Evaluating the suitability of coupled biophysical models for fishery management

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The potential role of coupled biophysical models in enhancing the conservation, management, and recovery of fish stocks is assessed, with emphasis on anchovy, cod, herring, and sprat in European waters. The assessment indicates that coupled biophysical models are currently capable of simulating transport patterns, along with temperature and prey fields within marine ecosystems; they therefore provide insight into the variability of early-life-stage dynamics and connectivity within stocks. Moreover, the influence of environmental variability on potential recruitment success may be discerned from model hindcasts. Based on case studies, biophysical modelling results are shown to be capable of shedding light on whether stock management frameworks need re-evaluation. Hence, key modelling products were identified that will contribute to the development of viable stock recovery plans and management strategies. The study also suggests that approaches combining observation, process knowledge, and numerical modelling could be a promising way forward in understanding and simulating the dynamics of marine fish populations.

Keywords: adaptive management strategies, applicability of biophysical models, collapsed fish stocks, early-life-stage survival, environmental variability.

Introduction

Greater biological realism is required in how fish stocks are assessed and managed (Morgan, 2008; Nash et al., 2008; Köster et al., 2009), particularly as the ecosystem approach to fisheries management becomes more widely adopted (Rice, 2009). However, accounting for more complexity could increase the uncertainty related to modelling and might not necessarily result in an improvement in management practice. Accounting for increased biological complexity could be detrimental if cause-and-effect relationships are not clearly described and/or understood (Basson, 1999; De Oliveira et al., 2006).

A potential pitfall of considering process information in fisheries management is that such information often complicates the understanding of relationships within marine ecosystems. However, coupled biophysical models that account for spatial and temporal dynamics provide insight into the basic physical and ecological processes within these systems and attempt to represent the spatio-temporal nature of such processes, without assuming that past system dynamics reflect future dynamics (Gallego et al., 2007). We evaluate and discuss whether coupled biophysical models can improve fisheries management significantly, concentrating on single-species management even though the models have other potential uses, including describing essential habitats, estimating connectivity and dispersion for closed areas, formulating metrics for estimating biodiversity, and investigating anthropogenic effects (North et al., 2008; Erftemeijer et al., 2009; Petitgas et al., 2010).

An attempt is also made to address how biophysical modelling can assist management efforts in rebuilding fish stocks, looking at how such models might help identify and understand bottom-up factors influencing the reproductive success (early-life-stage growth and survival) of marine fish, with emphasis on climate- and environment-driven changes in atmospheric and hydrographic forcing. The aim is not to provide an exhaustive summary of the worldwide use of coupled biophysical models in marine systems (for reviews, see Werner et al., 2001; Miller, 2007; North et al., 2009), but to focus on the development and application of individual-based models (IBMs) for selected fish stocks (anchovy, cod, herring, plaice, and sprat) in four European ecosystems (Bay of Biscay, North Sea, Barents Sea, and Baltic Sea). Specifically, we (i) evaluate the utility of biophysical IBMs for understanding the dynamics of early life stages of commercial fish, (ii) highlight how process knowledge gained on the selected fish stocks has been integrated into biophysical models, and (iii) comment on the fisheries management utility of IBMs, especially their potential role in developing recovery plans for overfished and depleted fish stocks.

Model approaches: from simple to complex

Because a population must perpetuate itself, one of the first steps in modelling stock dynamics is to understand the factors influencing recruitment (Allain *et al.*, 2007). Biophysical models allow an exploration of the effects of key abiotic and biotic factors on the growth and survival of early life stages by considering different interacting factors, including temperature, light, turbulence, current transport, and prey-field dynamics. They therefore provide a valuable means of disentangling various mechanisms affecting fisheries resources and their productivity by explicitly considering and incorporating processes acting at various spatio-temporal scales.

Many species use different locations for spawning, larval development, nurseries, and adult feeding. Connections between these different locations allow species to complete their life cycles. Patterns of connectivity (as influenced by variable hydrographic and atmospheric forcing conditions) influence the recruitment success of fish stocks via changes in retention or dispersion of larvae from spawning grounds to areas suitable (or unsuitable) for subsequent survival (Werner *et al.*, 1996; Heath and Gallego, 1997; Hinrichsen *et al.*, 2002; Bolle *et al.*, 2009).

Mesoscale transport processes have increasingly been studied using three-dimensional hydrodynamic models, and such well-validated models are now deemed essential in modelling early life history (Gallego *et al.*, 2007). However, the horizontal resolution of these models has to be fine enough to capture the appropriate horizontal mixing processes prevailing in the study area, e.g. smaller than the internal Rossby radius (Hinrichsen *et al.*, 2002), and wind-forced curl upwelling (Veneziani *et al.*, 2009). In addition, the vertical resolution must be fine enough to resolve the vertical profiles of currents and diffusivity, and the temporal resolution to resolve high-frequency processes such as tides (Huret *et al.*, 2007). Some recent models have used dispersion-kernel analysis to simulate the transport of passively drifting eggs and larvae and to provide statistically derived (quantifiable) results of these drift patterns (Edwards *et al.*, 2007; Peck *et al.*, 2009; Huret *et al.*, 2010).

