

## Increasing biological realism of fisheries stock assessment: towards hierarchical Bayesian methods

Anna Kuparinen, Samu Mäntyniemi, Jeffrey A. Hutchings, and Sakari Kuikka

**Abstract:** Excessively high rates of fishing mortality have led to rapid declines of several commercially important fish stocks. To harvest fish stocks sustainably, fisheries management requires accurate information about population dynamics, but the generation of this information, known as fisheries stock assessment, traditionally relies on conservative and rather narrowly data-driven modelling approaches. To improve the information available for fisheries management, there is a demand to increase the biological realism of stock-assessment practices and to better incorporate the available biological knowledge and theory. Here, we explore the development of fisheries stock-assessment models with an aim to increasing their biological realism, and focus particular attention on the possibilities provided by the hierarchical Bayesian modelling framework and ways to develop this approach as a means of efficiently incorporating different sources of information to construct more biologically realistic stock-assessment models. The main message emerging from our review is that to be able to efficiently improve the biological realism of stock-assessment models, fisheries scientists must go beyond the traditional stock-assessment data and explore the resources available in other fields of biological research, such as ecology, life-history theory and evolutionary biology, in addition to utilizing data available from other stocks of the same or comparable species. The hierarchical Bayesian framework provides a way of formally integrating these sources of knowledge into the stock-assessment protocol and to accumulate information from multiple sources and over time.

*Key words:* Bayesian statistics, fisheries management, harvesting, life histories, overfishing, stock assessment.

**Résumé :** Des taux de mortalité excessifs de poissons ont conduit à des déclin rapides de plusieurs stocks de poissons commerciaux importants. Afin de récolter de façon durable les stocks de poissons, l'aménagement des pêcheries nécessite une information précise sur la dynamique des populations, mais la génération de cette information, connue sous le nom d'évaluation des stocks de poissons, repose traditionnellement sur la conservation plutôt qu'à des approches de modélisation conduites à partir de données précises. Afin d'améliorer l'information disponible pour l'aménagement des pêcheries, on observe une demande croissante pour l'améliorer du réalisme biologique des pratiques d'évaluation des stocks et pour mieux incorporer la connaissance et la théorie biologique disponibles. Les auteurs examinent le développement de modèles d'évaluation des stocks de poissons avec l'objectif d'augmenter leur réalisme biologique, et de porter une attention particulière sur les possibilités provenant du cadre de modélisation bayésien ainsi que les façons de développer cette approche comme moyen d'incorporer efficacement différentes sources d'information permettant de construire des modèles plus réalistes pour l'évaluation des stocks. Le principal message émergeant de cette revue est à l'effet que pour arriver à améliorer efficacement le réalisme des modèles d'évaluation des stocks, les spécialistes des pêcheries doivent aller au-delà des données traditionnelles d'évaluation des stocks et explorer les ressources disponibles dans d'autres champs de recherche biologique, comme l'écologie, la théorie du cycle vital et la biologie évolutive, en plus d'utiliser les données disponibles à partir d'autres stocks de la même ou d'espèces comparables. Le cadre bayésien hiérarchique fournit une façon d'intégrer formellement ces sources de connaissances dans le protocole d'évaluation des stocks et d'accumuler de l'information à partir d'autres sources avec le temps.

*Mots-clés :* statistiques bayésiennes, aménagement des pêcheries, récolte, cycle vital, surpêche.

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## Introduction

Numerous commercially exploited fish stocks have rapidly declined as a result of excessively high rates of fishing mortality (FAO 2010). The demographic consequences of overexploitation have been realised through the collapses of several major fish stocks, followed by variable and often unexpectedly slow rates of recovery (Pauly et al. 1998; Hutchings 2000; Hutchings and Reynolds 2004). While risks associated with overfishing could be avoided simply by reducing fishing pressure, there is also a practical need to supply food for the increasing human population, such that fisheries management must constantly balance various trade-offs associated with harvesting interests and the long-term sustainability of fisheries (Hilborn and Walters 1992; McAllister and Kirkwood 1998). To this end, accurate information is needed about the size and dynamics of harvested fish populations to estimate the level of fishing mortality that can sustain high yields in the long run. The generation of this information is known as fisheries stock assessment (Hilborn and Walters 1992).

The failure of fisheries management to prevent stock collapses has partly resulted from a lack of political will to limit fishing pressure (e.g., Froese and Proelß 2010) but also from an inability of stock assessment to consistently provide reliable information about fish population dynamics (Schnute and Richards 2001). The latter is partly due to the lack of biological realism of the stock-assessment models as well as relevant information from the assessed stocks and species. Indeed, the constant tug-of-war among fisheries stakeholders has, in many instances, lead to strongly data-driven stock assessment practices, for which even obvious biological features may not be accounted for unless 'proven' by data (e.g., Schnute and Richards 2001; Cotter et al. 2004). Given a need for a more comprehensive understanding of fish population dynamics, there is also a demand to increase the realism of stock-assessment models and to have them better incorporate the available biological knowledge (e.g., Schnute and Richards 2001; Hilborn 2003; Peterman 2004).

The purpose of this review article is to explore the development of fisheries stock assessment models with an aim to increase their biological realism. To this end, we begin by reviewing existing biological knowledge of the drivers of fish population viability, and then explore the biological assumptions implicit to stock-assessment models, including their development, to better reflect the biology of a fish population. We focus particular attention on the possibilities provided by the hierarchical Bayesian modelling framework and sketch ways to further develop this approach and to efficiently incorporate different sources of information to construct more biologically realistic stock-assessment models.

## Biological perspective to the viability of a fish population

The viability of a natural population depends ultimately on its intrinsic rate of growth. Even though estimation of this metric is not the objective of fisheries stock assessment, from the population biology perspective it provides a well-established summary through which drivers of population dynamics can be viewed. Population growth rate can be described by the net reproductive rate,  $R_0$ , the expected number of offspring an individual produces over its life span

(Roff 2002).  $R_0$  is estimated as a sum over the products of age-specific survival probability and fecundity (summed over all possible ages). In a stable population,  $R_0$  is 1, such that each individual is replaced by another, whereas in a growing population  $R_0$  is larger than 1 and in a declining population less than 1. However, comparability of  $R_0$  is restricted by the fact that it is provisional on the generation time. To overcome this shortcoming, in biological research the population growth rate is often defined by  $r$ , the intrinsic rate of natural increase per unit time, which can be approximated as  $r = \log(R_0)/G$ , where  $G$  is the generation time (i.e., the average age of reproductive adults in the population) (Gotelli 2008). When viewed in this framework, the dynamics and demography of a fish population is regulated by the processes and factors that affect  $r$  through its subcomponents age-specific survival and fecundity. Given that the literature on these processes pertaining to fish is vast, the aim here is to provide an overview of their most relevant correlates for fisheries stock assessment.

