function. Finally, at the most complex end of the spectrum, “end-to-end” models create virtual ecosystems and industries allowing trade-offs between various, competing economic sectors and activities (e.g., fisheries, renewable energy, conservation) to be examined using a management evaluation framework (Fulton et al., 2011). All of these various tools can offer insight, to a greater or lesser extent, on the mechanisms acting to cause historical changes in distribution and productivity of living marine resources and allow projection of future trajectories. Plagányi (2007) provided a thorough review of the merits of various modelling tools in the context of ecosystem-based fisheries management while Travers et al. (2011) provided a retrospective on various modelling approaches leading to the design of size-based food web and end-to-end models.

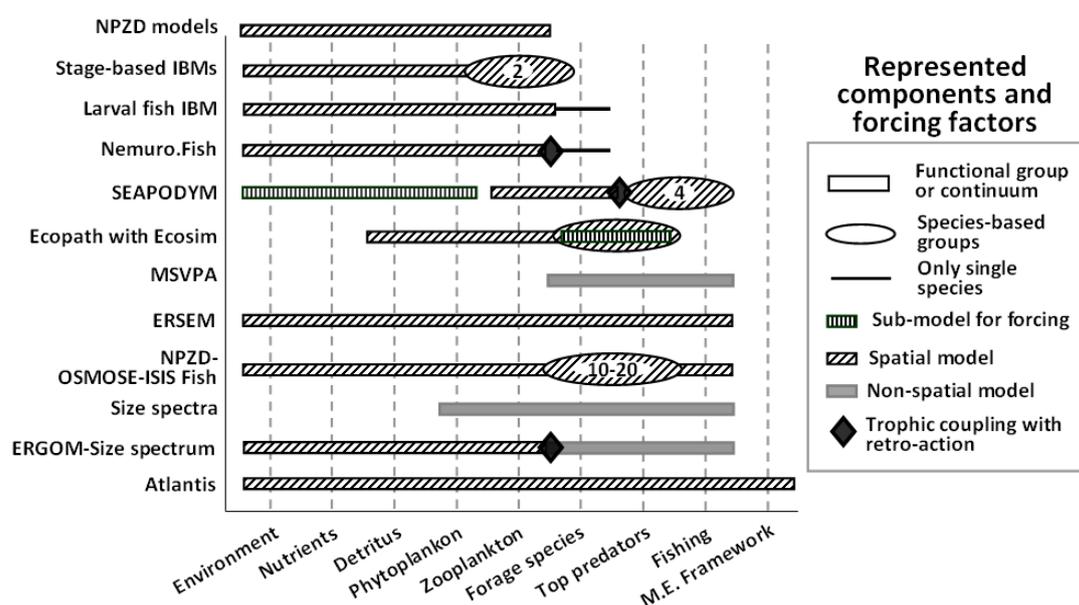


Figure 1 Schematic of the components within various types of models. Most models were characterized according to whether or not they were spatially-explicit and resolved species, functional groups or size spectra. M.E. = Management Evaluation. Model acronyms are explained in the text. The figure was adapted from one presented by Travers *et al.* (2007).

The present deliverable report compares five modelling approaches that have been developed to estimate changes in the distribution and productivity of living marine resources. The suitability of each method in understanding and projecting changes that arise from one or more interacting drivers is also examined. Model types include: 1) statistical modelling of habitat associations with a special subset being 2) bioclimate envelop models, 3) biophysical models of single species and/or life stages, 4) spatially-explicit food web models, and 5) end-to-end models. This list of approaches includes some that rely heavily on the statistical analysis of historical observations (1 and 2), others that are coupled physical-biological models that either include (3, 4, 5) or exclude (3) food web interactions. Examples of interacting state changes (and their pressures) include warming and acidification (climate change), decreases and increases in concentrations of dissolved O₂ and suspended particulate matter, respectively (eutrophication), changes in food web composition (introduction of invasive alien species), and reductions in biomass of stocks / populations (fisheries exploitation). We provide examples of

these various modelling approaches that have been applied within the European regional marine ecosystems (e.g., North Sea, Baltic Sea and Mediterranean Sea). These regions are case studies within “VECTORS” an EU marine research program charged with examining the impacts of multiple stressors and drivers on living marine resources and various economic sectors. Statements about the strengths and weaknesses of different modelling tools are examined as well as future research needs.

1. Statistical Analyses of Field Data (relative to Task 2.3)

1.1 Statistical Exploration of Temporal Changes

As our time series of living marine resources continue to grow, so does our understanding of the temporal dynamics of marine systems. Patterns include multi-decadal and decadal cycles of productivity influenced by climate variability such as the Atlantic Multidecadal Oscillation (Alheit et al., 2012) and the El Niño Southern Oscillation (Sugimoto et al., 2001), respectively. Time series analyses have also documented abrupt regime shifts in species composition and abundance associated with shifts from one ecosystem stable state to another as well as reciprocal shifts in adjacent trophic levels (trophic cascades). These ecosystem reorganizations often result from a combination of (over-) exploitation of marine resources and climate variability or change (Frank et al., 2005; Möllmann et al., 2008). Thus, developing tools that can disentangle the effects of these two pressures is important to building predictive capacity.

The first step in understanding potential causes of large-scale ecosystem reorganizations is to understand the temporal dynamics of the system. Statistical approaches to pinpoint the timing of the large-scale shifts are rapidly advancing. The empirical indicators method (Link et al., 2002) suggests the use of representative metrics derived from extended time-series databases which include human, abiotic and biotic factors, and the production of color-coded quintiles (as percentiles) of the empirical distribution of the selected metrics using average values for 5-year periods. Using this method major components of marine ecosystems can be assessed and an improved picture of the whole system can be provided. The empirical indicators method differs from the typical “traffic light” method (Halliday et al. 2001) into that no value judgement (i.e. good or bad) is assigned to any quintile (Link et al., 2002). The reduction of the multivariate dimensions to a smaller set of linear combinations through a Principal Component Analysis (PCA) tracked the most major trends across the time series, whereas a canonical correlation analysis evaluated the linear relationships between the multivariate response and explanatory metrics (Link et al., 2002).

More recently, Gröger et al. (2011) describe a method that relies on repeatedly conducting Principal Component Analyses (PCA) and analysing the results of the first principle component using a „shiftogram“, a series of 10 diagnostic plots. Both aggregate (full data set) and decomposed (by factor grouping) approaches can be utilized (Figure 2).

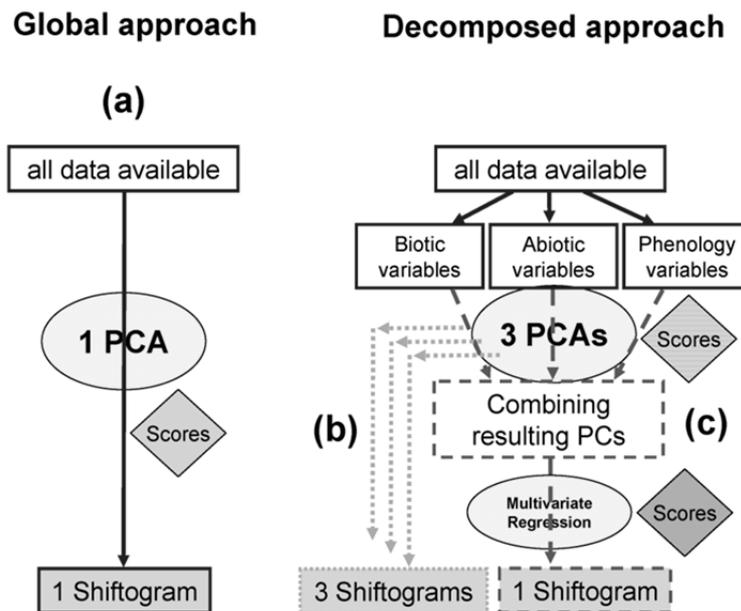


Figure 2 The analysis algorithm (a) for the global approach by applying a PCA based on all variables and generating one shiftogram using the resulting PC1 only, (b) for the decomposed approach by applying three PCAs (one per each factor grouping) and thus generating three shiftograms based on the three resulting PC1's, (c) for the decomposed approach by additionally combining all PCs produced in (b) using multivariate regression and generating one shiftogram based on the predicted values of PC1 of the biotic PCs.

The latter allows more information to be gleaned on occurrence, timing and type of abrupt changes in major factor groupings. The variable grouping results of the various PCAs can be illustrated using correlograms and/or cluster trees constructed through a PCA-based variable clustering method. This shiftogram technique has most recently been used to identify the environmental factors associated with changes in phenology and abundance of ichthyoplankton collected between 1975 and 2010 at spawning grounds in the Gulf of Riga (Arula et al., Submitted).

Time series analysis of field data is needed to build hypotheses on the processes controlling the dynamics of species or food webs (at least those observed at mesoscales). However, these techniques fail to provide process knowledge and a cause-and-effect understanding. PCA and hierarchical models do not provide predictive equations linking factors to changes in observations. These techniques are also not designed to allow projections of future changes. Indeed, a number of key assumptions may be violated by using analyses of historical time series to project future changes. First, the future may include novel combinations of abiotic and biotic factors forcing one to extrapolate beyond historical observations. Moreover, anthropogenic activities result in non-stationarity within natural systems such that fluctuations and variability noted in the past are unlikely in the future (Milly et al., 2008). The increased frequency of extreme events that has been observed in recent years and that is projected by future climate models helps to illustrate this point (IPCC, 2007).