Modelling efforts investigating the causes of mortality of fish larvae and juveniles have focused on the effects of advective and trophodynamic processes (Werner *et al.*, 1996; Hinrichsen *et al.*, 2002; Daewel *et al.*, 2008). Subcomponents of these models have been used to simulate the development of eggs and yolk-sac larvae in relation to key abiotic factors, as well as the drift, foraging, prey encounter, growth, and survival of feeding stages in specific time-steps. Model outputs have included (i) survival-dependent minimum rates of feeding and growth, (ii) days of starvation (when the quantity of food ingested does not cover metabolic costs), and (iii) the condition of larvae (weight) at specific lengths.

Within the four European systems investigated, biophysical modelling has become an essential component of integrated ocean-research efforts. The models have helped to identify the key mechanisms behind recruitment variability. These mechanisms are based on the observed explanatory abiotic and biotic variables in relation to retrospective deductions from the models about recruitment variation as the response variable. The utilization of these models for the development of recovery plans of depleted fish stocks is currently under discussion within different fisheries assessment working groups of ICES. The applicability of some model outputs is being tested, e.g. to assess the strength of the recruitment of Baltic sprat.

Case studies

Bay of Biscay

The anchovy (*Engraulis encrasicolus*) is a short-lived species with 1-year-olds typically representing 70–80% of the adult population within the Bay of Biscay. To derive a recruitment index for the stock, an IBM was developed of larval growth and survival, based on the analysis of daily rings in otoliths (Allain *et al.*, 2007). The growth model relates the daily increments in the otolith to environmental covariates, i.e. temperature and a stratification index. The IBM included mortality using a growth-dependent survival threshold, defined as the minimum growth rate at age observed among juvenile survivors. The IBM successfully predicted anchovy recruitment strength from 1997 to 1999 (Allain *et al.*, 2007), and it has recently been updated with new simulations covering a longer period (1998–2007). In the new configuration, eggs and larvae are transported in a 4-km-resolution hydrodynamic model accounting for larval behaviour and vertical mixing (Huret *et al.*, 2010), and growth is modelled as a function of age and temperature, following Allain *et al.* (2007). An annual index of potential survival was estimated, then evaluated in explaining the variability of annual indices of recruitment per unit of spawning-stock biomass (R/SSB; Figure 1). Although the relationship was positive, there are years when R/SSB proved to be poor, although potential survival was good, suggesting that other factors not yet included in the model, e.g. food limitation and spatially explicit predation, might occasionally have a marked effect on anchovy recruitment.

The modelling results also provide information on key habitats for spawning, as well as potential and realized early-life survival within the Bay of Biscay (Figure 2). Areas of high potential survival, i.e. those that contribute most to survival when spawning is assumed to be homogeneous in space (entire bay) and time (entire spawning season), were located over the mid-shelf, whereas potential survival proved relatively low in a narrow strip along the coast (Figure 2, left panels). Areas of realized survival (Figure 2, middle panels) were obtained by incorporating knowledge of the actual spawning areas by weighting potential survival according to the spatio-temporal evolution of spawning observed in the region. During the years simulated, realized survival was highest offshore of the Gironde estuary at 45.58°N, a key area
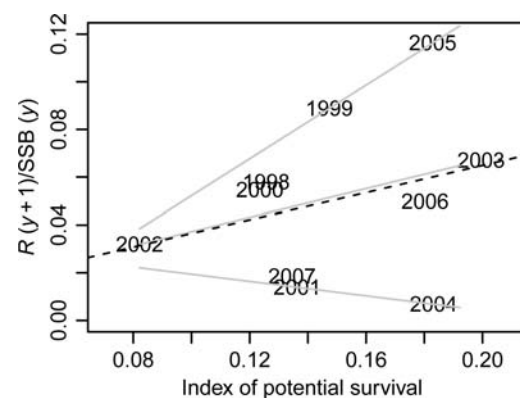

