



Original Article

Predicting reference points and associated uncertainty from life histories for risk and status assessment

Bernardo García-Carreras^{1*†}, Simon Jennings^{1,2}, and Will J. F. Le Quesne¹

¹Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft NR33 0HT, UK

²School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

*Corresponding author: e-mail: bgarciacarreras@gmail.com

†Present address: Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

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To assess status of fish populations and the risks of overexploitation, management bodies compare fishing mortality rates and abundance estimates with reference points (RP). Generic, “data-poor” methods for estimating RP are garnering attention because they are faster and cheaper to implement than those based on extensive life history data. Yet data-poor RP are subject to many unquantified uncertainties. Here, we predict fishing mortality RP based on five levels of increasingly comprehensive data, to quantify effects of parameter and structural uncertainty on RP. Level I RP (least data) are estimated solely from species’ maximum size and generic life history relationships, while level V RP (most data) are estimated from population-specific growth and maturity data. By estimating RP at all five data levels, for each of 12 North Sea populations, we demonstrate marked changes in the median RP values, and to a lesser extent uncertainty, when growth parameters come from data rather than life history relationships. As a simple rule, halving the median level I RP gives almost 90% probability that a level V median RP is not exceeded. RP and uncertainty were substantially affected by assumed gear selectivity; plausible changes in selectivity had a greater effect on RP than adding level V data. Calculations of RP using data for successive individual years from 1984 to 2014 showed that the median RP based on data for any given year would often fall outside the range of uncertainty for RP based on data from earlier or later years. This highlighted the benefits of frequent RP updates when suitable data are available. Our approach provides a quantitative method to inform risk-based management and decisions about acceptable targets for data collection and quality. Ultimately, however, the utility and extent of adoption of data-poor methods for estimating RP will depend on the risk aversion of managers.

Keywords: conservation, life history, management, reference points, selectivity, sensitivity, uncertainty.

Introduction

Around 65% of global marine fisheries landings come from unassessed stocks (Mahon, 1997; Andrew *et al.*, 2007; Branch *et al.*, 2011; Ricard *et al.*, 2012; Hilborn and Ovando, 2014). Consequently, management and conservation bodies often struggle to obtain essential information on stock or species status, risk, and potential yield. Calls for more and better information come from many regions, but the information gap is especially wide in poorer countries in the tropics and subtropics, where species and catch compositions are relatively diverse but resources for assessment are scarce (Mahon, 1997; Andrew *et al.*, 2007).

Several ways to reduce costs and data need for assessments have been tried (Clark, 1991; Beddington and Kirkwood, 2005;

Le Quesne and Jennings, 2012; Bentley, 2015; Hordyk *et al.*, 2015a, b; Prince *et al.*, 2015; Jardim *et al.*, 2015; Kokkalis *et al.*, 2015). Some approaches “borrow” information from similar stocks for which data are available (Brooks *et al.*, 2010; Prince *et al.*, 2015; Kokkalis *et al.*, 2015) to put bounds or impose penalties on parameter values and inform priors. When data are borrowed, models can be as sophisticated and ambitious as those used for the most thoroughly studied stocks (Brooks *et al.*, 2010; Kokkalis *et al.*, 2015), but defining and justifying “similar” species can be challenging in part because suitably analogous and well-studied species may not exist (Brooks *et al.*, 2010). Other approaches capitalize on established interspecific relationships among life history traits (e.g. between asymptotic body size and size at maturity) to

estimate values for population model parameters that are costly or difficult to measure (Pope *et al.*, 2000; Le Quesne and Jennings, 2012), building on established approaches to estimate natural mortality (e.g. Beverton and Holt, 1957, 1959; Beverton, 1963, 1987; Jensen, 1996; Charnov, 2008; Gislason *et al.*, 2008, 2010; Charnov *et al.*, 2013; Kenchington, 2014). The use of interspecific relationships among life history traits to reduce data demands is appealing because they are well established and apply to a wide range of taxa and geographical locations (e.g. Beverton and Holt, 1957; Jensen, 1996; Charnov, 2008; Gislason *et al.*, 2008, 2010; Charnov *et al.*, 2013; Kenchington, 2014). Uncertainties in such relationships are rarely reported, however, and the consequences of uncertainties are amplified when more parameters are predicted.

Typically, assessments of species status and risk are conducted by comparing fishing mortality rates (F) and abundance with reference points (RP) that indicate safe or sustainable F , abundance, and reproductive potential. Generic, “data-poor” methods for estimating RP may be applied when few data are available, but interpretation and adoption of these RP would be better informed by an understanding of the effects of estimation methods that draw on interspecific relationships among life history traits to provide parameters.

As well as contending with the absence of detailed life history data, assessors encounter the situation where these data are available but come from an earlier period. Temporal trends in life history traits within populations (e.g. Baudron *et al.*, 2011) suggest that, even when relatively comprehensive life history data are available for a population in a given year or years, these may lead to RP estimates that may not be the same as RP estimated from data collected in subsequent years. Web-accessible databases have markedly increased awareness of, and access to, older data, but the consequences of taking data from the past to estimate RP have not been systematically evaluated. For this reason, and because RP are not always re-estimated even when new data do become available, it is a priority to assess the consequences of temporal changes in life history traits on RP.

Here, we develop and apply a tiered approach for estimating RP. The approach allows us to quantify the effects and magnitude of parameter and structural uncertainty and to assess the effects of incorporating more data on uncertainty. The approach involves the development of yield-per-recruit (YPR; Beverton and Holt, 1957) and spawner-per-recruit (SPR; Mace and Sissenwine, 1993) models that are parameterized with minimal (maximum body size) or complete (growth and maturity) empirical data. Specifically, we aim to: (i) develop a model for predicting RP from life histories, (ii) quantify the uncertainty around output RP when using life history relationships to parameterize the model, (iii) discuss the impact of progressively introducing data on reference point estimates and uncertainty, thereby estimating the “cost” of using life history relationships in data-poor contexts, and (iv) assess the consequences of intraspecific temporal changes in life histories on RP and uncertainty.

Methods

Population model and biological RP

YPR (Beverton and Holt, 1957) and SPR (Mace and Sissenwine, 1993) models are widely used for calculating RP. Both models track cohorts, thus avoiding definition of a spawner–recruitment relationship. YPR RP reflect fisheries productivity, while SPR RP reflect reproductive potential and therefore have a greater conservation focus. YPR and SPR models share a common discrete time equilibrium population model (Beverton and Holt, 1957; Hilborn and

Walters, 1992), accounting for changes in abundance and biomass with growth and mortality due to fishing and natural causes. YPR is defined as the yield-per-recruit, summed across all age classes, as a function of F . SPR is defined as the spawning biomass per recruit summed across all age classes, as a function of F . SPR F RP are usually expressed as a percentage of the SPR in the unfished state (%SPR), such that %SPR denotes the reduction in reproductive potential due to fishing pressure.