1.2 Statistical Exploration of Spatiotemporal Changes

A number of approaches have been used to examine historical changes in the spatiotemporal distribution of species including Generalized Linear Models (GLM) (Hastie and Tibshirani, 1990), Generalized Additive Models (GAM), Classification and Regression Tree analysis (CART) (Breiman et al., 1984), Artificial Neural Networks (ANN) (Ripley, 1996), and Multivariate adaptive regression splines (MARS, Friedman, 1991). Thuiller (2003) briefly reviewed GLM, GAM, CART and ANN analyses and compared their performance in describing the distribution of 61 native tree taxa across Europe. The agreement between observed and predicted distributions was good in all four approaches the most accurate model varied between species. Leatherwick et al. (2006) reported similar capacities for GAM and MARS analyses to describe the distribution of 15 freshwater fish species. Most of these techniques have been used to infer historical changes of species due to climate-driven warming and to project future changes in terrestrial or freshwater systems with fewer applications within marine ecosystems.

Different types of GAMs have been utilized to investigate how spatiotemporal changes in environmental factors and in key players (fish, zooplankton, phytoplankton) corresponded with one another within a marine system. One of the first applications of threshold and spatial GAMs on marine fish was by Ciannelli et al. (2004, 2007) who examined the strength of association between environmental factors and density-dependent survival of early life stages of walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. The method could successfully distinguish subtle, non-linear effects such as temperature-dependent strengths of density dependent survival of specific life stages. Using GAMs and GLMs, different time periods can be distinguished that display common spatio-temporal distributions of specific taxa (groups/species of plankton, fish, etc.). Interactions among species or across different functional groups can also be examined. Within European waters, these techniques were applied by Llope et al. (2012) to examine spatiotemporal data on various plankton groups in the North Sea. The study by Llope et al. (2012) revealed a shift in the reliance of filter feeding zooplankton from diatoms to dinoflagellates in the early 1970s but this shift in bottom-up control was only apparent in eastern regions of that shelf sea ecosystem. Spatial or threshold GAMs can be applied to any taxa or variables for which sufficient spatial and temporal data are available. The outcomes of the model would be the identification of major spatial and temporal changes in distributions of fishes presented as maps that can be used for integration in other models. Employing threshold GAMs to describe spatially-explicit time series data on predators and prey or physical factors may help to identify factors that had a major influence on the spatial and/or temporal distribution of species (e.g., Kempf et al., 2013) but cannot be directly used for predictive scenarios.

Artificial neural network (ANN) models mimic intelligent machines that can learn from experience in a way that no conventional computer can and they are based on a “black box” approach which has great capacity in problem solving and predictive modelling (Lek and Guégan, 1999). The ANN models are able to describe relationships between state variables and forcing functions based on a heterogeneous database (Recknagel, 1997). According to Bandelj et al. (2009), an ANN model can be used to model the relationships between different benthic communities and a set of environmental parameters based on a back-propagation algorithm, which can be effectively applied when the communities' responses to environmental parameters are complex. Such models are easy and fast to apply and they give a close to optimum use of large datasets (Jørgensen, 2008). However, the ANN models are often not based on causality, they have reduced accuracy for future projections, and thus they could not completely abrogate the bio-geo-chemical models which are based on the conservation principles (Jørgensen, 2008).

Lewy and Kristensen (2009) presented a novel single-species spatially explicit geostatistical model that can be used to describe historical data on spatial distribution that are characterized by irregular sampling, many zeros and fluctuations in species abundance and distributions over time. The model, termed Log Gaussian Cox Process (LGCP) model, uses space and time correlations to model the number of individuals caught per sample. Assuming the numbers caught follow a Poisson distribution the spatio-temporal correlations and population parameters are estimated by maximum likelihood and used to predict abundance continuously through time and space. The LGCP model is a generic tool that can be used in any system where time series of spatially-explicit abundance (numbers per sample) are available. Thus far, the LGCP model has been applied to International Bottom Trawl Survey, fisheries, and CPR data from the North Sea and areas between the Baltic and North Seas (Skagerrak and Kattegat) to examine seasonal and decadal changes in the distribution of fish such as the larvae of mackerel (Jansen et al., 2012). The main advantages of the model are that no requirements are necessary regarding sampling grid, that uncertainty is accounted for and separated into model and observation error, that the impact of highly correlated observations automatically is down-weighted, and that over-dispersion is explicitly accounted for through a nugget effect. The main drawbacks are the demands with respect to computing time and that few biological processes so far have been incorporated. The LGCP model also assumes spatial and temporal continuity in the data and that an exponentially declining correlation of log density can be assumed both spatially and temporally.

1.3. Statistical Analyses of Historical and Future Distribution and Abundance

The approach known as 'bioclimatic envelope modelling' has become a commonplace technique used to predict present and project future distribution and relative abundance of marine fish and invertebrate species (e.g., Pearson and Dawson, 2003; Cheung et al., 2009). These models examine the relationship between key climatic variables and species distribution, mostly based on historical distributional data (i.e. they are largely correlative). By looking at the current range of environmental conditions tolerated by a species, it is assumed to be possible to project future distribution, if we know how the physical environment in an area will likely change in the future. Some of the more commonly applied 'bioclimatic envelope modelling' techniques include "Maxent", "BioMapper", the genetic algorithm "GARP", Aquamaps as well as GLMs and GAMs. These approaches have been applied to all sorts of marine organisms ranging from pathogens to seabirds, and including commercial fish (Phillips and Dudik, 2008).

The relative merits/skill of three different 'bioclimatic envelope modelling' (BEM) approaches (AquaMaps, MAXENT and DBEM) to predict distributions of marine fishes and invertebrates in the North Sea was recently explored by Jones et al. (2012). These three models make different assumptions. The AquaMaps approach uses simple, numerical descriptors of a species relationship with environmental variables to model its distribution using a trapezoidal distribution to find the absolute and 'preferred' preference ranges (Figure 3) (Kaschner et al., 2006; Ready et al., 2010; Jones et al., 2012). Maxent uses a complex generative approach (Phillips et al., 2006) to predict species habitat suitability from presence only, occurrence data and a suite of environmental variables. Maxent has been shown to compete well with alternative approaches in terms of model testing statistics (Elith et al., 2006; Phillips et al., 2006; Jones et al., 2012) and is robust to small sample sizes (Pearson et al., 2007). Finally, the Dynamic Bioclimatic Envelope Model (DBEM) (Cheung et al., 2011) uses a discriminative approach and attempts to avoid the bias that might be introduced by skewed distribution in many datasets due to sporadic sampling effort. The DBEM combines statistical and mechanistic approaches to predict species' distributions allowing one to explore (more mechanistically) the effects of multiple stressors. It differs from other BEMs in simulating

changes in the relative abundance of a species by incorporating a logistic population growth model (Cheung et al., 2008), larval dispersal as well as adult immigration-emigration and ecophysiological parameters.

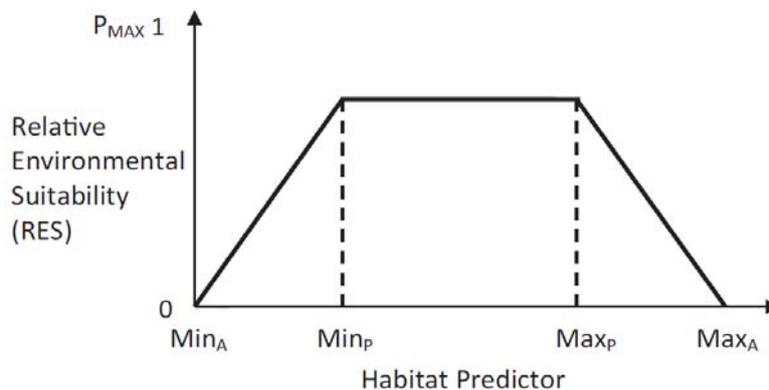


Figure 3 Trapezoidal species' response curve used in bioclimate envelope modelling, showing absolute minimum (Min_A) and maximum (Max_A) and preferred minimum (Min_p) and maximum (Max_p) levels of a habitat predictor, and the relative environmental suitability, the highest obtainable value being (P_{Max}) (see Jones *et al.*, 2012a).

Overall, the three types of bioclimate envelop models compared by Jones et al. (2012) did not vary greatly in the area or extent of occurrence predicted for each species, but differences in detailed patterns and values of predicted suitability existed within the extents of occurrence. The comparison by Jones et al. (2012) provides information about the robustness and uncertainty of the projections, which is thus important for spatial planning and developing management and conservation strategies. Currently, none of the 3 models takes account of food-web linkages but predator-prey interactions will be included in the next version of DBEM (Cheung et al., 2011). Within the DBEM modelling approach a new version of the model has been recently proposed to incorporate species interactions based on size-spectrum theory and habitat suitability (Fernandes et al., Submitted). The advantage is easy parameterisation and the disadvantage is that interactions are not specified (e.g. no diet matrix). However, a diet matrix is very hard to implement and assumes that a species will not change its diet to an opportunistic strategy. The proposed approach has the advantage that it is also able to handle new situations such as new predators invading an area and interacting with species for first time.