Figure 1. Bay of Biscay anchovy scatterplot of recruitment (R, number of individuals in year $y + 1$) per unit of SSB (in year y) vs. a calculated index of potential survival based on the output of an IBM constructed for anchovy larvae (dashed line, standard regression; solid lines, quantile regressions for $q = 0.1$, $q = 0.5$, and $q = 0.9$).
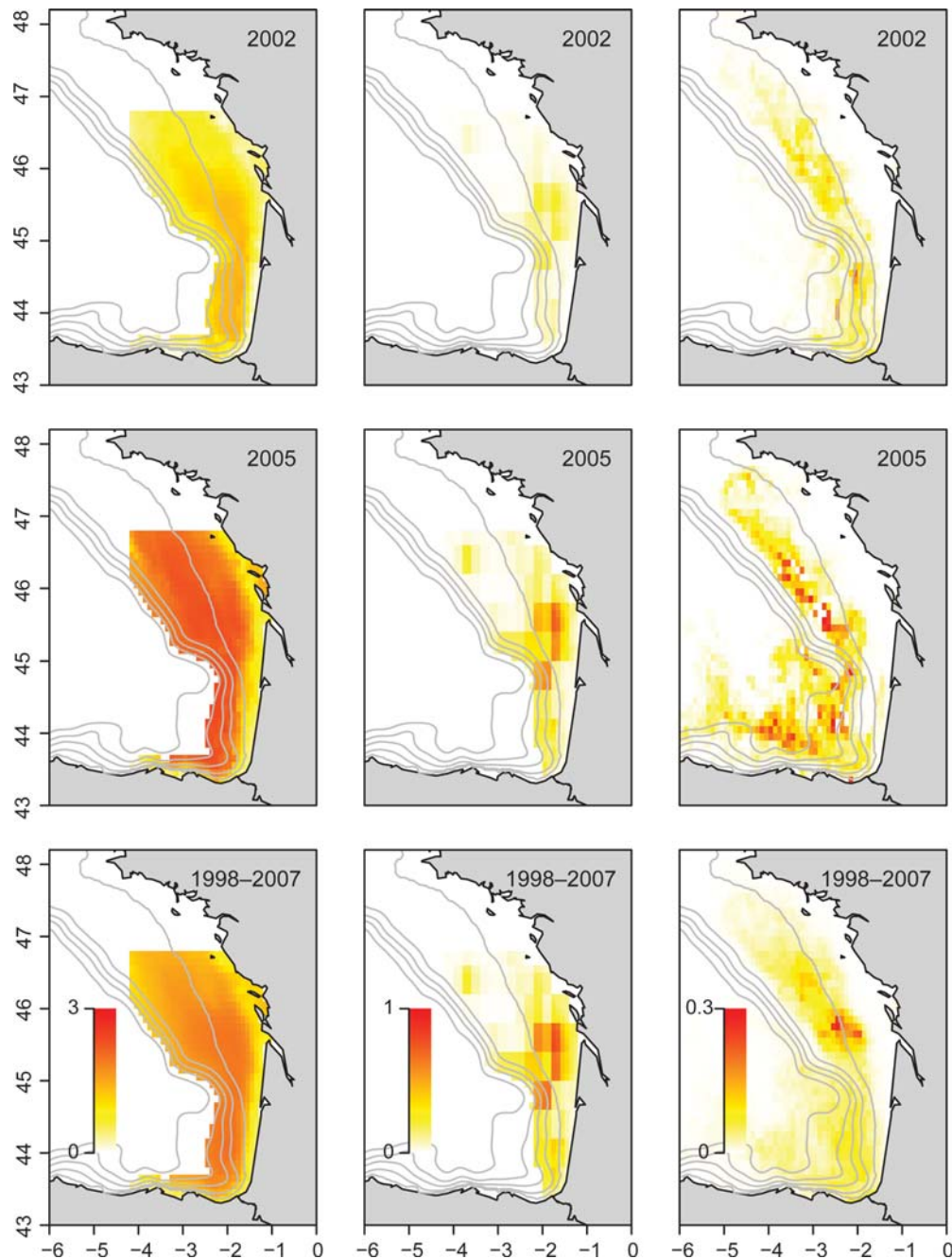
Figure 2. Bay of Biscay anchovy IBM estimates of the average distribution of potential survival (left, as a fraction of released particles per grid cell × 100), of realized survival from the entire spawning area (centre, as a fraction of total spawning × 104), and of survivors (right, as a fraction of released particles × 108) for 2002 (top), 2005 (centre), and as an average over the period 1998–2007 (bottom).

for both actual spawning and potential survival. Such map products could help define areas to protect because of their contribution to recruitment. The IBM also provides the location of survivors at a given age, indicating offshore aggregations of surviving juveniles in the south of the bay and also around the 100-m isobath at mid-latitudes (Figure 2, right panels). This product might be useful in identifying particular areas that need to be surveyed to find specific life stages, for instance to derive a recruitment index based on juvenile abundance. Variability in the spawning areas contributing to potential and realized larval