Here, we adopt four biological RP: F_{\max} and $F_{0.1}$ for YPR and $F_{10\% \text{ SPR}}$ and $F_{40\% \text{ SPR}}$ for SPR. F_{\max} , the F at which YPR is maximized, is considered to be an upper limit on the rate of sustainable fishing, while $F_{0.1}$, the F at which the slope of the YPR curve is 0.1 of the slope at the origin, is more conservative and reduces risk of collapse. $F_{10\% \text{ SPR}}$ and $F_{40\% \text{ SPR}}$ are defined as the F at which spawning-stock biomass (SSB) is reduced to 10 and 40% relative to the unfished level, respectively. $F_{10\% \text{ SPR}}$ is often viewed as the upper limit to F that allows for stock persistence (Mace and Sissenwine, 1993).

Uncertainty analysis

Parameters required for YPR and SPR models can be estimated directly from data or based on relationships among life history traits (see the “Life history model parameterization” section). A tiered approach to model parameterization was used to assess the effects of introducing more data on the values of RP and associated uncertainty. For level I (Table 1), we assumed no data on the stock were available, so the approach relied solely on a global estimate of L_{\max} obtained from FishBase (Froese and Pauly, 2015) and all other model parameters were derived from relationships between life history traits. At level II, we assumed the availability of local stock-specific body length data that could be used to refine the estimate of L_{\max} (giving a local L_{\max}), and at level III, body weight data were added to estimate parameters for the length–weight relationship (“Life history model parameterization” section). Level IV additionally required size at age information with which to estimate growth parameters, and finally, at level V, information on age and size at maturation was included, such that most model parameters were estimated from data (Table 1). YPR RP are the same for levels IV and V because maturity information is not required in the estimation of the YPR curve.

To enable the systematic comparison of the effects of increasing data availability on RP, the analysis focused on 12 North Sea stocks for which level V data were available. To conduct analyses at levels I–IV, we ignored parts of the available data for each stock. For the levels of analysis (II–V) where local L_{\max} , length–weight relationships, growth, or maturity were estimated with data, we used data from the North Sea International Bottom Trawl Survey database. This provides some of the data underpinning existing ICES

Table 1. The five levels of analysis that were used to assess the changes in RP that resulted from replacing parameters estimated using theoretical or empirical life history relationships with parameters estimated from data.

Level	Input parameters
I	Global L_{\max} (source: FishBase global maximum)
II	Local L_{\max} (source: local data)
III	Local L_{\max} , length–weight relationship (a, b)
IV	Length–weight relationship (a, b), growth (L_{∞}, K, t_0)
V	Length–weight relationship (a, b), growth (L_{∞}, K, t_0), maturity (m_t)

Input parameters refer to the model parameters generated directly from data. Any parameters not defined as *input parameters* were derived in the models.

stock assessments (ICES, 2012a; Supplementary Section S5). For the analysis of the effects of increasing data availability (as defined by levels I–V) on RP, we used 3 years’ data (2009–2011) to estimate the local L_{\max} and growth parameters, whereas data from 1984 to 2014 were used to obtain the parameters for the length–weight relationship and the proportion of individuals mature per age class (Supplementary Section S5). For the analysis of temporal changes in RP, we used data for each year for four stocks (cod, haddock, herring, and whiting) from 1984 to 2014 to produce annual RP estimates (“Temporal changes in life history traits and per recruit RP” section).

Uncertainty was introduced by running the population model using 10 000 random combinations of input parameters and life history relationships for each level of analysis. Coefficients were sampled from multivariate normal distributions, accounting for correlations between parameter estimates. The means of the distributions equal the estimated coefficients, and standard deviations equal the standard errors around the estimates.

Uncertainty was estimated as the width of the distribution of output RP (using quantiles). We characterized the differences between the output RP distributions and the distribution at level V using root-mean-square error (RMSE). The RMSE combines both the width of the RP distributions and the shift in the distributions relative to the data-rich level (V), and is defined as

$$\text{RMSE}_i = \sqrt{(\text{Var}(X_i) + (\text{Median}(X_i) - \text{Median}(X_{i=V}))^2)}, \quad (1)$$

for level i of the analysis, where X is the RP distribution for a given stock. A high RMSE can be attributed to a wide distribution, or a distribution shifted relative to that of level V. The RMSE for level V only quantifies the width of the distribution. A RMSE estimate is obtained per stock, RP, and level of analysis, and these are then averaged across stocks to give a mean RMSE per level and RP. Lower values of RMSE suggest RP distributions more similar to level V, the reference distribution. Values of the mean RMSE depend on the stocks used to estimate them. To assess the extent of this effect, the mean RMSE was also calculated using 1–12 stocks at a time, for all combinations.

Life history model parameterization

YPR and SPR model inputs are the mean size per age class (growth), natural mortality (M), proportion of mature individuals per age class, size selectivity of the fishery, and F . These may be estimated directly from data or from life history relationships, depending on the level of analysis. Central to our approach was the estimation of uncertainty resulting from the use of life history relationships. Consequently, several established relationships were recalculated to establish uncertainty in fits with more recent or more comprehensive data than those used in preceding studies.

Asymptotic size (L_{∞}) can be estimated using the statistical relationship with observed maximum size (Froese and Binohlan, 2000). We updated the relationship between L_{∞} and L_{\max} reported by Froese and Binohlan (2000) to include data added to FishBase since 1999 (provided by C. Binohlan, pers. comm.), while following the same filtering procedure used in the original study (Supplementary Section S1). The relationship between L_{∞} and L_{\max} , updated with data added to FishBase since 1999, was

$$\log_{10} L_{\infty} = 0.068260 (\pm 0.010451) + 0.969112 (\pm 0.006318) \log_{10} L_{\max} \quad (2)$$

(standard errors are shown in parentheses). Lengths were converted to weights (and vice-versa) using $W_t = aL_t^b$, with a and b assumed to be 0.01 and 3, respectively, at levels I and II.

Ontogenetic growth of fish is frequently modelled using the von Bertalanffy growth equation (VBGE; von Bertalanffy, 1934):

$$L_t = L_{\infty} (1 - \exp(-K(t - t_0))), \quad (3)$$

where L_t is the length at age t , K a growth parameter, and t_0 the hypothetical age at length zero. Where no stock-specific data were available, t_0 was assumed to be zero, and K was approximated using the relationship of Gislason *et al.* (2008). For this study, the equation of Gislason *et al.* (2008) was fitted to the larger database of life history parameters assembled by Gislason *et al.* (2010). The relationship relating K to L_{∞} using these data was

$$K = 2.15 (\pm 0.67) L_{\infty}^{-0.46 (\pm 0.09)}. \quad (4)$$

The proportion of individuals mature per age class, m_t , is estimated in some stock assessments (e.g. ICES, 2008, 2013), but we adopted an empirical relationship between knife-edge length at maturity (L_{α}) and L_{∞} (Gislason *et al.*, 2008) to estimate proportion mature by size:

$$L_{\alpha} = 0.64 (\pm 0.15) L_{\infty}^{0.95 (\pm 0.05)}, \quad (5)$$

as found by fitting the equation to data assembled from the literature by Gislason *et al.* (2008) for combined North Sea stocks.