The analysis of species–environment relationships (Whittaker RH, 1967; ter Braak and Prentice, 1988) and the predictive modeling of species distributions (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000) have been and will continue to be popular research endeavours. However, these methods often have limitations, mainly due to their lack of integration with ecological theory (Guisan and Thuiller, 2005). Among other shortcomings, species distribution models typically do not usually consider inter-specific competition and other biotic interactions, but assume that that different species respond to environmental conditions at an individual level (Gleason, 1939, Whittaker, 1967) and that community responses emerge from that response. Some attempts to incorporate biological interactions have been made (Leathwick and Austin, 2001). Bandelj *et al.* (2012) attempt to overcome these issues by focusing directly on the community level by combining fuzzy clustering techniques and direct gradient analysis rooted in the habitat meta-community concept.

1.4 Strengths and Weakness (Statistical Approaches)

A primary strength of all statistical approaches to describing and predicting the temporal dynamics as well as spatiotemporal dynamics of species distribution is that a standard set of diagnostic tools and procedures exists to evaluate model performance and predictive skill. The best predictive statistical model for time series data can be selected by using a bootstrap technique that tests the goodness of fit of a model to a random validation dataset (normally a subset of the data that were not used to parameterize the original model (Thuiller, 2003)). Using this technique, uncertainty of threshold years can be estimated, identifying the threshold years of major importance and assessing the speed of the change between the periods identified. This type of analysis helps reveal whether the observed temporal variability is related to a progressive and stable change or if it merely reflects natural oscillations of populations / stocks. For BEMs, the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot test statistic is typically used to assess model performance (Jones et al., 2012). The AUC is a widely used test statistic that allows a threshold-independent measure of model performance and can be calculated using pseudo-absences from a random sample of background pixels rather than true absences. In most cases, there is a lack of independent test datasets for BEMs but these models can be internally assessed, for example by 4-fold cross validation (Fielding and Bell, 1997) where occurrence datasets are separated into 4 sub-sets, each containing a randomly selected 75% of points for model training, and a corresponding 25% for model testing.

A key strength of the threshold GAMs as well as bioclimatic envelope modelling is that these techniques do not require extensive information from laboratory studies or physical (hydrodynamic) Lagrangian drift models. Rather, the approach can be applied to many different species, in different areas of the world – as long as some information is available on occurrence (not only dedicated survey data but also sporadic ‘sightings’) as well as appropriate datasets of environmental variables. In this context, bioclimatic envelope modelling have been utilized to provide projections of future expansion of invasive species in Europe such as the Chinese mitten crab (*Eriocheir sinensis*) (Herborg et al. 2007) and Pacific oysters (*Crassostrea gigas*) introduced from aquaculture farms (Jones et al., 2012). Although BEMs cannot be used to predict the transmission and trans-location of non-native species into new areas – since this is governed by human behaviour (e.g. shipping routes, importation of animals for aquaculture), BEMs can be used to model the spatial extent of habitats that could support the species once the species has arrived. Furthermore, the rate of the spread of an alien invasive species will depend upon life history characteristics (e.g., larval dispersal mechanisms and home range) which cannot be adequately assessed without additional modules. A second strength of BEMs is the ability to include additional data layers to examine additional factors such as oxygen concentration to examine the potential impacts of chronic eutrophication on species’ distributions. Since the approach is largely based upon correlations with environmental (or biotic) data layers, it should, in theory, be possible to account for multiple stressors by adding additional explanatory variables. This seems a relatively easy thing to do when applying BEMs to predict present distribution patterns, however it will be more challenging to project into the future, as the analysis would require spatial projections of those anthropogenic drivers (e.g. fishing effort, aggregate extraction, eutrophication, etc.).

These models are an essential step along the way from pattern recognition (what, where, when) to process understanding (how, why). However, they are fundamentally based on correlations, do not directly advance our mechanistic, cause-and-effect understanding and predictive capacity. The pitfalls of correlative approaches used to examine food webs (including fisheries examples) were demonstrated by Sugahara et al. (2012) who apply non-linear state-

space reconstruction to distinguish causality from correlation. A high profile example for correlation between the response of living marine resources and changes in environmental factors is the out-of-phase fluctuation of anchovy and sardine species in ecosystems around the world. In general, sardines and anchovies (in general) thrive during relatively cold and warm regimes, respectively. When applied to a long time series of anchovy and sardine in the California current, the technique suggested that the strength of the effect of temperature on sardine depends upon the state of the system, and that current management decisions, based upon a fixed temperature index for sardines, appear inadequate (Sugihara et al., 2012).

Although it may be evident to the reader of this report, it is important to note that the strength of the conclusions drawn from these statistical approaches depends upon the temporal and spatial resolution of observed data. An assumption is that the available subset of observations is representative of the true distribution of populations. Moreover, inferences regarding (explanatory) processes are also constrained by the availability of spatial and temporal dataset of good resolution such as physical and biological characteristics of the environment anthropogenic stressors (e.g., indices of fishing mortality). Concerns regarding the validity of BEMs have been expressed by Jennings and Brander (2010). First, it may not be possible to assess temperature preferences from current distributions because the observed distributions are modified by abundance, habitat, predator and prey abundance and competition. Second, there may be barriers to dispersal (although this is typically less of an issue in the sea than on land) and species will move at different rates and encounter different local ecologies as temperature changes (Davis et al., 1998). Also, BEMs make the assumption that each species is in pseudo-equilibrium with its environment (Guisan and Thuiller, 2005). Uncertainty is discussed in much greater detail by Jones et al. (2012a) and methods for summarising the outputs from ensembles of 'bioclimatic envelope modelling' are described by Jones et al., (2013) who projected changes in the distribution of threatened species and fisheries resources around UK waters.

Given the widespread use of bioclimatic envelope models in terrestrial and aquatic systems, a number of papers have proposed frameworks to improve their predictive capacity and utility. Recently, Huntley et al. (2010) presented a grid-based model for the distribution of terrestrial vegetation which includes various modules simulating: 1) climatic suitability, 2) habitat suitability, 3) population dynamics, and 4) dispersal. They point out that models integrating these four components are still in their infancy (Anderson et al., 2009). Understanding the inherent physiology of the study organisms such as thermal tolerance windows (Portner and Peck, 2010), as impacted by interacting drivers, can be used to parameterize the climatic suitability module. The habitat module takes into account key attributes of a species niche; for marine species this could be bottom sediment type, turbidity, depth or hydrographic properties such as frontal zones. Attributes of the niche of habitats of species may differ depending upon life stage (Petitgas et al., 2012). The habitat module is also where the effects of other drivers (e.g., eutrophication) could be implemented. The final two models simulate population dynamics (either mechanistically or statistically as functions of key environmental factors). The on-going steps to include physiological principles and interactions among marine species in the DBEM developed by Cheung et al. (2011) are similar to those outlined above for terrestrial organisms by Huntley et al. (2010).

2.0 Physiological-based, Biophysical Models (related to Task 2.2.2)

2.1 Utilizing Physiology to Advance Models

Incorporating physiology into models that provide spatial estimates of habitat characteristics can help one gain a mechanistic, cause-and-effect understanding behind observed changes in

productivity and distribution of organisms such as fishes (Pörtner and Peck, 2010). The benefits of using measurements of ecophysiology to shed light on how environmental change has affected species and their ecosystems (and to project future changes) is evidenced by the growth of the discipline termed conservation physiology (Seebacher and Franklin 2012). A practical example of how physiological measurements can inform policy is provided by Cooke et al. (2012) who describe applications relating to fisheries and gear interactions, disease and health and climate-driven warming in various Pacific salmon (*Oncorhynchus* spp) species in the Fraser River Basin as well as clam aquaculture in the Mediterranean (Melaku Canu *et al.*, 2011).

In terms of modelling the distribution and abundance of fishes and other living marine resources, Jørgensen et al. (2012) outlined how physiological knowledge could be infused at every level of model complexity (e.g., from global models of general patterns to models of individual within local habitats) to refine predictions. Those authors highlighted how metabolic (aerobic) scope (MS, a measure of the amount of oxygen potentially available to animals to fuel activities beyond those required for maintenance) provides a general framework for examining the potential effect of interacting stressors (e.g., reductions in ambient O₂ concentration due to eutrophication, warming temperatures due to climate variability or change, reductions in pH due to ocean acidification) on the fitness / performance of animals. Fry (1957& 1971) proposed using MS as a framework for examining interacting stressors many decades ago (Figure 4). Based upon new measurements made at the cellular, tissue and organismal level, MS has been re-introduced as a general framework (Pörtner and Knust, 2007, Pörtner and Peck, 2010; Pörtner, 2012).