survival was closely related to interannual variability of temperature, whereas the distribution of juveniles depended on circulation patterns. The influence of population age structure on the distribution of spawners (Petitgas *et al.*, 2003) and survival of the resulting larvae could also be examined with the model. For management purposes, IBM mortality estimates at the late larval stage are currently being used as input to the spatially explicit population dynamics model ISIS-Fish. Use of those estimates significantly improved the performance of ISIS-Fish, in the sense that it became more robust in evaluating population responses to
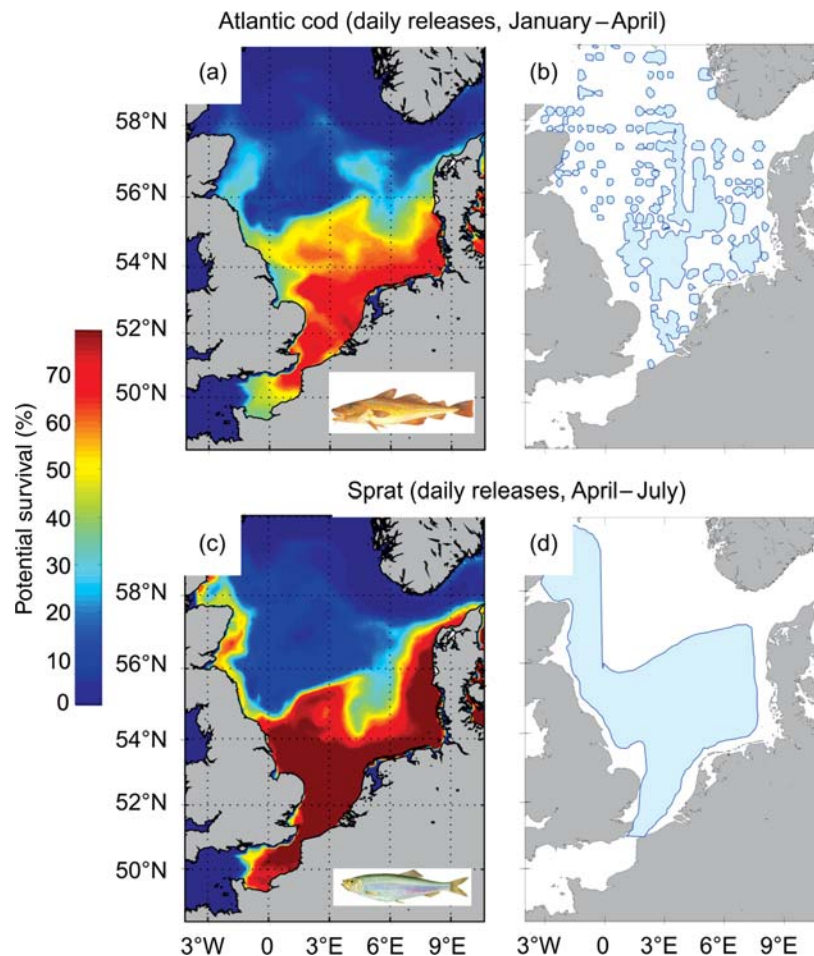
Figure 3. North Sea cod (a and b) and sprat (c and d; adapted from Daewel *et al.*, 2011) IBM–NPZD estimates of potential larval survival vs. spawning location. For each species, model estimates are illustrated for 1992 (a and c) and the modelled values compared with observed egg concentrations of cod (b; redrawn from ICES, 2005) and spawning locations of sprat (d; redrawn from Rogers *et al.*, 2001).

spatial management measures under different biological scenarios for stock recovery (Lehuta *et al.*, 2010).

North Sea

The North Sea is a challenging ecosystem for modellers, because of the large number of interacting species exhibiting different responses to climate and other drivers (Mackinson *et al.*, 2009; Petitgas *et al.*, 2009; Rijnsdorp *et al.*, 2009). Detailed, physiologically based models of feeding and growth have recently been developed to examine possible bottom-up controls on the survival of fish larvae (Peck and Daewel, 2007; Daewel *et al.*, 2008). Daewel *et al.* (2008, 2011) utilized coupled-model systems to identify spawning areas that potentially contributed to the survival of early life stages of sprat and cod. Their approach linked four models: (i) a core hydrodynamic model, (ii) a particle-tracking model, (iii) a physiologically based IBM for the foraging and growth of larvae, and (iv) a lower-trophic-level model involving nutrients, phytoplankton, zooplankton, and detritus (NPZD). Several relevant processes are embedded within the coupled models, including the direct effects of temperature and currents on the energy requirements and distribution of early life stages, and the indirect effects of climate-driven changes in physical forcing (stratification, nutrient dynamics) on prey fields of fish

larvae. In the model, eggs were released throughout the North Sea during the spawning periods of the two species (January–April for cod; May–July for sprat). The model sought to address the question of where adults had to spawn for their progeny to survive by generating spatially explicit maps of habitats delineating areas where early life stages had sufficient food (and experienced favourable levels of biotic factors, such as temperature, light, and turbulence) to survive and grow and those areas where larvae would starve as a result of there being inadequate prey. Predation pressure on early life stages was not included in these modelling efforts.