In fish, fecundity is known to be strongly regulated by female body size, age, and condition (e.g., Wootton 1998; Hutchings 2002; Green 2008; Marshall et al. 2008). Particularly old, experienced spawners have been shown to play a major role in a population's reproductive success in some species (Berkeley et al. 2004a; Birkeland and Dayton 2005; Venturelli et al. 2009, 2010). For example, in a meta-analysis of 25 marine species, Venturelli et al. (2009) showed that a population comprised of older, larger spawners has much higher growth rate than an equivalent population of younger, smaller fish, and that this discrepancy becomes even more pronounced at high reproductive life spans. Consequently, spawning stock biomass alone does not always provide a sufficient proxy of juvenile production; the age and size structure of the spawning population must be also accounted for. Conversely, preserving the reproductive ability of a population requires protection of the population age structure (Berkeley et al. 2004b).

Expected age-specific fecundity also depends on the probability of being mature at a given age, i.e., on the age-specific maturity ogives. Maturation on one hand increases current reproductive output but on the other hand affects future reproduction by reducing somatic growth and by increasing mortality through the survival cost of reproduction (Bell 1980; Hutchings 1993; Adams and Huntingford 1997; Bertschy and Fox 1999; Scarnecchia et al. 2007; Kuparinen et al. 2012a). The onset of maturation in fish is known to be partly genetically regulated (e.g., Mousseau and Roff 1987; Consuegra et al. 2005; Shimada et al. 2011) but also partly plastically modified by age-specific body size (e.g., Alm 1959; Reznick 1990), past growth (Morita and Fukuwaka 2006), temperature (Dhillon and Fox 2004; Gislason et al. 2010; Arendt 2011; Kuparinen et al. 2011), food (Uusi-Heikkilä et al. 2011), social interactions (Sohn 1977; Rodd et al. 1997), and habitat (Morita et al. 2009).

The survival of a fish to different ages in a harvested population depends on both natural and fishing mortality. Natural mortality is often linked to body size such that survival is enhanced among larger individuals both at the juvenile stage (Perez and Munch 2010) and later in life (Gislason et al. 2010). This can result, for example, from an enhanced ability to avoid predation and to achieve greater success during in-

traspecific competition. Juvenile and often also adult body size can be linked to the body size of the parents in some fish (e.g., Marshall et al. 2008; Thériault et al. 2007), such that the size structure of the spawning stock becomes again important in determining the survival of the next generation. As mentioned previously, the survival cost of reproduction (Bell 1980) is a relevant but, in fisheries science, frequently overlooked component of natural mortality. The relevance of the survival cost to fisheries science becomes apparent when one acknowledges that changes in maturation schedule will affect  $r$  and, thus, key variables of fisheries management, such as target values for spawning stock biomass and fishing mortality (Swain 2011; Jørgensen and Fiksen 2010; Hutchings and Rangeley 2011; Kuparinen et al. 2012a).

Fishing mortality is rarely evenly distributed among individuals but depends fundamentally on phenotypic traits such as body size, as described by gear-specific size- and age-selectivity curves (e.g., Millar and Fryer 1999; Kuparinen et al. 2009). Since fishing mortality is typically elevated among larger individuals, fishing is likely to target those age and size classes (older and larger) in a fish population that are most relevant for the renewal of the population (Venturelli et al. 2009). The often-considered ‘spawn-at-least-once strategy’ (Myers and Mertz 1998b) is generally not sufficient to overcome this if fishing mortality is high in older age classes, as the reproductive success of first-time spawners is typically very modest (e.g., Trippel 1998, 1999; Venturelli et al. 2010). As explicitly shown by Venturelli et al. (2009), fishing strategies most harmful to the population growth rate are those that severely truncate the age structure of a fish population towards younger age classes, thus forcing a bet-hedging, iteroparous species to spawn as if it was semelparous or nearly so.

Given that body size plays a fundamental role both in natural and fishing mortality, as well as fecundity, it is one of the key variables underlying population growth rate. Like ectotherms in general, fish growth is a highly plastic process showing great variability attributable to fluctuations in abiotic factors such as temperature and food (e.g., Atkinson and Sibly 1997; Berrigan and Charnov 1994). Changes in size-at-age trajectories are likely to alter maturity ogives and age and size at maturity (e.g., Kuparinen et al. 2008), age-specific fecundity (e.g., Marshall et al. 2008), and survival (Gislason et al. 2010) and, thereby, population growth rate (Hutchings 2011). Consequently, size-at-age trajectories should be routinely analyzed to track shifts in other relevant life-history processes and possible changes in population growth rate.

The previous brief overview of the major processes influencing population growth rate illustrates the great complexity associated with forecasting population viability and fluctuations in it resulting from changes in environmental conditions, species interactions, and population abundance, as well as fishing intensity and selectivity. However, perhaps the most important emerging message is that multiple factors simultaneously affecting population growth rate are tightly interlinked and, even more importantly, that any relevant trade-offs and interactions operate at the level of individual life histories (Roff 2002). For example, intensive fishing might reduce population density and reduce competition for food, leading to faster growth and earlier maturation, but this is ex-

pected to increase natural mortality (Bell 1980; Gislason et al. 2010) and decrease future fecundity because of declining growth rate and smaller final body size as a result of energy allocation to gonad development (e.g., Hutchings 2002, 2005). Based on life-history theory, there necessarily exists a trade-off between current and future reproductive success (integrating both survival and fecundity), such that life-history components that determine population growth rate can never be viewed independently of one another but as a combination constituting one life history (Gould and Lewontin 1979). In practice, this calls for a rigorous life-history approach when predicting how fish population dynamics are likely to respond to alternative fishing strategies and associated or parallel environmental changes. While stock-assessment models often estimate demographic parameters, such as maturity ogives or age-specific natural mortalities as free model parameters (see the following section), life-history theory can be used to identify most of the fundamental correlations between these features (Charnov 1993). Incorporating those into stock-assessment models has the potential to increase their realism and predictive ability, especially in cases where information is only available for a few relevant biological variables: accounting for the correlations can improve the precision of the predictions of the unknown variables (Gislason et al. 2010; Quesne and Jennings 2012).

Detailed life-history analyses may well be worthwhile to conduct for key species with particular economic, societal, and conservational relevance, such as Pacific (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) and Atlantic cod (*Gadus morhua*), but for many species this may be neither practical nor feasible. Instead, it may be very informative and applicable to identify major correlates of population growth rate ( $r$ ), which, in the absence of direct measurement of  $r$  itself, could be applied to identify populations likely to have very low  $r$  and, thus, low per-capita recruitment, high vulnerability to rapid declines, and slow recovery from intensive exploitation (Reynolds et al. 2005; Hutchings et al. 2012). Such an approach has been applied to study life-history correlates of marine fish harvested to low abundance, with the results clearly indicating that large-bodied, slow-growing, and late-maturing stocks have lower population growth rate and, thus, lower recovery potential at low abundances (Denney et al. 2002; Reynolds et al. 2005). These life-history types have also been found to be associated with low and strongly density-dependent recruitment, in contrast to small-bodied, early-maturing fish that tend to have high annual recruitment characterized by weak density dependence (Goodwin et al. 2006). It should be noted that several of the fisheries for small-bodied lower trophic-level fish have collapsed over the past years (Pinsky et al. 2011), underscoring that no life-history type can be considered resilient to fishing.