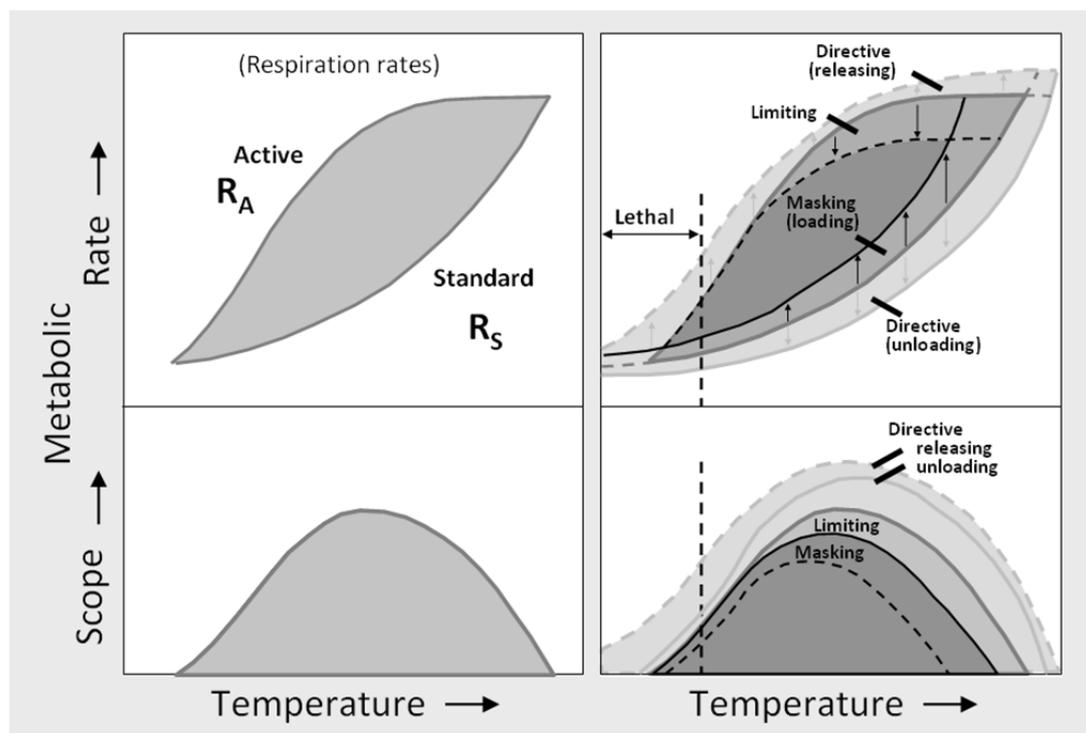


Figure 4 Changes in standard metabolic rate (R_S) and active metabolic rate (R_A) with temperature and the metabolic scope ($R_A - R_S$) versus temperature (Panels A&B). The right panels (C&D) indicate increases or decreases in metabolic rate and scope due to the interaction of other environmental factors superimposed on the controlling effect of temperature. The interacting factors can either reduce or expand the range of tolerable temperatures by either decreasing (loading) or increasing (unloading, releasing) metabolic scope (based on Fry, 1957).

The effect of interacting environmental factors on the MS of individuals is now being utilized (either directly or indirectly) in a variety of models projecting changes in the distribution and productivity of populations. For example, the DBEM approach uses MS-based principles to project the combined influence of warming and acidification on the future distribution of marine fishes (Cheung et al. 2011). Cucco et al. (2012) provide a thorough description of how aerobic scope can be measured and coupled to physical models to understand how temperature and ambient oxygen concentration interact to influence habitat suitability. Importantly, Cucco et al. (2012) demonstrate how seasonal migration patterns are coupled to physiological tolerance and to changes in habitat suitability, underscoring the need for models to capture not only long-term average characteristics but also short-term dynamics of the physical environment.

2.2 Biophysical models of plankton and fish early life stage

The coupling of physical and biological models for marine fish early life stages is considered a landmark achievement in terms of the tools available to generate and test hypotheses of the processes affecting early survival and growth (Werner et al., 2001). Physical (hydrodynamic) models with particle tracking subroutines are ideal tools to examine how changes in ocean circulation may influence the transport and distribution of organisms such as phyto-, zoo- and ichthyoplankton. With regard to ichthyoplankton, coupled hydrodynamic and individual-based models (IBMs) have become popular tools to investigate processes affecting the distribution and productivity of early life stages of a variety of marine fish species (Peck and Hufnagl, 2012). Biophysical early life stage IBMs have been constructed and applied for the larvae of a variety of European fish species within nearly all European regional seas (from the Mediterranean to the North and Baltic Seas). Examples of commercially important species examined using larval IBMs include four tuna species in the Mediterranean, European anchovy (*Engraulis encrasiocolis*) in the Bay of Biscay and Atlantic cod (*Gadus morhua*), sprat (*Spattus sprattus*) and Atlantic herring (*Clupea harengus*) in the North and/or Baltic Seas (see review by Peck and Hufnagl, 2012).

The structure and complexity of these biophysical models range from “simple” drift models including predator vulnerability and temperature-dependent larval growth functions to parameter-rich, physiological-based foraging and growth subroutines. The more complex models (which include mechanistic descriptions of feeding and growth bioenergetics) have been coupled to lower trophic level models (nutrient, phytoplankton, zooplankton, detritus – NPZD models) to represent how climate-driven changes in physical forcing can affect larval growth and survival both directly (via temperatures, and drift routes) and indirectly (by changes in the magnitude and timing of prey production) (Daewel et al., 2008 & 2011). Size-spectrum modelling (discussed in a later section) provides a relatively simple method of constructing prey fields from model-derived estimates of bulk zooplankton carbon. Suitable habitats are those having the correct mix of physical (hydrodynamic) and biological (prey and predator field) characteristics (Kühn et al., 2008; Daewel et al., 2011) (Figure 5).

Biophysical models of marine fish early life stages allow one to explore the processes affecting survival and dispersal. Since small changes in mortality rates of early life stages may cause large changes in marine fish recruitment, the tools may build predictive capacity of the factors affecting the year class success of commercially or ecologically important fishes. The intrinsic properties of marine fish larvae with respect to match-mismatch dynamics with prey (one of the key processes affecting early survival) and used to construct IBMs for early life stages was recently reviewed by Peck et al. (2012). Both simple (drift only) and more complex (drift, foraging and dynamic prey fields) models allow an examination of climate-driven changes in

the dispersal of passive (egg and larval) early life stages to key habitats, part of more complex, full life cycle approaches discussed in the next section.

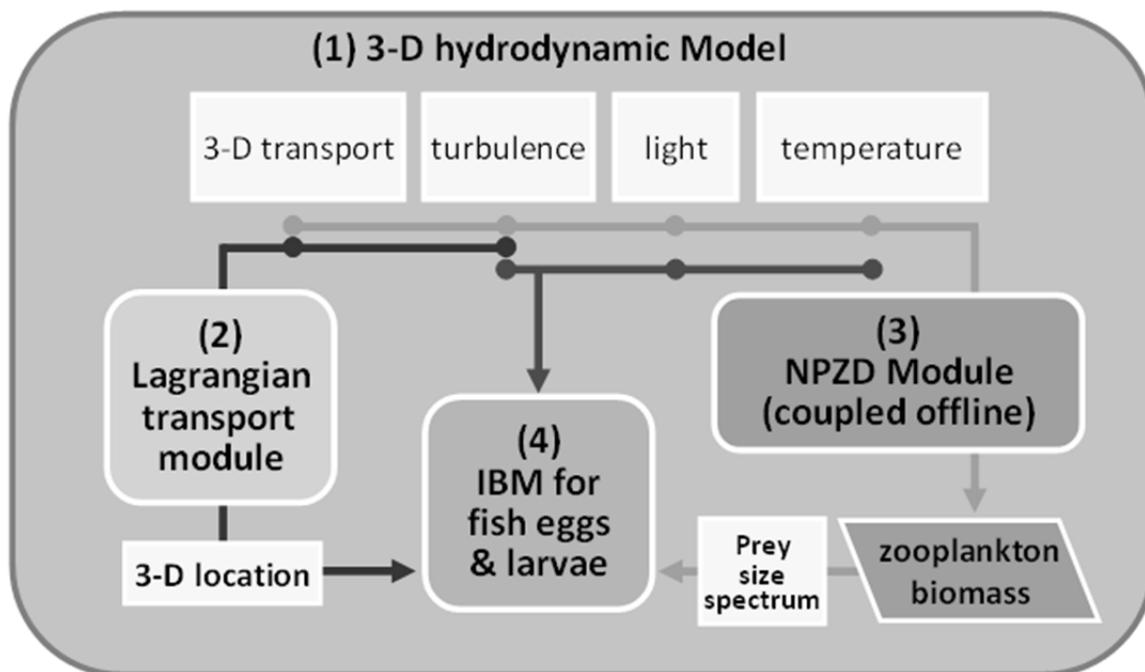


Figure 5 Coupled biophysical model for early life stages of marine fish. Various models include: 1) a physical (hydrodynamic) model core, 2) particle tracking model, 3) lower trophic level „ecosystem“ model (NPZD, etc.), and 4) an individual-based model for larval fish (foraging, physiology, etc.). A size-resolved prey field is derived from bulk zooplankton carbon using size spectrum theory. This scheme was adapted from Daewel *et al.* (2011).