By running the coupled-model system for different months and years, the southern North Sea proved to be an important nursery habitat for both cod and sprat, because the frontal zones in the area promoted survival of the larvae (Figure 3a and c). For both species, the spawning grounds predicted by the IBM–NPZD as favourable for the survival of early larvae (Daewel *et al.*, 2011) were largely in accord with the observed positions of spawning grounds (Figure 3b and d; Fox *et al.*, 2008; Munk *et al.*, 2009). The potential survival of cod was greatest in relatively cold years, but the estimates for sprat did not differ markedly between cold and warm years (Daewel *et al.*, 2011). The mechanisms for increased survival of cod included increased prey concentration and favourable

transport/drift routes. The latter appear as important factors in a variety of IBMs created for other fish species in the North Sea, particularly those with specific habitat requirements for nursery grounds. For example, changes in meteorology influenced larval development and likely recruitment in the southern North Sea through mediation of transport and sea temperature (Dickey-Collas et al., 2009). The outputs from the biophysical model on larval herring suggest a coincidence between years with stronger retention (reduced transport) of larvae and year-class strength. Finally, targeted research on the connectivity between spawning sites and nearshore, shallow-water nursery areas for flatfish has been examined for plaice (Pleuronectes platessa) by Bolle et al. (2009). The timing and the relative magnitude of the ingress of modelled plaice larvae to nearshore nursery areas agreed with observations obtained from surveys of tidal flats (Figure 8 of Bolle et al., 2009). An important aspect of that and other studies examining transport and connectivity is the sensitivity of model results to differences in the behaviour of larvae (Pineda et al., 2007; North et al., 2009), highlighting future research needed to increase the confidence in IBM transport and connectivity estimates.

The current approaches applied to the North Sea provide information on likely changes in fish stock productivity and in the carrying capacity of the ecosystem, information that can be integrated directly into strategic evaluation of potential management plans and into determining appropriate target and reference points. By considering the dynamics of recruitment variability under current and future environmental scenarios, coupled biophysical models provide one of the missing links in our understanding of stock–recruit relationships, by elucidating the connectivity of life stages.

Barents Sea

The resources in the Barents Sea undergo short- and long-term variations. A large spawning stock is often not sufficient to ensure good recruitment, because natural mortality (particularly of the early stages) might be highly variable in both time and space. Consequently, it is challenging to provide reliable advice on management measures that will dampen year-on-year variations in total catches and maximize sustainable yields.

To develop an ecosystem model that can simulate these stock fluctuations, information is needed on (i) relevant parts of the physical environment, (ii) temporal and spatial distributions of prey and predators, and (iii) individual physiological and behavioural responses to abiotic and biotic factors. The model must then be validated against empirical observations (Kristiansen et al., 2007).

In building IBMs for the larvae of Northeast Arctic cod and Norwegian spring-spawning herring, the physical environment of the Barents Sea ecosystem has been characterized using an Regional Ocean Model System (ROMS) with an ice-module component (Budgell, 2005). The horizontal resolution is 4 × 4 km, and daily averages are calculated and archived. Vertical forcing is effected using six-hourly information on ocean–atmosphere heat exchange and windstress. This approach appears to capture the main physical features of the habitats of the larvae of both cod and herring (Vikebø et al., 2010). Downscaled IPCC (International Panel on Climate Change) scenarios are available for predicting future changes in the early life history of fish (Vikebø et al., 2007a; Melsom et al., 2009). Other IBM activities have focused on simulating growth-related processes (Fiksen and

MacKenzie, 2002; Folkvord, 2005; Kristiansen et al., 2007; Vikebø et al., 2010), changes in spawning distribution (Sundby and Nakken, 2008), and patterns of ichthyoplankton dispersal (Vikebø et al., 2005, 2007b; Opdal et al., 2008). In addition, an IBM of the copepod prey species Calanus finmarchicus (Huse, 2005) has been successfully coupled with an IBM for cod larvae (Kristiansen et al., 2009). However, predation processes are not yet fully understood, and if included, are only considered in a simplistic manner (Vikebø et al., 2007b).

In terms of herring, a time-series analysis of observation and biophysical modelling results suggest that early hatching dates result in better survival (Figure 4), although the initial temperatures experienced by larvae are lower than later in the season (Husebø et al., 2009; Vikebø et al., 2010). The better survival of early-hatched larvae might be caused partly by a smaller spatio-temporal overlap with potential predators, along the drift route from spawning areas to the nursery grounds. Northward displacement of the larvae after 2 months was generally more noticeable when hatching was early in the season, and this effect appears to be more important for survival of larvae than ambient temperature (Figure 4). The model also revealed that transport was faster at shallow depths than deeper. Identifying the temporal and spatial distributions of the prey and predators of cod and herring larvae is essential if the existing models are to be improved and recruitment predictions enhanced.

Baltic Sea

For Baltic sprat, survival during the late larva and early juvenile stages is crucial for recruitment success (Köster et al., 2005; Baumann et al., 2006). As an aid in predicting interannual recruitment variability, a proxy representing larval transport from deep spawning basins to the coast has been developed, based on detailed drift-model simulations (Hinrichsen et al., 2006). Together with SSB, the index explained 82% of the annual recruitment variability of sprat (Baumann et al., 2006), suggesting that poor recruitment is associated with a strong larval displacement towards the coast and that recruitment is better in years when larvae are retained mainly within the deep basins. Relationships among environmental factors, spawner biomass, and recruitment have been used to simulate how Baltic sprat react to exploitation intensity and the variability in atmospheric forcing. Hindcast simulations (Figure 5) could mimic real annual recruitment with a high degree of accuracy. However, before this approach is included in stock–recruitment models, the underlying biological processes need to be resolved better. Nevertheless, use of the drift proxy is promising for projecting sprat recruitment, because it requires few data, is easy to use, and can be validated quantitatively (Hannah, 2007).