In a fisheries context, the evolution of life histories as responses to selective fishing has gained considerable attention recently. In principle, fishing selectively targeting large individuals can increase the relative reproductive success of small, early-maturing individuals and, depending on the extent to which these life-history types are heritable, can increase their relative abundance in a population (e.g., Heino and Godø 2002; Law 2007; Kuparinen and Merilä 2007). This, in turn, can cause long-term changes in maturity ogives, fecundity, and adult body size that can then feed

back to the demography of a fish population and alter recruitment and population growth rate (Hutchings 2005; Hutchings and Fraser 2008; Enberg et al. 2009; Kuparinen et al. 2012).

Notwithstanding discussions of 'Darwinian fisheries management' (Conover 2000; Jørgensen et al. 2007), possible shifts in life histories have generally not been accounted for when predicting future productivity of fish stocks. In principle, the evolution of fish life histories can have substantial influence on population growth: the slow recovery of North-west Atlantic cod (*Gadus morhua*), for example, has been hypothesized to be partly attributable to evolutionary shifts in fish life histories (Olsen et al. 2004; Swain et al. 2007; Hutchings and Rangeley 2011) that have reduced population growth rate through lower fecundity and elevated natural mortality (Hutchings and Reynolds 2004; Hutchings 2005; Swain 2011, but see Kuparinen and Hutchings 2012). Therefore, when it comes to practical fisheries management and stock assessment, evolutionary pressures associated with fishing strategies should be considered (Hutchings 2009) and stock size and productivity assessments should take into account the fact that vital population parameters can exhibit temporal trends. Such trends might be slowly reversible even if fishing is relaxed (e.g., Law and Grey 1989; Law 2007), thus having long-term impacts on the renewal and rebuilding capacity of a population (Hutchings 2005; Walsh et al. 2006). However, all else being equal, and because of their longer generation times, the time required for trait reversibility to occur will be longer for long-lived, late-maturing species.

### Current stock assessment practices

The primary purpose of fisheries stock assessment is to provide quantitative predictions about the reactions of fish populations to alternative management choices (Hilborn and Walters 1992; Schnute and Richards 2001; Hilborn 2003). This is independent of the goal of the management, which is usually a mixture of conservation and harvesting (Hilborn and Walters 1992; McAllister and Kirkwood 1998) and usually includes socio-economic elements (Symes 1997). To make predictions about the future state of a fish stock, information on current status, dynamics, and productivity should be available. These can be obtained by observing the previous behaviour of the stock in question, which can also be supplemented by knowledge of other stocks of the same or taxonomically related species (Hilborn and Liermann 1998). Information that is considered relevant for a particular population comes typically from two sources:

1. Basic biological knowledge about the species in question. This includes basic ecology and life-cycle of the species as well as plausible ranges of the population level demographic parameters.
2. Observations made about the population. Typical data comprise reported commercial catches, together with sampled length distributions and commonly also age and weight distributions. Similar measurements are often also collected by scientific survey fishing vessels. In the following, these two types of data (commercial and fisheries-independent survey catches and variables sampled from those) are jointly called 'stock-assessment data'.

While the latter source can be characterized as a set of 'facts' or observations, the former can be viewed as a set of

expectations about the population and its dynamics. These expectations can be formulated into mathematical models to describe the overall pattern of the population dynamics and the details of the dynamics are then given by the model parameters. These parameter values are typically estimated through a statistical fit of the model to stock-assessment data (Schnute and Richards 2001).

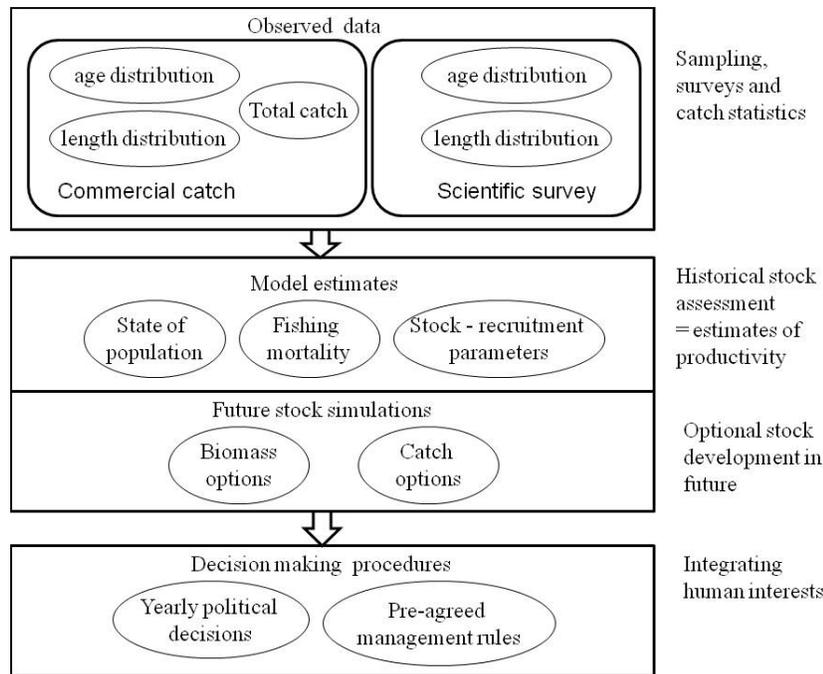
The steps of a typical stock assessment process are illustrated in Fig. 1. Catch sampling is used to approximate the age and length structures and body weights in the fisheries catches and to estimate growth of individuals. These are then utilized to estimate catch in numbers in different age groups, which comprise the input data for most age-structured stock assessment models (i.e., the model operates at the level of discrete age-classes) that estimate the size of the population through removals. Surveys can be utilized to provide biomass estimates of the stock size and they currently have high importance particularly in the estimation of stock size in the last year (so called 'terminal year'), which is a key estimate when predicting future harvesting options. Historical stock development provides estimates of stock productivity which, in turn, are applied to forecast future stock dynamics in response to alternative management options. Often, data from the most recent years have more weight in the estimation of current biomass than older data. In practice, most commonly the management options investigated are alternative sizes for the annual total allowable catch (TAC). TAC can either be directly estimated, based on a pre-agreed harvest-control rule, or the criteria for calculating TAC can vary from year to year.

### Biological assumptions of mainstream stock assessment models

In this section, we summarize the biological assumptions made in most mainstream stock assessment models. When appropriate, we also provide examples of stock assessments that go beyond the typical methods in terms of their biological plausibility. For clarity, theoretical modelling approaches, general methodology, and related software packages are not our primary focus here, although these are reflected in the following section, where we discuss steps that can be and already have been taken to improve the use of biological knowledge in fisheries stock assessments. Most of the stock assessments carried out around the Atlantic Ocean are based on principles of Virtual Population Analysis (VPA) introduced by Gulland (1965), but in other areas the variety of methods is larger (Butterworth and Rademeyer 2008; ICES 2010d; Hilborn 2012). Here, we consider the VPA approach as the primary mainstream method and concentrate on the biological assumptions used in this context (e.g., Punt 1997).