2.3 Full-life cycle models

There is a recognition that, in many cases, predicting changes in the productivity and distribution of marine species will not be possible without taking into account processes acting on all life stages (Petitgas *et al.*, 2012). Areas used for spawning, larval and juvenile nurseries, and for feeding by larger juvenile and adult fish are often separate habitats and, due to differences in developmental morphology and physiology, different life stages are susceptible to different anthropogenic pressures to different degrees (Rijnsdorp *et al.*, 2009; Pörtner and Peck, 2010). A clear example is the different habitats required by temperate marine flatfish species, which include offshore banks (spawning), nearshore shallow waters (young juveniles) and offshore deeper waters (feeding areas) (Petitgas *et al.*, 2012). Rochette *et al.* (In Press) have developed a full-lifecycle model for sole (*Solea solea*) in the Eastern Channel which include different modules representing key processes acting in specific, spatially separated habitats including 1) a population model for adults, 2) a Lagrangian drift model for eggs and larvae settling to different near-shore nursery areas, and 3) a juvenile habitat suitability module (Figure 6). The model was built within the hierarchical Bayesian modelling framework, a valuable approach for embedding complex demographic models within statistical models for various (often noisy and incomplete) sources of data. The approach also appraises the uncertainty around estimates and predictions (Thomas *et al.*, 2005; Buckland *et al.*, 2007; Parent and Rivot, 2012).

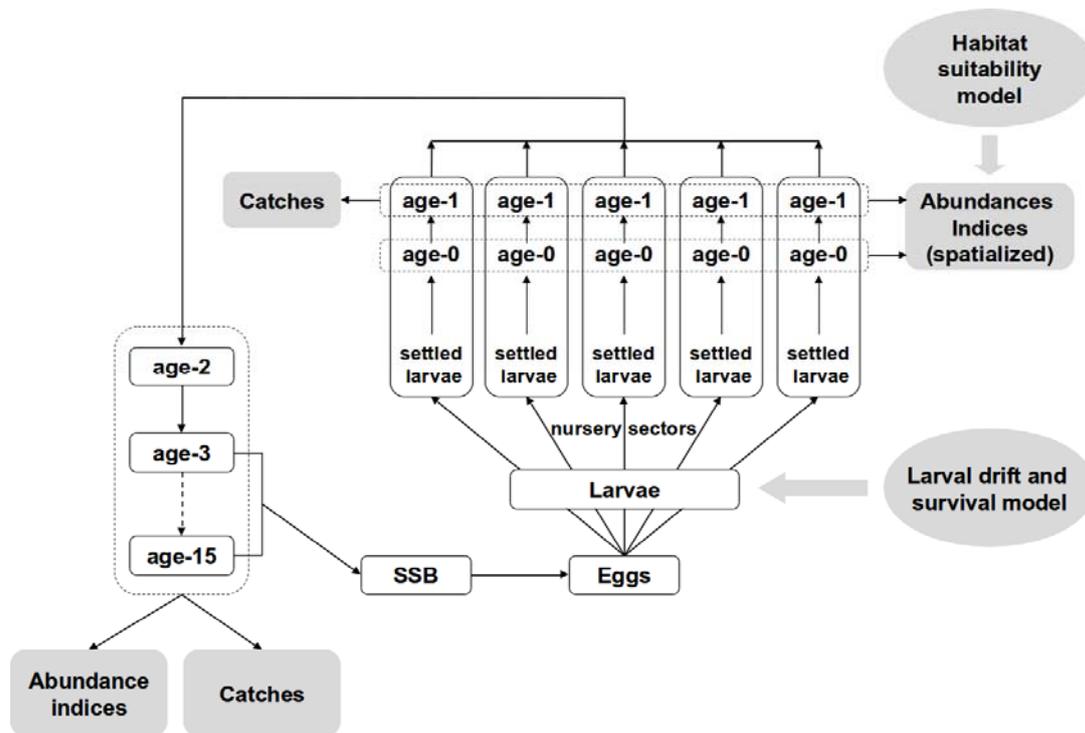


Figure 6. Scheme of a hierarchical, full life-cycle model used to examine flatfish species. White boxes represent a hidden population dynamic model whereas grey boxes represent processes and observations. The two ellipses with large arrows represent inputs from other models (see Rochette *et al.*, In Press)

The model framework described by Rochette *et al.* (In Press) allows various interacting pressures to be examined, including fisheries-induced changes in adult demographics, climate-driven variability in drift routes of pelagic larvae, and coastal habitat degradation due to aggregate extraction and dredging of juvenile nursery areas. It has the potential to provide tools applicable for predicting the effect of spatial management measures. This coupled model approach produced reliable, unbiased and precise estimates of time series of abundance at age (and in particular the total recruitment) and of fishing mortality at age with low bias and uncertainty. Simulations performed by Rochette *et al.* (In Press) were also able to estimate the different carrying capacities of coastal nursery grounds, despite missing data and misspecification of larval drift. Currently, the approach does not include explicit trophic interactions but the Bayesian framework easily enables one to include this information throughout the life cycle through estimates from correlations, expert knowledge, or other sources of data.

The advances in individual-based models of zooplankton populations provide additional examples of the importance of examining all life stages within model frameworks. Maar *et al.* (2012) coupled stage-structured models of two key, copepod congeners (*Calanus helgolandicus* and *C. finmarchicus*) within a 3D coupled hydrodynamic–biogeochemical model. The *Calanus* models were validated against Continuous Plankton Recorder (CPR) data as well as in situ data on vertical distributions north of the Dogger Bank. The validated model was used to investigate how the distribution of these zooplankton species responded to changes in sea water temperatures, overwintering, and oceanic inflow in the North Sea. It incorporates empirical relationships between mortality, growth and reproduction within five life stages (including diapause), and suggested that both changes in the strength of slope-shelf water exchange (hydrodynamics) and the general warming of the area have been causal agents to

the decreases in *C. finmarchicus* (a boreal species) and *C. helgolandicus* (a more Lusitanian species). In a warmer climate (2°C increase from 2005 levels), the peak abundance of both species was expected to occur about two weeks earlier.

2.4 Physiologically-based Life Cycle Models

More than three decades ago, balanced bioenergetics that include parameters for energy gain (from prey consumption and growth) and energy loss (metabolism and assimilation efficiency of food) and the effects of temperature and prey availability were linked to models of the physical environment and utilized to test habitat suitability for invertebrates such as clams (Solidoro *et al.*, 2000) and juvenile and adult fish (Hanson *et al.*, 1997; Durbin and Durbin, 1998; Rose *et al.*, 1999). Some models now include all life stages of species including dynamic coupling of fish to physical and biological characteristics of the environment such as migration patterns linked to temperature and/or prey availability (Megrey *et al.*, 2007). These coupled biophysical, physiological-based approaches allow resource managers to take advantage of the developing capacity of global climate models to project future, regional ocean conditions (Stock *et al.*, 2011). The continued development of physiological-based, full life cycle models will provide a greater capacity to examine the impacts of multiple stressors that may affect different parts of marine ecosystems to different extents.

In recent years there has been an upsurge in the parameterization and utilization of Dynamic Energy Budget (DEB) models (Kooijman, 2010). A DEB model is similar to a traditional bioenergetics model in that both approaches describe the effects of key intrinsic (body size, maturity) and extrinsic (temperature, food) factors on physiological processes (feeding, growth and reproduction) within an organism Nisbet *et al.* (2012) provide a thorough comparison of the “theory-driven” DEB and traditional, “data-driven” bioenergetics parameters. In contrast to standard bioenergetics budgets, a DEB model describes an organism by using three state variables: structural body volume (Structure, V , cm³), reserves (Reserve, E , Joules) and reproduction buffer (Maturity or Reproduction Buffer, R , Joules). The energy flow between the sources, sinks and state variables is described by various processes allowing the effects of environmental perturbation to be examined with respect to resource partitioning, such as the timing and magnitude of spawning (Figure 7).

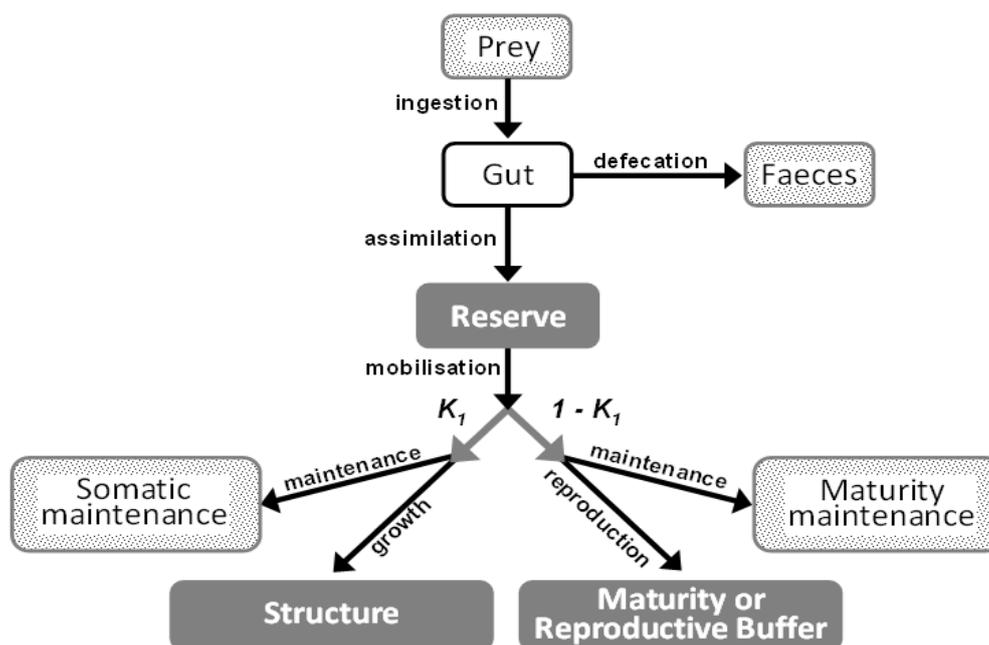


Figure 7 A schematic representation of the standard dynamic energy budget (DEB) model showing the paths of energy flow through an organism. Blue boxes represent sources or sinks of energy, red boxes indicate the three state variables describing the organism. Processes affecting energy flows are described by black arrows (see Teal *et al.*, 2012).