Natural mortality M is notoriously difficult to estimate, even for well-understood stocks. A few assessments estimate M_t , but many others assume M to be constant across all age classes, including data-poor methods (Brooks *et al.*, 2010; Punt *et al.*, 2011; Hordyk *et al.*, 2015b). Gislason *et al.* (2010) provide convincing evidence for the strong size-dependence of M and fit a model accounting for species’ realized and asymptotic size to data. Charnov *et al.* (2013) simplified this relationship to

$$\ln M_t = -0.063 (\pm 0.07) + 0.998 (\pm 0.06) \ln \left[K \left(\frac{L_t}{L_{\infty}} \right)^{-1.5} \right]. \quad (6)$$

The intercept and slope were not statistically significant from 0 and 1, respectively, simplifying the relationship, at the cost of a poorer fit to the data. We estimate M_t using the relationship of Charnov *et al.* (2013), but also consider how results change when using M_t from Gislason *et al.* (2010).

Size selectivity depends on gear type and target stock combination. For the purposes of this analysis, we idealize selectivities using sigmoidal (relevant for most active gears) or bell-shaped (for most passive gears) functions (Huse *et al.*, 2000). The idealized selectivity curves are generated from the logistic distribution; active gears with the cumulative distribution function (cdf), and passive gears with the probability density function (pdf). The cdf and pdf of the logistic distribution can be described using two parameters: location and scale. Location defines the length at which half the individuals are selected (L_{50}) for active gears, and the target length for passive gears. The scale refers to the smoothness of the selectivity curve for active gears, and the width of the selectivity curve for passive gears (Supplementary Section S2). To verify the sensitivity of results to assumptions about selectivity, we use five location

parameters and three scale parameters for both active and passive gears, yielding a total of 30 different selectivity curves.

General methods

RP were estimated by generating YPR and %SPR curves for the range $0 \leq F \leq 3$, in 0.001 increments for each level of analysis and stock. Age classes were discretized by month, and the average size of an individual was calculated at the midpoint of each age class. Since the relationships of Gislason *et al.* (2010) and Charnov *et al.* (2013) overestimate M for the small size classes, we assume that individuals are recruited to the population at age three months or 2% of L_{\max} , whichever is greater. Spawning is assumed to take place during the first quarter (January–March) for levels I–IV of the analysis. For the data-rich case (level V), spawning time is stock-dependent, and taken from Daan *et al.* (1990). We also consider the effect of using different definitions of spawning seasons on RP. Outside the spawning season, the proportion of mature individuals was set to zero. “Plus” age classes were added to stabilize output RP, and assumed to have the same parameter values as those used for the terminal year class before this addition. All simulations were run in R (R Core Team, 2013).

RP estimated in this study are routinely provided in several North Sea stock assessments. We developed a version of the model that would allow direct comparison of outputs to RP published in stock assessments, and also investigated the effect of changing the width of an age class on output RP (Supplementary Figure S4), because stock assessments use age classes of one year rather than one month. The process is described in Supplementary Section S3 and the comparison of the output in Supplementary Table S1. While values of RP estimated with our model were comparable to those reported in stock assessments, they were rarely the same.

Temporal changes in life history traits and per recruit RP

Life history traits change over time in response to environmental and human pressures (e.g. Baudron *et al.*, 2011). Consequently, RP that depend on life history may vary through time. To investigate how RP change through time, we ran the analyses using annual data from 1984 onwards, for four of the North Sea stocks with good temporal data (cod, haddock, herring, and whiting). For this analysis, we excluded the level I case (RP from global L_{\max} only) because the global L_{\max} is assumed to be time invariant. Parameters estimated from data were calculated year by year. In reality, one year’s data will often be insufficient to obtain good estimates of life history parameters such as maturity, but using data for several years would average out any underlying trends. For this reason, we accept the necessary compromise of poorer and more uncertain life history parameter and RP estimates, for the sake of capturing temporal changes in RP. Outputs provided distributions of RP, per year, level, and stock. For each RP in these distributions, we calculated the number of consecutive years when the value remained within the 95% uncertainty envelope (estimated using the distributions and running forward in time) to produce distributions of numbers of years, per year, level, and stock.

Results

The impact of data on RP estimates

As more data are used to estimate the RP, absolute values often change, although uncertainty around these values remains relatively stable for all species except herring and plaice (Figures 1 and 2, and Table 2). Over 61% of the median RP for data-poor levels (I–III)

were lower than the median estimate for the data-rich level (V). Level V SPR RP for haddock are highly uncertain owing to substantial uncertainty in maturity parameters (Table 2). F_{\max} is more sensitive to changes in parameter inputs than $F_{0.1}$ (uncertainty intervals are wider), and $F_{10\% \text{ SPR}}$ (excluding haddock at level V) is more sensitive than $F_{40\% \text{ SPR}}$.

When empirically derived growth data were excluded from RP calculations (levels I–III), the median RP estimate fell outside the 95% uncertainty interval of the level V RP almost half of the time (Figure 1). The inclusion of growth data were especially important for haddock, Norway pout, saithe, sole, and whiting. Uncertainty intervals for all the data-rich (level V) RP that could be calculated for cod included the median values for RP at all lower levels of analysis, except $F_{40\% \text{ SPR}}$ at level I and $F_{10\% \text{ SPR}}$ (Figure 1). For haddock, the median estimates of $F_{0.1}$ that excluded growth data (levels I–III) were lower and fell outside the uncertainty intervals in data-richer levels (IV and V). $F_{40\% \text{ SPR}}$ and $F_{10\% \text{ SPR}}$ tended to be higher with more data (levels IV and V; Figure 1). For herring and plaice, $F_{0.1}$ and $F_{40\% \text{ SPR}}$ showed little change with level of analysis. For herring, the median estimates of F_{\max} estimated using global or local L_{\max} (levels I–II) were outside the range of uncertainty of the data-rich levels (IV and V). For plaice, the median values of F_{\max} at all lower levels (I–III, data poor) were within the uncertainty interval of the data-rich levels (IV and V; Figure 1). For sole, the median $F_{0.1}$ estimates that excluded growth data (levels I–III) were higher and, excepting level I, were also outside the range of uncertainty of data-rich RP (levels IV and V), whereas for F_{\max} , the median RP values for levels I to III were outside the uncertainty interval at levels IV and V. For $F_{10\% \text{ SPR}}$, the median RP values at levels II and III were higher and outside the uncertainty interval at level V (Figure 1). The median values of all RP for whiting that excluded growth data (levels I–III) were outside the uncertainty intervals at level V (Figure 1). The mean RMSE values (Figure 3) confirm the importance of growth data in determining the absolute value of YPR RP. Adding growth data also reduced the mean RMSE for SPR RP, but for $F_{10\% \text{ SPR}}$, adding maturity data had an even greater impact. The mean RMSE was usually insensitive to the number of stocks used to calculate the estimates (Supplementary Figures S45–S48).