While the biological knowledge of fish population dynamics stresses the role of the size and age structure of the spawning population in reproduction (Lambert 2008; see also previous section), typical stock assessment models define the expected number of juveniles (recruits) as a function of mature female biomass (spawning-stock biomass) (Quinn and Deriso 1999). In practice, this stock-recruitment function usually takes the form of a Ricker model, Beverton-Holt model, segmented regression or a constant recruitment (Quinn and Deriso 1999; Patterson et al. 2001; Cotter et al. 2004). Even though these functions (except constant recruit-

**Fig. 1.** The use of information in typical stock-assessment practices. Data originating from commercial fisheries catches and survey fishing are fed into the population model to produce estimates of the stock size and the historical productivity of the stock. These estimates are then utilized to simulate future catches and population biomasses which, in turn, provide information about the consequences of alternative management options. The final harvesting decision is a compromise between conservation and commercial interests, thus balancing the long-term development of the population biomass with short-term fisheries catches.



ment) reflect to some degree a biological interpretation (e.g., Brännström and Sumpter 2005), the choice of the function is typically based on statistical goodness-of-fit measures in relation to estimates of the stock biomass and the corresponding recruitment. In rare cases, the biological background of the stock-recruitment relationship is implemented by defining the stock-recruitment function as a model for the density-dependent survival of eggs (e.g., Köster et al. 2003; Michielsens et al. 2008; Michielsens et al. 2006a). Similarly, biological features of the stock are rarely used as criteria for selecting the stock-recruitment function, i.e., the case-specific datasets are considered to be more informative in model selection than general biological knowledge. Typically the choice of stock-recruitment relationship does not affect the estimates of the past development of the population, but is often fundamental for the prediction of the future development under alternative management actions.

From the management point of view, the stock-recruitment relationship is considered to be the most stochastic, but also the most critical, link between the current and the future of a population and, thus, its renewal ability and persistence (e.g., Hilborn and Walters 1992). Nonetheless, it is commonplace to assume that the parameters of the stock-recruitment function are estimated but the uncertainty regarding the estimates is ignored and random variation is then produced for recruitment projections based on the estimated residual variation obtained from the statistical curve fitting (Patterson et al. 2001). However, in more advanced cases, prior information about the parameters of the stock-recruitment function is explicitly transported from other populations of the same or similar species (e.g., Su et al. 2004), and also uncertainty associated to the form of the function is taken into account

(e.g., Patterson 1999; Michielsens and McAllister 2004; Mäntyniemi et al. 2009).

Sensitivity analyses worldwide suggest that the estimated population size is most sensitive to information about natural mortality but, simultaneously, natural mortality is difficult to estimate from the data sets typically available (Cotter et al. 2004). Given both the sensitivity and estimation difficulties, it is counterintuitive that most stock assessments treat the natural mortality parameter as a known constant (Patterson et al. 2001; Cotter et al. 2004; Gislason et al. 2010). Natural mortality is commonly assumed to be independent of the age and (or) size of an individual and the population density, and it is also not assumed to reflect environmental variability (Schnute and Richards 2001). The rates of natural mortality typically arise from published estimates for similar populations. Variation in natural mortality owing to starvation or predation are not typically accounted for in routine stock assessment, although a few exceptions do exist (e.g., Vinther 2001; ICES 2010b) and in many cases it would be technically feasible (Köster et al. 2003). Some assessments that go beyond the routine methods incorporate the assumption that natural mortality decreases with the age of an individual (ICES 2008, 2010a, 2010b; Kolody et al. 2008; ISC 2008), and the most advanced studies account for uncertainty and temporal variability in natural mortality (ICES 2008). In rare cases, the uncertainty about the rate of natural mortality is also accounted for (e.g., ICES 2008; Kolody et al. 2008).

Compared to natural mortality, fishing mortality is typically modelled in much finer detail and is assumed to vary in time and space and across size and age groups (e.g., Patterson et al. 2001). While natural mortality is often assumed to be known without error, such an assumption about fishing

mortality is typically not made. However, it is commonplace to assume separable age and year effects in the fishing mortality so that they reflect the selectivity of the fishing process and temporal changes in overall fishing pressure (e.g., Pope and Shepherd 1982). Should any information about size-selectivity of fishing be available (obtained for example from gear-selectivity studies; Millar and Fryer 1999), this is typically accounted for indirectly, by converting this into age-selectivity by using the size-at-age data (e.g., Rahikainen et al. 2004). If fishing effort is known, standard models assume a linear relationship between instantaneous fishing mortality and fishing effort (Quinn and Deriso 1999).

Despite recent calls for size-based stock assessments (Pope et al. 2006; Beyer 1989; Froese et al. 2008), stock assessments to date typically do not explicitly model the growth trajectories of individual fish (Patterson et al. 2001). However, assumptions about growth are often made when preparing the data for stock assessments: typically only length distributions are directly sampled from the catches and the age distributions are constructed based on an assumed age-length relationship (Fridriksson 1934). This conversion is made because, in practice, most stock assessment models track changes in the age structure of a population rather than the size structure. Some of these age-based models also track the average size-at-age (e.g., Kolody et al. 2008; ICCAT 2010), but entirely size-based assessments remain rare. A notable exception is that assessments of aquatic invertebrates tend to use size-structured models (e.g., Breen et al. 2003). If the growth is explicitly modelled, then the growth parameters are not typically estimated annually from the stock assessment data but are fixed, based on external sources of information, such as separate growth data from the same or other population of the same species, scientific literature, or data from growth experiments (Patterson et al. 2001).

Maturity is typically assumed to depend on only the age of an individual, and the maturation schedule is assumed to be known exactly in most assessments (Patterson et al. 2001). However, the most advanced assessments do acknowledge uncertainties in the maturation process and also incorporate information about male maturity (Michielsens et al. 2008; Michielsens et al. 2006b; ICES 2008; Smith and Punt 1998). There also exist few exceptions, where maturity has been assumed to depend on body size or growth rate (Smith and Punt 1998; Brattey et al. 2004). The information about maturity typically originates from samples obtained from fisheries catches or from fisheries-independent sampling of the population.

While water temperature, salinity, and currents are considered important drivers of fish population dynamics (e.g. Köster et al. 2003), mainstream stock assessment models do not utilize data on environmental variables for model parameter estimation or for predictions (e.g. Walters and Collie 1988; Köster et al. 2003). In VPA-based assessments, one potential means of using information about the environment would be to base the estimate of natural mortality on the abundance of predators (e.g., Vinther 2001), but this is rarely implemented in practice (for an example of an exception, see ICES 2010b). Beyond the mainstream approaches, environmental conditions such as water temperature, upwelling and discharge are sometimes used to predict recruitment and movements of fish (e.g., ICES 2000; PSC 2010), as well as the efficiency of sur-

vey gears (e.g., Mäntyniemi and Romakkaniemi 2002; ICES 2008). Research papers discussing the potential use of environmental covariates are still common (e.g., Köster et al. 2003; Megrey et al. 2005; Kell et al. 2005b). The main message emerging from this research is that population dynamic parameters often vary with environmental variables, but the main challenge hindering their use in population predictions is the difficulty in predicting the future values of the environmental variables (e.g., Walters and Collie 1988).