In European waters, DEB models have been parameterised for many different taxa including commercially important fishes such as plaice (*Pleuronectes platessa*) (van der Veer *et al.*, 2009) and sole (Freitas *et al.*, 2011). The models have been used to describe how environmental conditions (temperature and food conditions) impact on the physiological performance (growth and reproduction) of various life stages of these species. Differences in the quality of habitat (growth potential) under different climate scenarios can be projected. Used in this manner, a DEB model examines habitat quality for single species. Teal *et al.* (2012) utilized a DEB model linked (offline) to an ecosystem model providing spatially-explicit estimates of the availability of total benthic prey organisms (GETM-ERSEM-BFM (Stips *et al.*, 2004). (see http://www.nioz.nl/northsea_model). Coupling a DEB to ERSEM allowed Teal *et al.* (2012) to examine the effects of climate variability by comparing suitable habitats for both species across two years (1989 and 2002) with contrasting conditions. Predictions (modelled) and observed distributions matched well with the model capturing the well-known, ontogenetic shifts in depth distribution as well as the migration of juveniles of the population towards deeper waters (outside the protection of the “plaice box” closed area) associated with warming.

2.5 Strengths and weaknesses of physiological life cycle models

The main strengths of using DEB theory are that models and their parameters are generic and that models can be applied to the full life cycle of different species using species-specific parameters. The methodology for estimating DEB parameters from available data is rapidly advancing and recent publications (Lika *et al.*, 2011a&b) discuss methods that help ensure that parameters are developed in a consistent manner across species, allowing interspecific comparisons based purely on the parameters (Kooijman, 2009). A library of DEB parameters for various species of marine animals (from shellfish to roundfish) has been compiled and is

available online (Kooijman, 2009). The use of non-standardized parameters and different functional forms is a weakness of standard bioenergetics models. However, both approaches often suffer from “parameter stealing” due to a lack of physiological data on modelled species (such as feeding behaviour and rates of food uptake). Another weakness of the DEB approach is that the output is strongly driven by the thermal tolerance range of a species and size-dependent optimal temperature for growth which is often not known for species (Pörtner and Peck, 2010; Freitas et al., 2011). However, an upsurge in measurements of organismal-level physiology has occurred concomitant with research programs examining climate change and ocean acidification. The availability of these new data will aid in the development of physiological-based modelling approaches.

3.0 Models Simulating Ecosystem Dynamics

3.1 Food Web Models

Anthropogenic changes in marine habitats are known to influence predator-prey dynamics (Altiere, 2008), hence food-web models offer an important tool to assess potential changes in productivity or distribution resulting from such changes. Food web models designed for marine habitats originate from advancements made decades ago by Polivina (1984) that have led to the development of Ecopath with Ecosim (EwE) in 1995 and Ecospace in 1998 (Christensen and Walters, 2004). While Ecopath provides a static representation of a food web, Ecosim includes the temporal dynamics of abundance and trophic relationships of species within a food web while Ecospace extends this approach so that it is spatially-explicit. EwE has been widely used and applications include evaluations of the effectiveness of Marine Protected Areas (Libralato *et al.*, 2012). Coll and Libralato (2012) provided a review of applications of EwE in the Mediterranean Sea.

One of the latest incarnations of spatially-explicit food web modelling is OSMOSE (Object-oriented Simulator of Marine eCOsystems Exploitation) (Shin and Cury, 2001 & 2004). OSMOSE simulates the vital rates (growth, mortality, feeding and reproduction) of individual super particles (composed of many individuals) that can move across a spatial grid (Figure 8). It is a multi-species model explicitly representing trophodynamic interactions between 10 to 20 species (depending upon the ecosystem) and it also models the whole life cycle of fish from eggs and larvae up to juveniles and adults. Super-individuals represent schools of organisms of the same species having the same size and age. These schools interact through opportunistic, size-based predation regulated by the extent of spatio-temporal co-occurrence and size adequacy of predators and its prey. Using this approach, no a priori food web or diet matrix are utilized, but these facets emerge from local trophic interactions which makes this model suitable for addressing effects of global changes on marine ecosystems (Travers et al., 2009).

OSMOSE has been applied to simulate the influence of Marine Protected Areas (Yemane et al., 2009), fishing moratoriums (Marzloff et al., 2009), overexploitation (Shin et al., 2004, Travers et al., 2010), combined effects of climate change and overexploitation (Travers et al. in prep) on the productivity and distribution of fishes. Within European waters, OSMOSE has recently been parameterized to represent a 10-species food web within the eastern English Channel (corresponding to the ICES VIIId zone). The 10 species included in that application account for about 75% of the fish community biomass as sample during the CGFS survey. Within the eastern English Channel region, two-way coupling exists between OSMOSE and the lower trophic level model “MARS3D”. The latter NPZD-type model includes pico-nanoplankton, dinoflagellates, diatoms, microzooplankton and mesozooplankton. Benthic prey fields are derived from area surveys. Similar to the larval fish IBM example, coupling lower and upper trophic level models allows climate-driven dynamics (via changes in bottom-up forcing) to be

transferred up the food web. Biological interactions constitute the basis of OSMOSE, making this model suitable for investigating trophodynamic (predation and competition) relationships that can vary in strength in time and space and according to forcing factors such as fishing pressure. It is also one of the few food web-based models that can examine the impact of invasive species on the distribution and abundance of living marine resources (Plagányi, 2007).

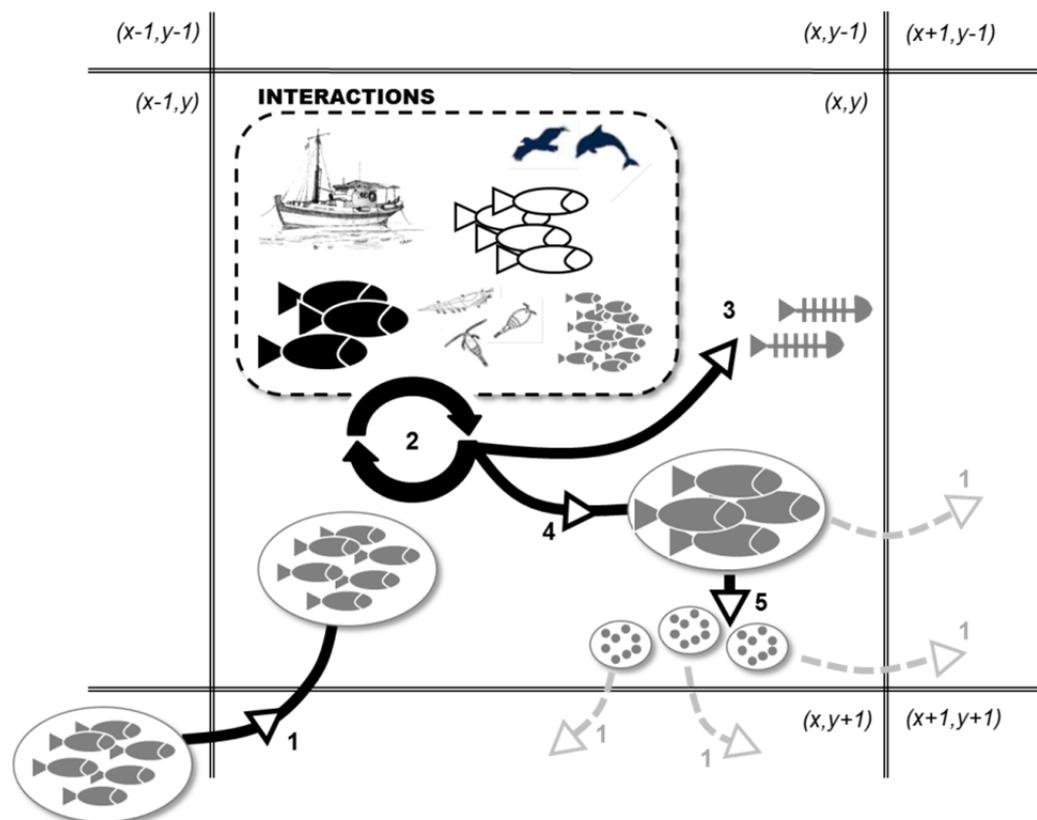


Figure 8 Diagram of spatial interactions with a grid box of the OSMOSE model. Processes occurring within each grid cell include: (1) movement (either random or data-driven), losses of individuals within super particles driven by (2) predation with is separated into three components: i), explicit predation mortality, ii) other natural mortality (including due to top predators), and iii) losses due to fishing activities, and (3) starvation, (4) growth, and (5) reproduction and recruitment (see Travers *et al.*, 2012).