Selectivity

Changes in assumed selectivity have a substantial impact on the uncertainty around RP (Figure 4). For active gears, increases in the minimum landing size (L_{50} , expressed relative to L_{∞}) are linked to greater uncertainty around RP for most stocks (Figure 4), but assumptions about the smoothness of the selectivity curve had little impact on uncertainty (Supplementary Figure S32). Changes in the widths of the uncertainty intervals around RP along the y -axes of Figure 4 are comparable to or greater than those along the x -axes, implying that the impact of changes in L_{50} on uncertainty can be greater than those caused by the introduction of data to estimate growth and maturity parameters. Active gears targeting large individuals, and passive gears in general, frequently failed to produce RP within $[0, 3]$, because the impact on the stock was comparatively small (e.g. Figure 4, and Supplementary Figure S33).

Temporal changes

Observed changes in life history parameters through time led to marked variation and trends in values of RP (Figures 5 and 6). Trends over time are particularly evident for haddock (top panels of Figure 5) due to underlying trends in growth parameters

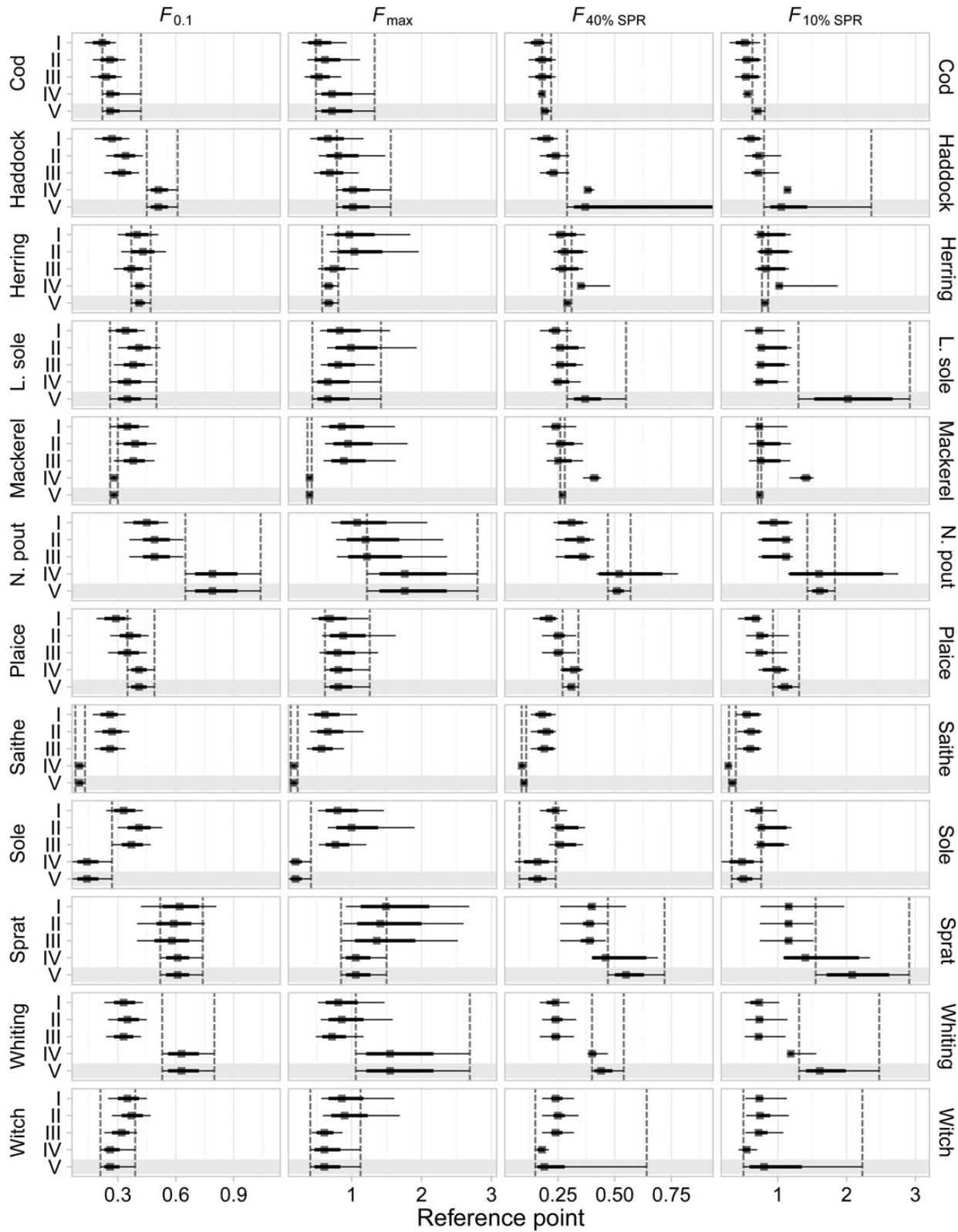


Figure 1. Median RP (squares), and uncertainty intervals (thin line: 95%; thick line: 75%) for each of the five level of analysis (Table 1). Rows of panels correspond to stocks, and columns of panels to the four RP. Each uncertainty interval summarizes the distribution of RP estimated from 10 000 simulations (RP distributions are provided in Supplementary Figures S13–S24). The upper limit of the $F_{40\% SPR}$ uncertainty interval for haddock level V has been truncated for clarity but reached 2.47. Level IV and V YPR RP are identical because maturity data are not required to estimate the YPR curve. The selectivity profile is assumed to be that of an active gear, with $L_{50} = 1/3L_{\infty}$, and with an intermediate smoothness (Supplementary Section S2). Additional results for different selectivity curves are shown in Supplementary Figures S25–S27.