### Gap between biological knowledge and its use in stock assessment

Based on discussions depicted in stock assessment working group reports (e.g., ICES 2010a, 2010c, 2010d; ICCAT 2010), it seems unlikely that scientists actively involved with stock assessment lack an appreciation for the fact that biological processes are more complex than the assumptions made in the stock-assessment models. Therefore, a reasonable and relevant question to ask is: Why is existing knowledge on fish biology and fish population dynamics not fully reflected in stock-assessment practices? In brief, we identify what we perceive to be three primary issues:

1. Philosophical reasons. It is a common view that all the free-model parameters must be estimable directly from the data observed and that the use of external sources of information reduces the objectivity of the stock assessment. Typical stock assessment data do not provide sufficient information about all the relevant biological processes underlying the dynamics of the population. Therefore, the stock-assessment model structure is simplified to facilitate the estimation of at least a few of the parameters. Even though the limitations of current practices are widely acknowledged, new less tested approaches are not easily accepted to replace well-established practices.
2. Computational difficulties. While analysts aim to include their knowledge into the stock-assessment models, practical problems arising from the computation time and the convergence of the parameter estimates often set practical limits to what can be done.
3. Lack of resources. Time and funding constraints often limit the possibilities to incorporate more biological realism into stock-assessment models and to gather together existing information and (or) to collect new data required for the use of such models.

The first reason has its roots in the traditional principles of statistical inference. To date, most of the applied statistical methods have their roots in the branch of statistics known as exploratory data analysis and information theory, where the objective is to describe the observed data with as simple a model as possible (e.g., Reza 1961; Tukey 1977, Burnham and Anderson 1998). Fisheries scientists have been strongly encouraged to aim at a simple, parsimonious model and to use information theoretic methods for model selection (e.g., Patterson et al. 2001; Schnute and Richards 2001; Cotter et al. 2004; ICES 2010d). In practice, this means that the models have far fewer unknown parameters than there are data points, such that the identification and estimation of model parameters can be based solely on the observed stock-assessment data. If the number of free model parameters was substantially increased, it would become difficult to estimate the parameters based on the data available. Consequently, in a

data-poor fishery, either simple models with few parameters are used or no quantitative stock assessment is performed at all. Generally, however, those parameters that are estimated by stock-assessment models will be estimated with high precision, as guaranteed by the use of information theoretic criteria.

If more data on the targeted population become available, this will facilitate the identification and estimation of a larger number of parameters than used previously (e.g., Schnute and Richards 2001; Patterson et al. 2001). As the data accumulate, the model assumptions slowly become more and more biologically realistic. This ideal is often expressed by stock-assessment scientists in their discussions: more data would have made it possible to fit a more realistic model but stock-assessment data available were not sufficient to estimate extra parameters (e.g., ISC 2008; Wyatt 2002; Patterson et al. 2001). An obvious side effect of the increasing biological realism of the stock-assessment models along with the accumulation of data is that the uncertainty associated with the population size estimates and the parameters describing population dynamics will remain the same or even increase over time, despite the increased amount of data available.

### **Towards biologically more realistic models**

The actions required to improve the use of biological knowledge in fisheries stock assessment and management depend on the reasons identified in the previous section. If the modelling philosophy constitutes the primary reason for resistance to change, then the entire modelling approach should be viewed critically and changed accordingly. However, certain aspects can be facilitated within the traditional point-estimation approach: biological knowledge could be better used in the development of the model structures and in the choices of those parameter values that need to be fixed to be identifiable. For example, the traditional assumption that natural mortality is constant over time and independent of the age and size of an individual can be replaced by a fixed function of relevant covariates, e.g., mortality can be described to decrease as a function of size. Following the same logic, the entire model can be built to reflect the dependence of the population dynamics on phenotypic traits, and the first step towards this would be to build an age- and size-structured model to account for age- and size-dependent reproductive rates. Biological knowledge could be used to fix those parameters having the most certain prior knowledge. One could then statistically estimate as many uncertain parameters as possible, using the available stock-assessment data. This would clearly improve the biological credibility of the stock assessment, but it nonetheless remains a far from optimal situation, particularly when it comes to the desire of explicitly accounting for uncertainty (e.g., Patterson et al. 2001; Mäntyniemi et al. 2009).

The fact that point-estimation-based assessment approaches are inevitably oversimplified in terms of their biological plausibility has already been widely recognised (e.g., Patterson et al. 2001; Schnute and Richards 2001), but they remain to be used in practical stock assessments, mainly because they are easy to use (e.g., Hilborn 2003). To better deal with the uncertainty involved in stock assessment and management decisions, an approach called management strategy evaluation

(MSE; e.g., Punt and Smith 1999; Kell et al. 2005a, 2006) has become a recommended practice (ICES 2010d). The MSE procedure includes an operational model that is applied to simulate the real behaviour of a fish stock and fishery. Sampling models are then coupled with the operational model to describe how the assessment data become generated. The fishery system is repeatedly simulated and new hypothetical assessment datasets are generated. These datasets are then analysed using a simplified stock-assessment model, and the management advice is generated based on each dataset separately. The consequences of each management advice are then simulated using the operational model. This procedure facilitates the evaluation that the management procedure works in a satisfactory manner together with the applied stock-assessment approach. As a result, the management procedure can be adjusted to tolerate the biases arising from the simplified stock-assessment model, as well as to incorporate variation of point estimates arising from the sampling of the stock-assessment data. In the MSE framework, the detailed biological knowledge is built into the operational model and, in principle, no limits are set to the degree of complexity of the model's features and the interactions that the model can incorporate. The MSE framework has already been applied to several fish stocks worldwide (e.g., Butterworth and Punt 1999; Kell et al. 2006), as well as by the International Whaling Commission (e.g., Kirkwood 1997; Punt and Donovan 2007). However, the MSE approach has also been criticized because of the numerous assumptions included, and because of the difficulties involved in the interpretation of simulation results (Rochet and Rice 2009; Butterworth et al. 2010; Kraak et al. 2010).

The Bayesian approach to statistical inference has become increasingly popular in fisheries stock assessments over the past decades (e.g., Punt and Hilborn 1997; McAllister and Kirkwood 1998; Meyer and Millar 1999; Hilborn 2003). The rationale of the Bayesian approach is to encode the existing knowledge about the population dynamics into a probabilistic form, that is, into prior distributions of the model parameters and, by fitting the model to stock-assessment data, to update these distributions into posterior distributions that describe the new state of knowledge. The prior distribution assigns a probability for each combination of parameter values, where the probability is understood as a degree of belief on the hypothesis that the particular combination would be the true combination of the parameters (e.g., Jaynes 2003). These probabilities are then revised in the light of data by multiplying them by the likelihood values implied by assumed model structure and observed data. The revised probability distribution then describes what is known about the parameter combinations after observing the dataset. In principle, the procedure is repeated each time new data become available, using former posterior distributions as new priors (e.g., Jeffreys 1961; Jaynes 2003). Forecasts of the future of a population under alternative management actions integrate the uncertainty about model structures and parameters as well as inherent stochasticity of the population dynamics (e.g., Patterson 1999; Mäntyniemi et al. 2009).