For eastern Baltic cod, the spatial distribution of larvae and early juveniles was examined using a hydrodynamic model (Hinrichsen et al., 2009). The results revealed that successful settlement of the juveniles depended on wind-induced drift of the larvae (Figure 6). The characteristics of surviving juveniles have been investigated by otolith microstructure analysis and backtracking the drift via hydrodynamic modelling (Huwer, 2009). Back-calculated hatching locations of pelagic juvenile cod were characterized using various factors, including water depth, survival probability derived from an IBM (Hinrichsen et al., 2002), and the extent of a marine protected area (MPA) in the Bornholm Basin. Back-calculated hatching locations (Figure 7a) were generally distributed around the edge (60–80 m isobaths) of the Bornholm Basin spawning area, with only a modest percentage (18%) lying
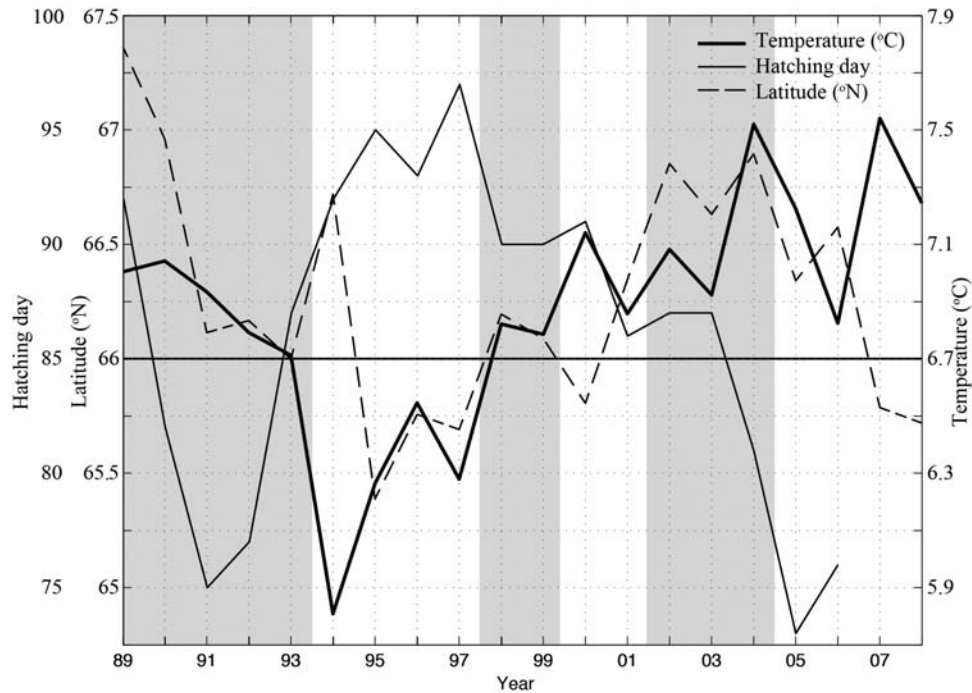
Figure 4. Norwegian spring-spawning herring: mean hatch day, simulated annual average latitude after 60 d of drift, and average ambient temperature encountered, 1989–2008. Years for which enhanced survival was observed are shaded (redrawn from Vikebø *et al.*, 2010).
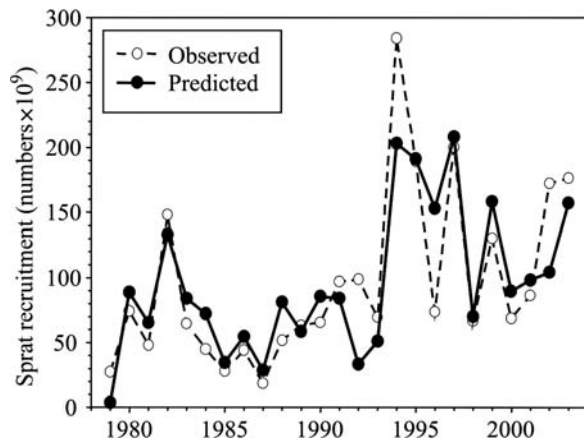

Figure 5. Baltic sprat time-series of observed and modelled recruitments based on hindcasting, 1979–2003.

within the deep portion of the Basin. Centres of the survivor origin were located north and east of Bornholm and at the southern edge of the Basin. Comparing the observed survivor origin in 2000 (Figure 7a) with the average survival probability of cod larvae obtained when the simulated abundance of *Pseudocalanus acuspes* was low (Figure 7b) is revealing in its agreement. High probabilities of simulated cod larva survival were associated with distinct centres of origin in the northwestern parts of the spawning ground, both north and east of Bornholm Island.