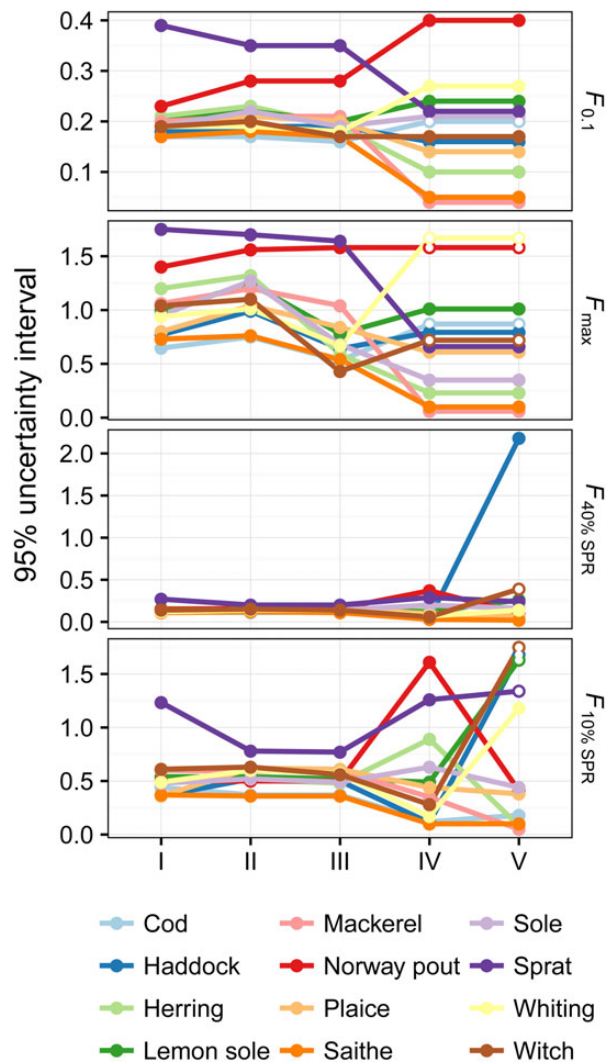


Figure 2. Width of the uncertainty intervals (95%) of RP estimates for the 12 stocks as a function of the five levels of analysis (Table 1). The selectivity profile is assumed to be that of an active gear, with $L_{50} = 1/3L_{\infty}$, and with an intermediate smoothness (Supplementary Section S2). Simulations that yielded fewer than 90% of RP in the range $[0, 3]$ are shown using hollow circles. Level IV and V YPR RP are identical because maturity data are not required to estimate the YPR curve. Distributions underlying the summaries in this plot are shown in Supplementary Figures S13–S24, and additional results for different selectivity profiles are provided in Supplementary Figures S28–S30.

(Supplementary Section S5.3). Temporal variability and trends affect the length of time over which RP may be perceived as valid (bottom panels of Figure 5). For haddock, YPR and SPR RP can move outside the range of uncertainty at any point in time within a few years. RP for other stocks, for instance, cod (Figure 6), are variable through time but do not show consistent temporal trends.

Examples shown in Figures 5 and 6 are representative of the range of patterns observed for other stocks at levels IV and V (Supplementary Figures S34–S41). Models relying on life history relationships (levels II and III) lead to lower temporal variability in RP. RP at levels IV and V are more variable and consequently remain within a given range for fewer consecutive years. Uncertainty envelopes for SPR RP tend to be larger and RP tended to remain within these

intervals for longer periods (Supplementary Figures S38–S41). Introduction of maturity data at level V substantially increases uncertainty around the time-series for some stocks (e.g. haddock), because fits of the maturity curves to annual data can be weak and variable (Table 2 and Supplementary Figure S11).

Discussion

In situations where little is known about a particular stock, the adoption of data-poor methods for estimating RP that draw on life history relationships can be appealing. Our analysis of uncertainties associated with these methods shows that parameters estimated from data do not necessarily lead to less uncertainty in RP than those based on life history relationships. However, the median estimate of a RP based on limited data (levels I–III) frequently fell outside the 95% uncertainty interval for a RP based on complete data (level V) when empirically derived growth data were excluded from RP estimation. The median estimates using all available data (level V) were often similar to estimates for level IV (except for herring). Usually, the introduction of growth data also had the greatest effect on the mean RMSE. Distributions of RP calculated with growth parameters derived from data may be higher or lower than those calculated with growth parameters estimated from life history relationships. We did not identify any predictors of the direction of change. Consequently, when minimal life history data are used to calculate fishing mortality RP (i.e. levels I–III in this analysis), some level of precaution is needed by managers if they seek to reduce the risk of surpassing the true value. For example, based on this analysis, if an assessor cannot access contemporary growth and maturity data and applies a level I–III method, then adoption of the lower 95% uncertainty interval of the RP distribution as a RP would ensure that this RP fell above the median value for the data-rich RP in just under 20% of cases on average (based on all stock and RP combinations considered; Supplementary Figure S50). However, given the span of the 95% uncertainty intervals is often ~ 0.6 of the median value of all RP distributions (except for F_{\max} where the value is ~ 1.2 ; Supplementary Figure S49), achieving this level of risk reduction would also lead to significant loss of potential yield. Using the median values from levels I to III (based on no growth and maturity data) could, in some cases, put over half the stocks at risk of exceeding the median RP at level V (full growth and maturity data). Halving the median values of RP for levels I–III would give a higher probability that a median data-rich RP would not be exceeded (Supplementary Figure S50), but is a more conservative approach than using the lower 95% uncertainty interval and would lead to greater loss of yield. Clearly, if basic life history information is used to define RP then it is necessary to adopt a high level of precaution if the aim is to minimize the probability of exceeding median RP based on growth data.

Per recruit models are sensitive to changes in input parameters (also emphasized by Hordyk et al., 2015b). However, uncertainty was greater for F_{\max} and $F_{10\% \text{ SPR}}$ than $F_{0.1}$ and $F_{40\% \text{ SPR}}$, respectively. $F_{10\% \text{ SPR}}$ is expected to be more sensitive to changes in input parameters than $F_{40\% \text{ SPR}}$ because the slope of the SPR curve becomes shallower with increasing fishing pressure; at 10% SPR, the slope of the curve is less than at 40% SPR, so any small change in the curve leads to larger changes in F at 10% SPR than at 40% SPR. The shape of the YPR curve and hence the values of RP, especially F_{\max} , are particularly sensitive to small changes in input parameters such as K and M , because these may lead to flat-topped curves with maxima that are difficult to define, as reported elsewhere (Chen, 1997; ICES, 2012b; Hordyk et al., 2015a).

Table 2. Parameter estimates, and standard errors in parentheses, used to estimate RP.