In contrast to the traditional point estimation, where model parameters and structures either have to be fixed or fully unknown, Bayesian stock assessment methods can incorporate any existing relevant biological knowledge as long as it can

be represented by alternative model formulations and prior distributions of the model parameters (e.g., Mäntyniemi et al. 2009; Rivot et al. 2001; Martell et al. 2008). Additionally, limitations on the amount of available data do not pose technical restrictions to the biological plausibility of the stock-assessment model. Uncertainty associated with the choice between alternative models is handled via model averaging, using probabilities of alternative hypotheses (models) as weights. These probabilities can arise from prior knowledge about the plausibility of competing biological models (Berger and Jefferys 1992; Hoeting et al. 1999; Brandon and Wade 2006). Thus, in the Bayesian framework the biological assumptions built into the alternative model structures and their weights, as well as into prior distributions of the model parameters, can be seen as the start point for stock assessment, while the stock-assessment data comprise an additional source of information used to localize the general knowledge into a specific population.

The benefits associated with the incorporation of any available knowledge into informative priors are most pronounced in data-poor fisheries (e.g., Conn et al. 2010). In an extreme case, there may be no direct observations from the population to be assessed, but prior knowledge can still be obtained from other stocks of the same or similar species, scientific literature, experimental research and biological theory (e.g., Myers et al. 2002; Uusitalo et al. 2005; Mäntyniemi et al. 2009). As direct observations from the assessed stock become available, the information provided by the model gradually accumulates and uncertainty decreases.

One example of the gains of using prior knowledge from other stocks of the same species is illustrated in Fig. 2. This example shows the estimation process of the slope parameters of the stock-recruitment curves for six herring (*Clupea harengus*) stocks in the Baltic Sea and in the Atlantic Ocean. The modelling is conducted both using a hierarchical meta-analysis model that accounts for the estimates of the other stocks, and a non-hierarchical model that estimates the parameter for each stock independently. In the case of the hierarchical model, the uncertainty about the parameter estimate decreases faster and for most of the stocks the parameter estimates also converge towards the final ones faster. Moreover, the year-to-year variations are smaller, which, in practice, implies greater stability in the annual production of TAC advice.

Owing to the obvious benefits associated with the Bayesian approach, one might expect to see a wide range of biologically realistic Bayesian stock assessment models in use, but in practice this is not the case. Following the information theory argument, simple 'identifiable' models are also often strongly preferred over more complex ones in the Bayesian framework (e.g., Wyatt 2002, 2003; Hobbs and Hilborn 2006; Kinas and Andrade 2007), such that the full utility of the Bayesian approach has remained unemployed and problems associated with model choice are similar to those described in the context of traditional point-estimation. This is partly understandable, as simple models face far fewer computational problems than biologically more realistic but complex models. These models involve numerical integration over a highly dimensional parameter space, which requires considerable computing power, modelling skills, and time. Not surprisingly, the lack of scientists with suitable skills has

been considered the major obstacle for the use of assessment models that, in theory, would be preferred over the simplified ones (e.g., Hilborn 2003; ICES 2010*d*).

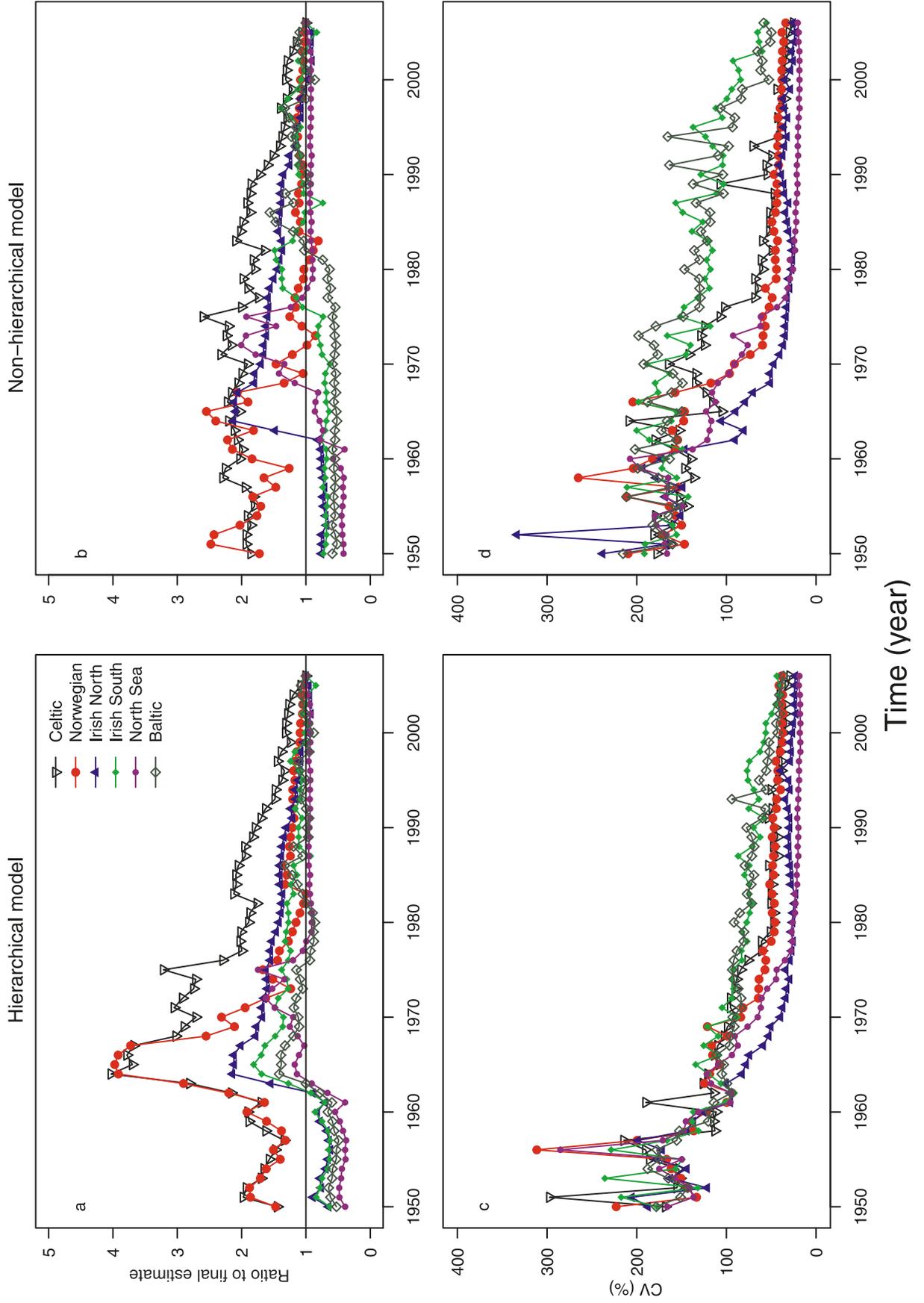
### Ideas for future model development

In this section, we outline possible ways to account for the biological processes identified in the second section above in fisheries stock assessment. Following the view that the Bayesian approach represents both the state-of-art and the future of the fisheries stock assessment (e.g., Hilborn 2003; Peterman 2004), we formulate the ideas in the Bayesian state-space modelling framework (Millar and Meyer 2000*a*, 2000*b*; Buckland et al. 2007; Rivot et al. 2008). However, the same suggested ideas can also be formulated, for example, into the operational model in the MSE framework, as well as into a few existing flexible modelling frameworks that are capable of either partial or full Bayesian estimation (e.g., Quinn and Deriso 1999; Hampton and Fournier 2001; Methot 1990; Bull et al. 2002). However, it should be noted that the latter are not able to represent full state-space formulation of the population dynamics, that is, the population dynamics equations are deterministic.