Huwer's (2009) back-calculation approach may be used to evaluate potential sites for MPAs to restore the Baltic cod stock. As illustrated in Figure 7a, only few juvenile survivors (26%) originate in the current MPA and fewer still (6%) in the central part,

which was protected by the MPA. Therefore, given current environmental conditions in the Baltic (characterized by stagnation and declining salinities), the current location of the Bornholm Basin MPA seems to have limited potential for enhancing the Baltic cod stock by protecting spawning aggregations. Biophysical modelling results suggest that spawning locations outside the MPA, particularly those in the northwestern Bornholm Basin, exhibit the greatest probability for enhanced survival of cod larvae and subsequent recruitment to the stock. Nonetheless, the influence of the MPA on factors such as egg production (Hinrichsen *et al.*, 2007) and fishing mortality of adults (Kraus *et al.*, 2009), as well as interactions with other conservation measures (e.g. seasonal closures), need to be considered.

Summary and conclusions

Coupled biophysical models have proved to have great potential for use in fisheries management. Their utility includes estimating the connectivity within stocks, the transport of larval and early juvenile stages, and spatio-temporal differences in potential survival. Although transport processes in marine ecosystems are usually assumed to be relevant over relatively large spatial scales (Reiss *et al.*, 2009), marine fish populations are often demographically structured at smaller spatial scales (Sinclair, 1988; Jones *et al.*, 2005; Cowen *et al.*, 2006). These types of model could improve simulations of within-population variability and ecosystem dynamics (Miller, 2007).

Coupled models have markedly advanced our understanding of the important biophysical processes regulating the productivity of fish stocks, by revealing the effects of temperature and prey fields on the transport of early life stages, survival, and the settlement probability of juvenile fish, and allowing the quantification of spatio-temporal scales of connectivity within fish stocks (Palumbi, 2001; Cowen *et al.*, 2003; Kell *et al.*, 2009). They
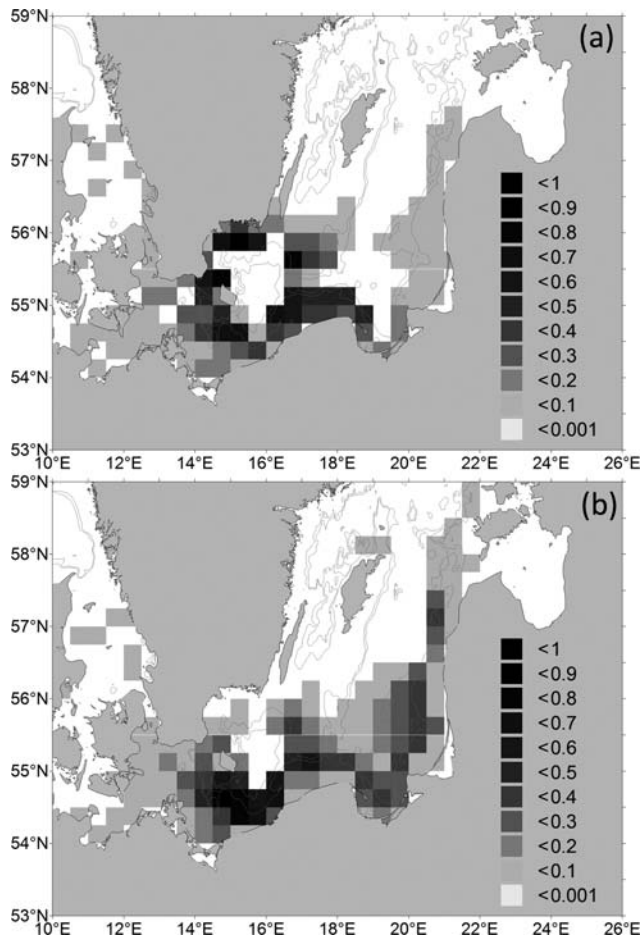
Figure 6. Baltic sprat wind-induced variability of potential nursery areas produced by Bornholm Basin spawners during periods having a (a) high or (b) low Baltic Sea Index (BSI: high during periods of high westerly winds, low during periods of high easterly winds).

could also help to validate some of the biological assumptions underlying general fisheries models or be used to evaluate the effectiveness of management measures such as closed areas. In some cases, the results can be incorporated in stock–recruitment relationships or provide information relevant to scenario- and hypothesis-testing (Miller, 2007).

Overall, biophysical modelling results can shed light on whether stock management frameworks need to be re-evaluated. As stock assessment and projection tools develop, it should become easier to include additional environmental and ecological information into models of population dynamics (Aarts and Poos, 2009) using Bayesian methods, statistical catch-at-age models (Kell et al., 2007), and other approaches. Existing tools for management strategy evaluation, such as ATLANTIS (Fulton et al., 2007), can already incorporate spatially explicit estimates of distributions of early life stages, as well as information on areas supporting their growth and survival.