	Cod	Haddock	Herring	Lemon sole	Mackerel	Norway pout	Plaice	Saithe	Sole	Sprat	Whiting	Witch
Level I: Global L_{max} (source: FishBase)												
L_{max}	200	112	45	65	60	35	100	130	70	16	70	60
L_{∞}	199 (2.254)	113 (0.950)	47 (0.262)	67 (0.409)	62 (0.365)	37 (0.202)	102 (0.799)	131 (1.176)	72 (0.466)	17 (0.138)	72 (0.466)	62 (0.365)
K	0.19 (0.034)	0.24 (0.036)	0.36 (0.041)	0.31 (0.038)	0.32 (0.038)	0.41 (0.044)	0.25 (0.036)	0.23 (0.035)	0.30 (0.038)	0.58 (0.068)	0.30 (0.038)	0.32 (0.038)
L_{α}	101.0 (4.76)	59.6 (2.38)	26.0 (1.38)	36.3 (1.68)	33.8 (1.62)	20.7 (1.27)	53.8 (2.15)	68.3 (2.88)	38.9 (1.69)	10.1 (0.89)	38.9 (1.69)	33.8 (1.62)
Level II: Local L_{max} (source: local observations)												
L_{max}	123	68	37	45	48	28	56	56	41	18	58	51
L_{∞}	124 (1.101)	70 (0.447)	39 (0.217)	47 (0.255)	50 (0.274)	30 (0.176)	58 (0.341)	114 (0.949)	43 (0.238)	19 (0.145)	60 (0.358)	53 (0.295)
K	0.23 (0.035)	0.30 (0.038)	0.40 (0.044)	0.36 (0.041)	0.35 (0.040)	0.45 (0.049)	0.33 (0.039)	0.24 (0.035)	0.38 (0.043)	0.55 (0.063)	0.33 (0.039)	0.34 (0.039)
L_{α}	64.9 (2.61)	37.8 (1.66)	21.7 (1.27)	26.0 (1.42)	27.6 (1.46)	16.9 (1.16)	31.7 (1.51)	60.1 (2.50)	23.9 (1.33)	11.3 (0.95)	32.7 (1.53)	29.1 (1.50)
Level III: Length – weight relationship												
a	0.006 (0.0001)	0.005 (0.0001)	0.002 (0.0000)	0.006 (0.0003)	0.007 (0.0002)	0.008 (0.0002)	0.008 (0.0001)	0.005 (0.0001)	0.004 (0.0004)	0.007 (0.0001)	0.005 (0.0001)	0.001 (0.0001)
b	3.142 (0.004)	3.168 (0.003)	3.402 (0.005)	3.206 (0.014)	3.055 (0.009)	2.983 (0.008)	3.053 (0.004)	3.154 (0.005)	3.290 (0.030)	3.042 (0.005)	3.157 (0.003)	3.478 (0.018)
Level IV: Growth												
L_{∞}	126.7 (1.822)	41.1 (0.114)	31.4 (0.052)	33.6 (0.661)	36.4 (0.129)	20.6 (0.164)	35.0 (0.182)	111.3 (2.234)	37.3 (2.973)	14.5 (0.067)	38.5 (0.128)	44.6 (0.964)
K	0.20 (0.005)	0.52 (0.005)	0.49 (0.003)	0.32 (0.024)	0.45 (0.010)	0.75 (0.020)	0.37 (0.008)	0.12 (0.005)	0.26 (0.065)	0.74 (0.017)	0.49 (0.005)	0.25 (0.013)
t_0	0.33 (0.013)	-0.03 (0.010)	-0.24 (0.008)	-0.27 (0.144)	-0.92 (0.043)	-0.02 (0.017)	-0.17 (0.037)	-0.59 (0.065)	-1.09 (0.420)	-0.07 (0.023)	0.03 (0.009)	0.31 (0.057)
Level V: Maturity												
α	2.03 (0.09)	3.33 (4.13)	3.04 (0.33)	0.56 (0.18)	4.27 (0.39)	4.91 (0.88)	0.88 (0.03)	1.20 (0.06)	2.16 (0.63)	1.77 (0.48)	2.08 (0.43)	0.22 (0.07)
β	-6.17 (0.20)	-6.75 (8.20)	-7.45 (0.65)	-0.12 (0.56)	-9.28 (0.75)	-6.50 (0.97)	-2.50 (0.10)	-5.85 (0.27)	-5.45 (1.69)	-2.07 (0.75)	-3.18 (0.75)	-2.55 (0.33)
L_{α}	53.0 (0.74)	27.4 (11.49)	23.2 (0.34)	5.6 (3.76)	27.4 (0.16)	13.5 (0.41)	23.9 (0.13)	52.7 (0.37)	23.0 (0.98)	8.8 (1.01)	20.7 (1.26)	42.0 (1.41)

L_{α} refers to the knife-edge length at maturity for life history parameters (levels I–IV). α and β are the intercept and slope, respectively, of the logistic regressions describing the proportion of individuals mature at age. An estimate of the length at which 50% of individuals become mature (L_{α} for level V) is given for comparison with the L_{α} assumed at levels I–IV. The species used are cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), lemon sole (*Microstomus kitt*), mackerel (*Scomber scombrus*), Norway pout (*Trisopterus esmarkii*), plaice (*Pleuronectes platessa*), saithe (*Pollachius virens*), sole (*Solea solea*), sprat (*Sprattus sprattus*), whiting (*Merlangius merlangus*), and witch (*Glyptocephalus cynoglossus*).

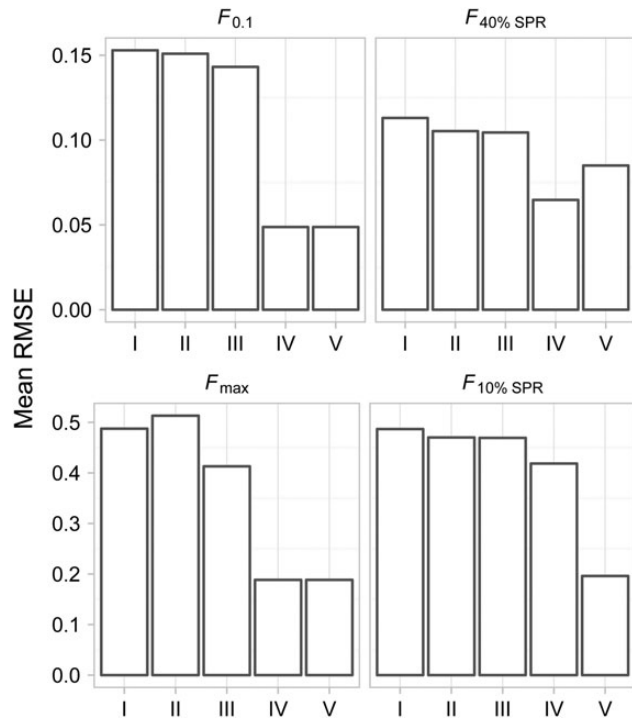


Figure 3. Mean RMSE for all 12 stocks at the five levels of analysis (Table 1). The selectivity profile is assumed to be that of an active gear, with $L_{50} = 1/3L_{\infty}$, and with an intermediate smoothness (see Supplementary Section S2). Level IV and V YPR RP are identical because maturity data are not required to estimate the YPR curve. Results for other selectivity profiles are given in Supplementary Figures S42 – S44.