Growth and body size are fundamental variables affecting stock productivity and, therefore, the stock assessment model should be able to account for these variables explicitly. This can be done (1) by structuring the model by body size or (2) by structuring the model by age and then modelling the average growth along cohorts (e.g., ICCAT 2010; Bull et al. 2002; Hampton and Fournier 2001). However, if a model contains size-structure only, it is difficult to utilize observations about the age distribution (e.g., Bull et al. 2002), and both the previously mentioned alternatives make it difficult to model variation in growth within a population, which is necessarily present in any fish population and is expected to affect predictions of the stock dynamics (e.g., Punt and Smith 1999). Alternatively, growth trajectories could be modelled by structuring the population by age and growth parameters, which then together enable calculation of length-at-age. This type of modelling option already exists in the software packages CASAL (Bull et al. 2002) and SS3 (Methot 1990, 2010).

Both fishing and natural mortality depend on phenotypic traits of a fish, most importantly the body size. Therefore, the rates of natural and fishing mortality should be modelled as functions of phenotypic traits relevant for the species and the gear in question, and the first step towards this objective is to properly account for the role of body size in mortality. While in the context of fishing mortality the selectivity curves are commonly formulated as a function of body size (Millar and Fryer 1999; Kuparinen et al. 2009), for natural mortality such relationships have only very recently been developed (Gislason et al. 2010). Size-dependent mortality rates coupled with an age- and growth-parameter-structured model (as sketched previously in the text) would realistically account for the fact that survival up to reproduction depends on the growth trajectory of the individual. Having knowledge about the biological processes that influence the natural mortality will help both the estimation of the past natural mortality (and therefore abundance) and prediction of the natural mortality in the future. Since mortality depends on body size, coupling natural mortality and growth is expected to

**Fig. 2.** *Clupea harengus*. The accumulation of information about the parameters of the stock-recruitment function for six herring stocks, using hierarchical and non-hierarchical models. Both models use all the data available, but the hierarchical model enables sharing of information among stocks while the non-hierarchical model analyses each stock separately. Uncertainty about the parameter estimates is described through the deviation from the final estimate (in percentage) and through the coefficient of variation (CV). For most stocks, the hierarchical models (on the left) converge more rapidly towards the final parameter estimate and the uncertainty about the estimate (CV) decreases more rapidly than in the non-hierarchical model (on the right). The figure is redrawn from the same estimates as used in Hillary et al. (2012).



give more plausible basis for forecasting than just having good estimates of annual age-specific estimates of mortality in the past. Similarly, maturity and fecundity also depend on the body size and age, which should be reflected in the model structures. It should be pointed that considering body size as a covariate of processes such as mortality and reproduction does not necessarily involve prior assumptions about whether the correlation is negative or positive, but in the absence of strong prior knowledge the strength and sign of the correlation are properties emerging from the model fitting.

Population density is also a largely ignored yet potentially highly relevant covariate of population productivity through density-dependent somatic growth and also through the so-called Allee effect, that is, a reduction in the population productivity at a low abundance (Courchamp et al. 2008). Allee effects can have marked implications for fisheries management (Berec et al. 2007) as it has been hypothesized to contribute fishery collapses and reduce the rate of population recovery from overfishing (Shepherd and Partington 1995; Babcock and Keesing 1999; Nash et al. 2009; Hutchings and Reynolds 2004; Keith and Hutchings 2012).

In an age- and growth-structured model, the distribution of growth rates can be explicitly modelled, so that the proportions of eggs produced by each growth group can be tracked. One obvious problem then arises: How should one allocate the eggs among the growth groups for the future time steps? If individuals only mated within their own growth-groups and if the growth parameters were fully heritable, then eggs would remain in the same group that produced them. This is hardly realistic, so a model for allocating the eggs among different growth groups is required. Mathematically, this can be formulated as a simple transition matrix, and knowledge about the spawning behaviour and the inheritance of growth and body size (e.g., Mousseau and Roff 1987) can be incorporated to provide informative priors for the transition probabilities in the matrix. Interestingly, this type of a model structure also has the potential to account for fisheries-induced evolutionary trends in fish life-histories (see section 2).

The survival of eggs up to a larval stage and onwards up to a body size at which a fish can be caught by commercial and survey fishing depends on competition for food and shelter and on external sources of mortality such as predation, so that that the survival process should be modelled as a case of negative density-dependence but positively associated with body size. The nature of competition and knowledge about the sources of mortality, e.g., cannibalism, could be utilized to construct priors for the alternative shapes of the stock-recruitment functions. Particularly in these model structures, external information incorporated into the priors is likely to be important, as typical stock-assessment data are not very informative about the shape of the stock-recruitment function (e.g., Mäntyniemi et al. 2009; Martell et al. 2008).

Life-history stages described previously are generally regulated by the environment through, for instance, temperature, salinity, and climatic oscillations (e.g., Pörtner and Peck 2010). Consequently, information about the potential environmental covariates is likely to improve a model's ability to explain and predict fluctuations in population dynamics (Walters and Collie 1988). In the absence of direct observations on environmental covariates, a red-noise process can be introduced to mimic the typical behaviour of environmental

variables (e.g., Ruokolainen et al. 2009); this inclusion is expected to improve the precision of short-term forecasts for stock development.

### Practical considerations

The model structures outlined in the previous text are not particularly complex or difficult to implement. However, a more challenging part of the work is that the model should be conditioned on all stock-assessment data available and it should fully integrate the resulting knowledge into probability distributions (e.g., Peterman 2004). The modelling should also be done as expeditiously as possible to support the annual decision making in fisheries management (ICES 2010d). Nonetheless, complex hierarchical models are not free from computational problems (e.g., Newman et al. 2009), which implies that, in practice, some trade-offs between computation speed and the biological realism of the model need to be made. To this end, we suggest the following order of simplifications:

1. Decrease the model dimension by reducing the number of age and growth classes and by combining time steps.
2. Treat a few of the less uncertain model parameters as fixed ones.
3. Simplify the biological assumptions.