A recent trend in modelling food web dynamics has been to eliminate species in favour of size spectra (numbers of organisms versus their size) observed within marine ecosystems. Simple size spectrum models can distribute the biomass of marine organisms across multiple sizes, based on empirically observed patterns (Sheldon *et al.*, 1972; Kerr and Dickie, 2001; Nogueira *et al.*, 2004) or theoretical predictions (Platt and Denman, 1977, Kerr and Dickie, 2001; Brown *et al.*, 2004). In an oligotrophic aquatic system in a steady state, for example, the biomass B of organisms with an individual biomass m tends to be proportional to m raised to a power s (the normalized biomass spectrum slope) of approximately -1.2 (Platt and Denman, 1977; Kerr and Dickie, 2001). This assumes a continuous range that can be integrated of m while in practice B is usually divided into discrete size bins, thus the need for normalization. More complex size spectrum models use a combination of empirical and mechanistic relationships to predict variability in s (e.g., Zhou *et al.*, 2010). A size spectrum model can be used alone or coupled to other, species-specific models. An example of the latter is a length-based partial ecosystem model developed by Speirs *et al.* (2010). That model was able to capture important temporal dynamics within food webs such as prey-to-predator loops – in that case the importance of

predation by a pelagic fish (herring) on early life stages of a top predator (Atlantic cod) (Speirs et al., 2010).

Size spectrum models have made an important, practical contribution to the advancement of models examining spatial dynamics of productivity and distribution of living marine resources. For instance, size-spectrum theory has been used to couple lower and upper trophic level models, an approach that 1) reduces model complexity while still capturing the dynamic responses of systems to pressures such as climate and/or fishing in cases where detailed information on specific species is not needed. For example, size spectrum theory was used by Daewel et al. (2008) to link a physiologically-based fish IBM to an NPZD model. In that study, bulk carbon estimates from the NPZD were converted to a size-resolved prey field needed for optimal foraging routines. In a second IBM application, estimates of the survival and growth of larvae was shown to be quite sensitive to assumptions made regarding the slope of the size spectrum (Hufnagl and Peck, 2010) suggesting the importance of appropriately modelling both spatial and temporal changes in the zooplankton spectrum. A simple model that predicts seasonal changes in the biomass and size spectrum of zooplankton (from inputs of chlorophyll concentration and water temperature) was developed by Zhou et al. (2010). At the whole ecosystem level, Blanchard et al. (2012) coupled a physical–biogeochemical model with a dynamic, size-based food web model to predict the future effects of climate change on fish biomass and production in 11 large regional shelf seas with and without fishing effects. In that study, changes in fish production closely mirrored changes in phytoplankton productivity, indicating the need to understand the dynamics of lower trophic levels.

3.2 Strengths and weaknesses of food web models

Understanding the strength of food web connections is fundamental to projecting the response of ecosystems to anthropogenic perturbations such as climate-driven changes in temperature regime or over-exploitation of living marine resources. Food web models are, therefore, an indispensable tool. However, these models require estimates of the extent of interactions between species including quantitative estimates of predator-prey relationships, which is a “data hungry” exercise. Evaluating the impacts of the introduction of novel species requires extensive knowledge on the diet and suitability of the species as prey prior to assessing potential impacts. Within Europe, many European regional sea food web models are parameterized based upon diet data that were collected more than two decades ago (Hislop et al., 1997; ICES, 2010). New diet data may be needed to make robust estimates of the impacts of novel predator-prey dynamics that may have developed in the interim (e.g., due to climate-driven shifts in species composition, abundance and distribution). The role of species that are not commercially important in the ecosystem is frequently unknown or only partly understood due to limited availability of broad-scale data on the abundance, distribution and diets of these ecosystem players (Garcia et al., 2003).

3.3 Incorporating Human Sectors and Pressures and Creating End—to-end Models

In the last decade, one of the most active areas of research has been to model the impacts of activities of various economic sectors on marine species, with particular emphasis on marine fisheries. One of the first models developed to assess spatially-explicit fisheries impacts in European waters was ISIS Fish (Mahévas and Pelletier, 2004). ISIS Fish providing a flexible multi-species, multi-fisheries deterministic modelling platform which includes three spatially explicit sub models of population dynamics, fisheries dynamics and management. It enables one to project scenarios on one or several of those compartments and has been used to compare different management measures such as different TACs or the implementation of MPAs on the mixed hake (*Merluccius merluccius*) – Norway lobster (*Nephrops norvegicus*)

fishery in the Bay of Biscay (Drouineau et al., 2006), the Bay of Biscay anchovy (*Engraulis encrasicolus*) fishery (Lehuta et al., 2010) or the New Zealand hoki (*Macruronus novaezelandiae*) (Marchal et al., 2009). However, ISIS Fish does not explicitly integrate ecological processes (physics and biology) of the modeled systems. This, more integrative approach, is taken by a more complex class of models known as “end-to-end”.

We use the term “end-to-end” to reflect models that attempt to represent all trophic levels (from phytoplankton to fish) and include human pressures (such as fisheries) affecting marine systems (Rose et al., 2010). One of the first models developed to assess spatially-explicit fisheries impacts in European waters was ISIS Fish ((Mahévas and Pelletier, 2004). ISIS-Fish model has been specifically developed to investigate the consequences of management measures with special emphasis on spatial measures (Pelletier and Mahévas 2005). It has already been applied to various European fisheries to assess the impact of Marine Protected areas (e.g. hake-nephrops fishery in the Bay of Biscay (Drouineau et al 2006), cod fishery in the Baltic Sea (Kraus et al 2009), or pelagic fishery in the Bay of Biscay (Lehuta et al 2010). The model uses a joint approach for the description of marine populations and exploitation spatially explicit dynamics on a regular 2D-grid. ISIS-Fish is a matrix model that accounts for mortality, growth, reproduction and migrations to update population numbers monthly, spatially and per population stage. It computes fishing mortality based on the dynamically allocated effort of the fishing fleets in the areas where populations and fishing overlap. A management dynamics sub-model enforces regulation constraints on exploitation monthly and spatially as well as fishermen reactions to those constraints. Pelletier et al. (2009) provide full details of the model and the software can be freely downloaded (<http://www.isisfish.org/download.html>). The ISIS-fish mode is currently being developed for the eastern Channel where it is expected to provide recommendations for the management of flatfishes taking into account habitat alterations due to the construction of windfarms and expansion of regions of aggregate extraction (Gasche et al., In Prep).

This class of whole system models (e.g. Atlantis, InVitro) dynamically couples oceanography, biogeochemistry, food web, habitat, fish population and human sector (e.g. fisheries, tourism, economics, coastal development etc.) models. While broad in scope, these models cover interacting processes and feedbacks of critical importance in marine and coastal systems. Their complexity does make them potentially unwieldy but they form a solid upper end to the model continuum considered in this brief review. In her review of 20 models designed for fisheries management questions, Plagányi (2007) discussed the ability of different models to address 14 different research questions. Most models (16 of 20) were only designed to examine a subset of the ecosystem in a very detailed way, some (8 of 20) could examine changes in physical characteristics, but very few could also examine the potential impacts of introduced species (4 models) and habitat modification (2 models). Atlantis was one of the few models suitable to explore the introduced species and habitat modification. Atlantis is already being used as a management advisory tool and has been applied in many regions to consider fisheries, conservation, and multiple use management of marine and coastal resources (Fulton et al., 2011; Morzari-Luna et al., 2012) including the exploration of potential impacts of climate change on natural resources and ecosystems (Fulton, 2011; Griffith et al., 2012; Kaplan et al., 2012). Within European waters, Atlantis models are being developed for the Channel, the North Sea, Baltic Sea and Straights of Sicily (VECTORS cite report). The spatial overlap between ATLANTIS models developed within the Channel and North Sea on the one hand and the Baltic and North Seas on the other, will allow a more complete coverage and links between regional seas. Primary stressors being examined in these developing tools will be the trade-offs among setting aside areas for conservation (e.g., Natura2000) while at the same time

expanding renewable energy platforms (windfarm development) and maintaining healthy, productive fisheries.

3.4 Strengths and Weaknesses of End-to-end Models

End-to-end models may include a great number of species, a high biological and functional variability and an increased number of potentially interacting components / features. A clear shortcoming is the large number of parameters and associated uncertainties that exist (Pikitch et al., 2004). For example, model estimates are sensitive to assumptions made on food web interactions such as the functional response of predators (Magnusson, 1995; Fulton et al., 2003). The data needed to allow one to choose between alternative parameter estimates are often lacking (FAO, 2008). In addition, the spatio-temporal scales at which processes occur may differ by many orders of magnitude, whereas complexity may be increased due to the direct and indirect effects of anthropogenic impacts (i.e. fisheries) (Travers et al., 2007). Assessing the validity of estimates derived from end-to-end models is crucial to convince stakeholders of the relevance of such complex models to support the decision-making process.