An important utility of biophysical models is that, by incorporating high-resolution (temporal and spatial) sets of oceanographic data, they can be used to hindcast likely developments that have not been observed directly. These datasets, most of which are freely available, combined with existing empirical datasets (typically from surveys), allow detailed analyses of ecological and
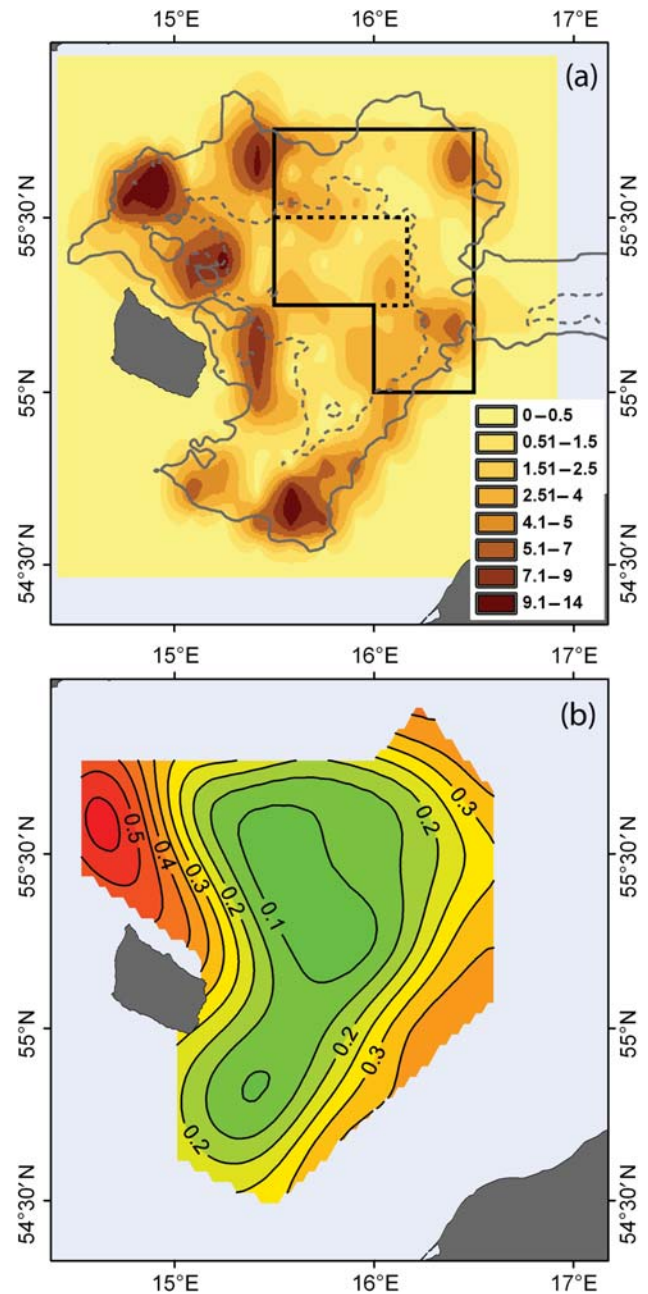

Figure 7. Baltic cod spawning activity and survival success of early life stages in the Bornholm Basin: (a) back-calculated hatching positions of pelagic juvenile survivors (colour scale) and location of the MPA (thick black line, current extent; thick dashed line, extent in 2000; thin grey line, 60 m isobath; thin dashed line, 80 m isobath); (b) average survival probability of larvae based on an IBM simulation utilizing low abundances of P. acuspes nauplii (redrawn after Hinrichsen et al., 2002).

environmental interactions and may be used to describe suitable habitats and probable distributions of cohorts (Röckmann et al., 2011). Few areas on the European continental shelf now lack physical oceanographic data at the scale or resolution relevant to their application in this type of modelling study.

In future, approaches that combine observation, process knowledge, and numerical modelling will be a promising way

forward in simulating the dynamics of marine fish populations and in increasing our understanding of their dynamics. Operationally, this can be pursued by coupling the early-life-stage transport patterns obtained from online hydrodynamic models to continuing (and perhaps real time) field-sampling programmes. Philosophically, the overarching challenge will be to work back from complex coupled ecosystem models to crafting relevant and easily understood management advice or to use a phrase of Elizabeth North (University of Maryland, MD, USA, pers. comm.): "turning the gigabytes of information from a coupled biophysical model into a simple spreadsheet table of options for managers". As such, the modelling results will have to be transparent for managers, scientists, stakeholders, and other users to ensure that the results are interpreted correctly and applied appropriately. The strongest approach will be an amalgam of information obtained from laboratory, field, and modelling studies (Gallego *et al.*, 2007).

Acknowledgements

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