The disadvantages of the first two suggestions are that some information can get lost with the reduction in model resolution and, on the other hand, some uncertainty is omitted as full knowledge is assumed in fixed parameters even though in reality the information necessarily is imperfect. Nonetheless, the biological assumptions about the population dynamics should be the last ones to become simplified, to retain the realism of the model and to be able to plausibly predict the future stock development in response to alternative management actions.

One of the main messages emerging from the biological knowledge is that several phenotypic traits and processes affecting the population dynamics are interconnected at the level of individual life-histories and through density-dependencies at the population level. Many of these connections are already known in the fields of life-history theory and population ecology, if not as functional relationships then at least at the level of the trade-offs (i.e., existence of negative correlations among variables). These connections can be utilized in the development of model structures and, specifically, correlations among prior distributions for parameters: information about one parameter provides indirect information about the likely values of the others (for an example, see He et al. 2006; Pulkkinen et al. 2011). Building such linkages into a stock-assessment model can make it more complex in terms of the number of parameters, but it also promotes the accumulation and the more efficient use of information as parameters are no longer considered independent. For instance, while hierarchical meta-analysis is an efficient tool for pooling information about population dynamic parameters from multiple fish stocks (e.g., Liermann and Hilborn 1997; Hilborn and Liermann 1998; Myers 2001; Helser and Lai 2004; see also Fig. 2), the incorporation of correlations among population parameters has proven to further improve the method (Pulkkinen et al. 2011). Another important enhancement is to use geographical distance between populations as an explanatory factor for the de-

gree of similarity between neighbouring populations (e.g., Pyper et al. 2001; Su et al. 2004). Biological databases such as FishBase (Froese and Pauly 2011) and RAM II (Ricard et al. 2012) can serve as a good source for population-specific parameters to be used in meta-analysis. To this end, biological databases could also perform hierarchical meta-analysis internally to provide users with prior distributions of key population parameters as well as correlations among them. The benefits of such an approach are persuasive. For example, while natural mortality is an essential parameter for population dynamics, stock-specific estimates are often not available. To overcome this shortcoming, scientists can utilize the probabilistic relationships among the rate of natural mortality and such correlated variables that are easier and cheaper to estimate.

It should be noted, however, that the gathering of information from databases and existing publications to be used in meta-analysis can also involve problems (e.g., Pulkkinen et al. 2011). Current scientific publication practices may not provide entirely unbiased views about the states and causalities of populations and ecosystems. The common practice of publishing only ‘statistically significant’ results easily leads to the publication of detected correlations only, while negative results often remain unpublished. This publication bias is widely discussed in medical and genetic studies (e.g., Dickersin 1990; Easterbrook et al. 1991; Lohmueller et al. 2003), but rarely dealt in the fisheries context (for exceptions, see Myers and Mertz 1998a; Myers 1998). Another weakness of the current publishing system is that it does not fully support the accumulation of information (especially if traditional point estimation is applied). In the Bayesian framework, however, a posterior of one study can serve as a prior of another study (for an example, see Uusitalo et al. 2005 and Michielsens et al. 2008), so that the publication of posterior distributions is important to promote future modelling. In genetics research, it has become a practice to archive sequencing data to publicly available sources; a similar approach would be highly useful in the fisheries research context and the establishment of the RAM Legacy Stock Assessment Database (Ricard et al. 2012) represents a very important step in this regard.

### Further avenues for biological realism in fisheries research

In the present study, we have focussed on stock-assessment models typically used in the management of commercial fisheries, and explored their biological realism and outlined relatively feasible ways to overcome some of the most striking oversimplifications related to the biological assumptions. However, obviously the biological complexity driving fish population dynamics is vast, so that understanding, capturing, and predicting even a few aspects of that requires research that extends far beyond from what has been covered in this article. For instance, we have only focussed on single-species models, while predator–prey interactions and the entire food web can also affect a population targeted by fisheries. Ecosystem-based fisheries management has been frequently called upon and scientific implementations exist (Smith et al. 2008) but its wider incorporation into models remain uncommon (Link 2010). However, model developments sketched previously may prove to be useful also in the ecosystem-based management context: this approach will create a need

to assess the risks associated to by-catch (accidentally caught) species, but from those there typically exist even less data than from the targeted species, so that any available prior information becomes highly required.

Behavioural traits, such as habitat preferences (Köster et al. 2003; Rivot et al. 2008), schooling behaviour (Parrish 1999; Mäntyniemi and Romakkaniemi 2002; Lindén and Mäntyniemi 2011; Thorson et al. 2011), and vulnerability to fishing gears (e.g., Biro and Post 2008) are also likely to underlie some variations in the stock assessment data and further affect population viability (e.g., Uusi-Heikkilä et al. 2008), thus suggesting that these might be relevant covariates to be accounted for in the models and management. So far, behavioural aspects have gained most attention in the analysis of risks associated to recreational fisheries, while in the context of commercial fisheries the available knowledge has not been fully utilized. Existing recreation fisheries studies, as well as those stemming from more traditional behavioural ecological research, could provide the first source of prior information about the role of behaviour in fishing selectivity and fish population dynamics. More generally, closer interactions between the fields of commercial and recreational fisheries research might prove to be useful for stock assessment and management: recreational catch records may provide an additional data source for stock assessment (e.g., ICES 2008; MSFCA 2006), while harvest rates arising from recreational fishing may be so substantial that they should be better accounted for in fisheries management (Post et al. 2002; Coleman et al. 2004; Cooke and Cowx 2006).

### Conclusions

The philosophy of utilizing the existing biological knowledge in the development of fisheries stock assessment models can be summarized by the words of Ludwig Wittgenstein: “A picture depicts reality by representing a possibility of existence and non-existence of state of affairs” (Wittgenstein 2001). Ecological and life-history theory, scientific literature in these fields, as well as what is known about comparable populations and species, are sources of knowledge that can help a fisheries scientist to make assumptions about the assessed stock and the likely causalities and interactions affecting its dynamics. One of the emerging messages of this review is that to be able to efficiently improve the biological realism of stock assessment models, fisheries scientists must go beyond the traditional stock-assessment data and explore the resources available in other fields of biological research. The hierarchical Bayesian framework provides a way of formally integrating this knowledge into the stock-assessment protocol and to accumulate information from multiple sources and over time. Similarly, the framework accounts for the inherent stochasticity and uncertainty in population dynamics, and integrates it into uncertainty about the management advice and forecasts of the population’s future.

It is obvious that most fisheries in the European Union as well as many other heavily exploited fisheries worldwide are not likely to attain the goals set at the 2002 World Summit on Sustainable Development in Johannesburg; that is, to rebuild exploited fish stocks back to the levels where the sustainable yield is maximized by 2015 (STECF 2005; Froese and Proelß 2010). Even if fishing pressures were dramatically

reduced for the remaining years, heavily exploited stocks would not have sufficient time to increase their biomass even close to the targeted levels. Fisheries science has a critical task to produce estimates about how much catch potential is lost every year because past exploitation rates were not controlled properly. Without such estimates, it is difficult to imagine success in negotiations that aim to limit fisheries catches today to provide better catches in the future. Scientific information provides both an incentive and a common language for these negotiations.

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