RP and associated uncertainties were substantially affected by assumptions about gear selectivity and often these uncertainties exceed those attributed to the absence of biological data. This result, while expected, raises an important but sometimes overlooked point: it is essential to have reliable information on the size selectivity that different fishing gears may have on target and non-target stocks to reliably estimate RP. In the context of data-poor stocks, gathering this information could be challenging and development of simple and effective methods to estimate size-selection, based on characteristics of species and gears, remains a priority.

Per recruit RP are frequently used in stock assessments as proxies for more complex and difficult to estimate RP. For example, F_{max} is still used in the North Sea cod stock assessment as a proxy for F_{MSY} because estimates of the latter were found to be too contingent on the stock–recruitment model assumed (ICES, 2013). F_{max} is particularly sensitive to changes in inputs, and changes in the parameterization of the models not only affected the width of the 95% uncertainty intervals, but also the point estimates and central tendencies of the RP. RP are not only uncertain (even at level V), they are also affected qualitatively and quantitatively by assumptions about gear selectivity (Figure 4), and by structural uncertainties, such as the choice of approach for estimating M , the number of age classes used per year, or spawning season (Supplementary Figures S3–S5). RP were shown to be very variable over time at levels IV and V, proving that it is insufficient to implicitly assume RP are relatively stable. Temporal variability was much reduced for levels II and III because the uncertainty introduced by life history relationships is greater than the underlying temporal variability in

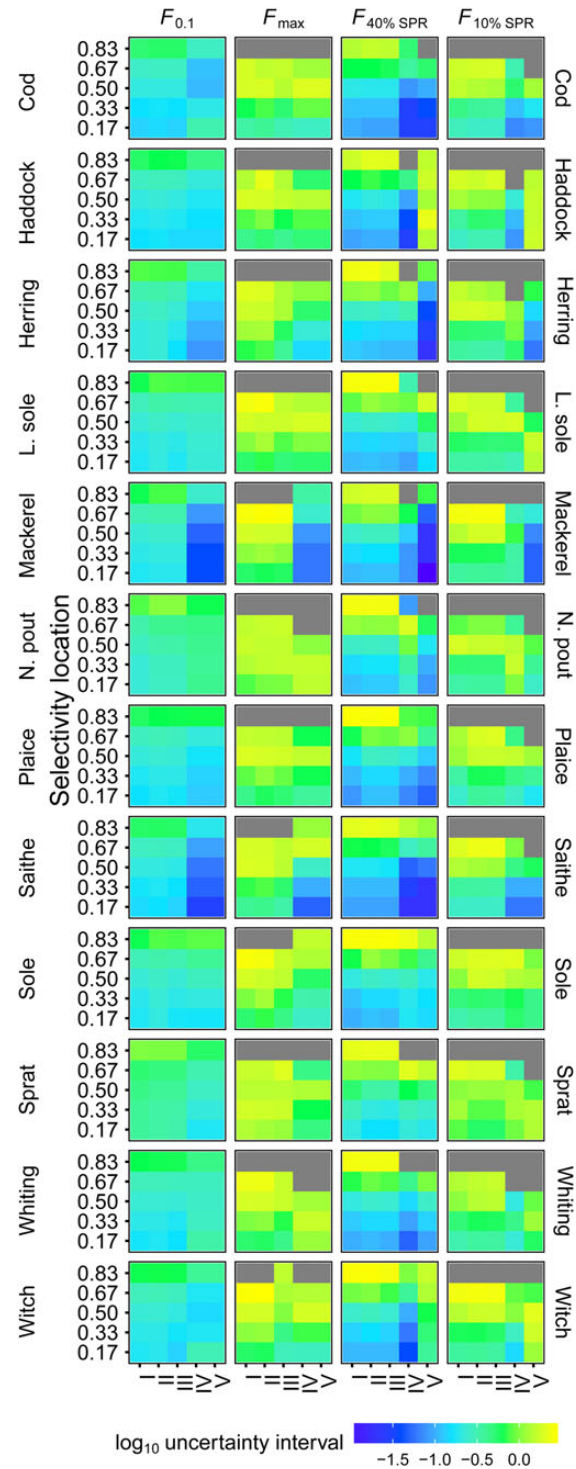


Figure 4. Effects of changes in selectivity (location of L_{50} relative to L_{∞}) on the width of the RP uncertainty intervals, by species for the five levels of analysis (Table 1). The colour of the tiles represents the width of the uncertainty intervals (on \log_{10} scale for clarity). In each panel, results for $L_{50} = 0.33$ correspond to those shown in Figures 1 (the widths of the 95% uncertainty intervals) and 2. Combinations for which no RP in the range $[0, 3]$ were produced are shown as grey tiles. Results for level IV and V YPR RP are identical because maturity data are not required to estimate the YPR curve. The selectivity curve is assumed to be that of an active gear, with a profile of intermediate smoothness (Supplementary Section S2).