Testing the validity of models incorporating human sectors and pressures is an active area of research. For example, Marchal et al. (2011) have recently examined the relevance of the info-gap method to assess the robustness of diagnostics within ISIS Fish. For more complex, end-to-end models, two methods (perturbation analysis and the bounded parameterization) have been proposed for handling uncertainty and for assessing model sensitivity. The perturbation analysis includes the intentional perturbation (decrease, increase, or systematic change) of the different components of the ecosystem and the mapping of the flow of consequences to all other components (Fulton, 2010). The bounded parameterizations method considers the most pessimistic, middle and optimistic version for each of the major dimensions of the system (e.g. productivity and vulnerability, human impacts) (Fulton, 2010). Risk assessment for different management decisions can only be conducted by discussing the uncertainty in parameter values (estimation error), or model structure (process error).

The advancement of these more complex models is essential if one hopes to fully quantify and evaluate predictions of different ecosystem-based management strategies (Degnbol, 2002; FAO, 2008). Different end-to-end models have been developed for different reasons. For example, Atlantis offers a framework to assist in strategic management decisions (comparison of the 'relative' but not necessarily the 'absolute' changes in costs and trade-offs due to direct and indirect effects of different management actions). The right level of complexity needs to be found that is in line with the level of process understanding and data availability (Fulton et al., 2003). The end-to-end models may seem as an ideal tool to be used in ecosystem-based approaches, but their use in management related forecasts should be restricted until their performance can be adequately tested and their critical knowledge gaps are identified (Rose et al., 2010).

4.0 Discussion and Conclusions

Multiple pressures such as climate change, eutrophication and pollution, biological resource harvesting, habitat alteration, and introduced/alien species are causing state changes to marine ecosystems including altered productivities and distributions of living marine resources (Bax *et al.*, 2003, FAO 2007, Díaz and Rosenberg, 2008; Barange and Perry, 2009; Rabalais *et al.*, 2010). Furthermore, a variety of activities in shallow, coastal areas (e.g., dredging, aggregate extraction, windfarm construction) cause direct physical alteration of bottom habitats with deleterious short- and potentially long-term consequences for resident biota (Lindiboom *et al.*,

2011; Melaku Canu et al., 2011). These pressures acting on the marine environment, when combined with land-based pressures, are causing a loss of global biodiversity and biological natural capital at an unprecedented rate in earth's history (Barnosky *et al.* 2011) with similar trends observed in European waters (Fortibuoni *et al.*, 2011). It is paramount to develop tools that can project future changes and provide sufficient information to decision makers on how to best manage natural systems.

Our brief review has highlighted the current state-of-the art in tools that help one detect patterns and key associations, formulate hypotheses on processes, test those processes and advance predictive capacity of changes in the distribution and abundance of living marine resources. It is important to note that all modelling tools have strengths and weaknesses and that our separation of various approaches into different categories (statistical analyses, physiological-based biophysical models, full life cycle models, food-web models, and end-to-end models) was often an imperfect, oversimplification. Clearly some modelling examples that we discussed bridge the gap across categories (Figure 9).

There is a growing consensus that we need to create flexible tools that capture information on how various interacting pressures affect key species and their food web interactions. Process knowledge on how multiple factors interact to affect individuals, populations and food web dynamics is needed. At each level of biological organization, gaps in knowledge exist that need to be filled to improve our predictive capacity in models. These gaps in knowledge include:

- 1) Individual-level: For many species, there is a general lack of knowledge on how abiotic factors interact to control the vital rates (survival, growth, feeding, reproduction). This makes it difficult to parameterize models that can provide robust projections of the cumulative impacts caused by, for example, warming, reduced dissolve oxygen concentrations and decreased values of pH. A mechanistic, cause-and-effect understanding of how key abiotic factors interact to affect vital rates (including optimal and suboptimal limits defining the fundamental niche) is needed (Pörtner and Peck, 2010). Moreover, individuals pass through different life stages and each life stage may have a unique tolerance or sensitivity to environmental factors due to morphological, developmental and behavioural differences (Rijnsdorp et al., 2009; Petitgas et al., 2012). Finally, abiotic factors may interact with biotic factors in unexpected ways to change the potential for growth, survival and reproduction.
- 2) Population-level: Moving from projections of individual- to population-level responses to interacting stressors requires knowledge on additional, key processes. These processes include intrinsic differences such as the extent of phenotypic plasticity of key traits that may alter a population's ability to adapt to environmental change (Chown et al., 2007). Attempts to incorporate adaptive capacity within spatially-explicit marine system models are still in their infancy (Solidoro et al., 2009). It will also be important to account for extrinsic differences among populations; different populations often persist in unique environmental settings that may be impacted to greater or lesser degrees by physical and biological changes to habitats. Examples include differences in the strength of connectivity between suitable habitats for subsequent life stages (e.g., geographic features) or the presence or absence of predators and competitors. Thus, species-level responses to habitat change caused by multiple, interacting stressors will likely differ among populations.
- 3) Ecosystem-level: One of the most intractable challenges is projecting changes in ecosystem structure and function that result from perturbations to the abundance and

productivity of individual species, altered species composition (including novel species) and small- and large-scale changes in habitat characteristics. Ecosystem-level projections must account for changes in the strength of species interactions via bottom-up, top-down and intraguild processes. It is important to note that ecosystem-level effects will emerge from the aggregate response of individual species, many of which have a physiological-basis. In a recent example, Kempf et al. (2012) used habitat modelling to examine temporal changes in the distribution of 0-group cod and grey gurnard (*Eutriglia gurnardus*) at different spatial scales. Their results highlight how physiological-based differences in preferred habitat characteristics control the strength of food web coupling that may ultimately limit the productivity of a species. An important, on-going development which should produce more realistic dynamics within food web models is the two-way coupling between upper and lower trophic levels (Travers et al., 2007) offered in many end-to-end approaches.

In general, the predictive power of models attempting to explain the causes (and consequences of) changes in the distribution and productivity of species is seriously hampered by the following factors. First, analytical models cannot include all of an ecosystem's components and abiotic factors, our emphasis is normally on a few taxa or taxonomic / functional groups or resources and the remaining ecosystem components are either simply ignored or oversimplified. Second, a multitude of anthropogenic drivers interact to simultaneously cause state changes in environments and it is difficult to disentangle cause-and-effect relationships. Moreover, we are limited in our ability to conduct experiments at appropriate (large) scales and patterns observed and processes inferred from the result of small-scale experiments may differ from those at larger (field) scales. Finally, there needs to be recognition that, at every step (from observations, to conceptual and predictive models) that error and variability exists (Planque 2011) and that the validity of any model depends upon the criteria used to assess it (Allen et al., 2007). Several authors have promoted the use of specific metrics that reflect various aspects of model skill (correlation, efficiency, accuracy) and have provided more quantitative elements for model evaluation (Jolliff et al., 2009). Sensitivity analyses are also efficient, mathematical tools to assess the validity of the estimates obtained from complex models (Lehuta et al., 2010 & In Press; Peck and Hufnagl, 2012). More complex, end-to-end approaches include different techniques to examine model sensitivity (Fulton, 2010). Standardized reporting of model sensitivity, precision and accuracy is needed. For all models examined here, parallel efforts are needed to increase both the capacity of models (such as complex, end-to-end approaches) and the collection of data required to parameterize models (and that can be used to challenge their predictions).

It is clear from the present review that different models are able to capture different processes that may interact to cause changes in the distribution and productivity of living marine resources. A clear message from this review is that the different models need to be coupled to most effectively advance predictive capacity. An assemblage model approach has been recommended by various authors (Planque et al., 2011; Robinson et al., 2011; Kempf et al., 2012) that can combine the strength of different model types. For instance, biophysical IBMs of early life stages can be used to test whether historical changes in distribution can be reproduced by bottom-up, climate-driven processes such as changes in the advection and survival of fish eggs and larvae (e.g., Daewel et al., 2011; Peck and Hufnagl, 2012). Physiologically-based models can be used to determine the fundamental habitat (Sykes et al., 1996; Pearson and Dawson, 2003) as well as understand factors causing temporal (seasonal) movements among different habitats (Cucco et al., 2012). A comparison between fundamental and realized habitat may point towards the underlying causal processes relationships affecting

individual species. This process knowledge can help advance spatially-explicit food web models such as ECOSPACE and OSMOSE that can then be used to test how novel combinations of pressures (e.g., climate-driven changes in temperature and pH, eutrophication, fishing pressure, species introductions) may be translated to ecosystem-level impacts. Finally, spatially-explicit models incorporating one or more economic sectors such as ISIS Fish (Mahévas and Pelletier, 2004) or Atlantis (Fulton et al., 2011; Griffith et al., 2012) will then be able to use scenarios to estimate how various economic sectors (the drivers behind various pressures) will likely impact the system and the costs and trade-offs to various management options.

Based upon this review, potential links between the modelling approaches outlined in deliverable report 2.2.3 are being reviewed. The comparison of the outputs of those models will be attempted within the regional seas work package, particularly the North Sea (WP4.2), where a number of models have been advanced and utilized. This inter-model comparison and the potential for linking various models will be discussed in deliverable report 4.2.1 and 4.2.2 (Month 42).

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