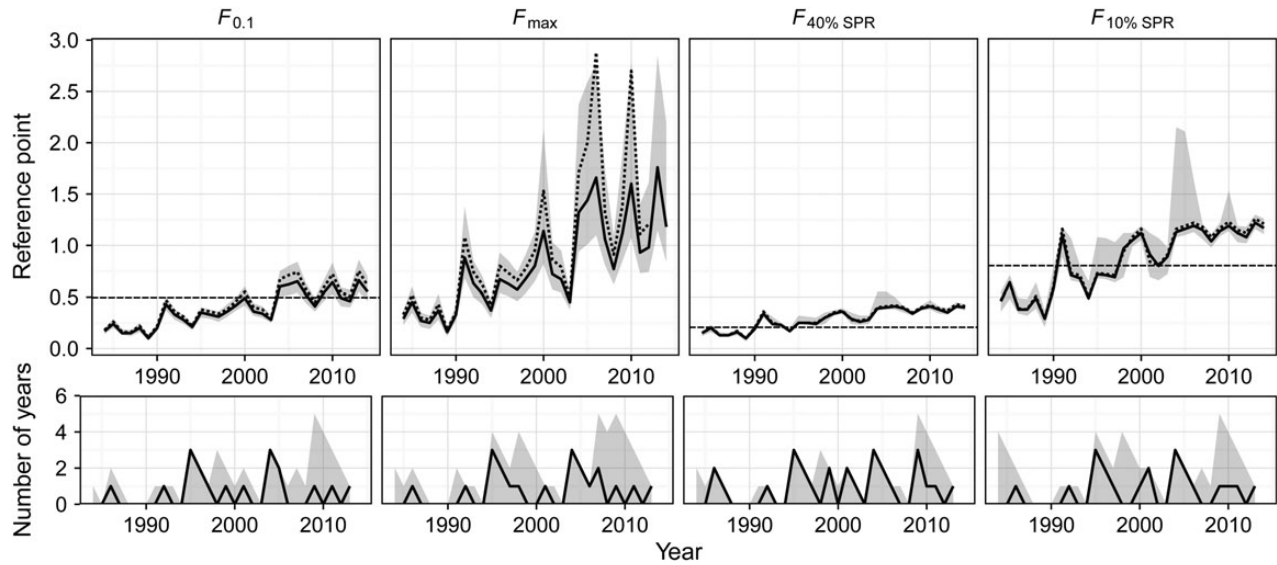


Figure 5. *Top panels:* Time-series of RP for North Sea haddock, at level IV. The solid line is the median RP, the dotted line is the point estimate (no uncertainty), the horizontal dashed lines show the RP obtained with a stock assessment version of the model (Supplementary Section S3; no value is produced for F_{max} because the YPR curve does not peak within $F = [0, 3]$), and the shaded areas are the 95% uncertainty envelopes. The selectivity profile is assumed to be that of an active gear, with $L_{50} = 1/3L_{\infty}$, and with an intermediate smoothness (Supplementary Section S2). *Bottom panels:* Sequential number of years for which RP remain within the 95% uncertainty envelopes presented in the top panels (see “Methods”). The solid line is the median number of years, and the shaded areas are the 95% uncertainty envelopes. Results for other stocks and levels of analysis are provided in Supplementary Figures S34 to S41.

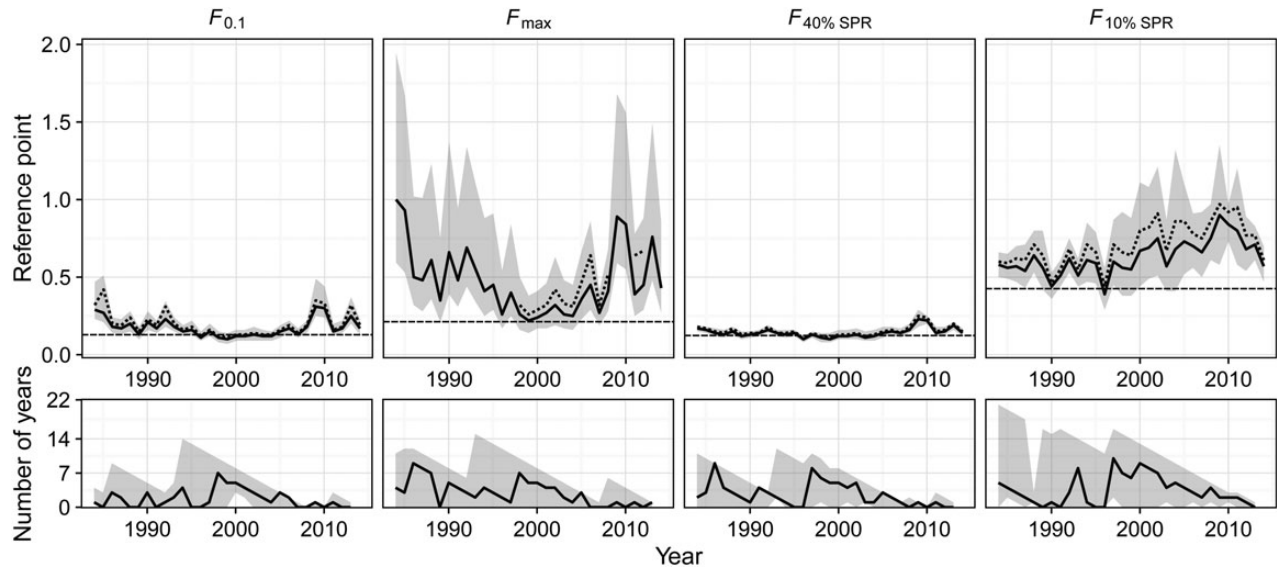


Figure 6. *Top panels:* Time-series of RP for North Sea cod, at level V. The solid line is the median RP, the dotted line is the point estimate (no uncertainty), the horizontal dashed lines show the RP obtained with a stock assessment version of the model (Supplementary Section S3), and the shaded areas are the 95% uncertainty envelopes. The selectivity profile is assumed to be that of an active gear, with $L_{50} = 1/3L_{\infty}$, and with an intermediate smoothness (Supplementary Section S2). *Bottom panels:* Sequential number of years for which RP remain within the 95% uncertainty envelopes presented in the top panels (see the “Methods” section). The solid line is the median number of years, and the shaded areas are the 95% uncertainty envelopes. Results for other stocks and levels of analysis are provided in Supplementary Figures S34–S41.

L_{max} or the length–weight relationship (Supplementary Sections S5.1 and S5.2). Given known and ongoing changes in the life histories of many stocks under the influence of climate change and fishing (Baudron *et al.*, 2011), it is desirable to revisit RP frequently when time-series data are available.

Although life history models are cheap compared with the data-driven counterparts, they can only be as good as the empirical relationships upon which they rely (see also Thorson *et al.*, 2014). Refinements in data analysis and model development could both contribute to reducing uncertainties. Some of the variability in

existing relationships could be obfuscating systematic differences (Gislason *et al.*, 2008; Thorson *et al.*, 2014; Prince *et al.*, 2015). For example, life history relationships for elasmobranchs differ from those for teleosts (e.g. Frisk *et al.*, 2001; Gislason *et al.*, 2008, Thorson *et al.*, 2014). Further research on how life history traits might vary across different taxonomic groups, or indeed across different environments (for instance, how relationships change with temperature) might help improve the quality of the fits and widen the applicability of the method. The life history model currently relies on a global estimate of L_{\max} . For this model, RP clearly depend on size (Supplementary Section S4), and the maximum size in a location of interest could differ substantially from the global estimate. It should be possible to use the observed temperature dependence of some life history traits (such as body size: Brunel and Dickey-Collas, 2010), to obtain a more precise estimate of local L_{\max} , and therefore more locally relevant RP.

The value of data is made clear by our analysis, particularly because it quantifies temporal changes in life history traits and hence in RP. However, there is potential for uncertainty around RP to be reduced. We used the most accepted fish growth model: the VBGE. While it has been justified in the past on bioenergetic grounds and as a relatively good statistical description of growth for many fish species, it has also been questioned (e.g. Roff, 1980). We found that the growth equation can be difficult to fit, particularly when there is little evidence of any reduction in the rate of growth with size. This has been well documented for North Sea saithe (e.g. Bolle *et al.*, 2004) but was also apparent for North Sea cod in the late 1990s owing, in part, to underrepresentation of larger size classes in survey data.

Uncertainty can describe different types of variability: within a population or stock, between populations (of the same species), and between species (Ralston *et al.*, 2011). The nature of uncertainty changes across the levels of analysis: uncertainties in life history relationships describe interspecific variability, whereas the use of data in levels III–V introduces intra-stock variability. To compare the magnitudes of these different types of variability, substantial amounts of data would be required. For example, Brunel and Dickey-Collas (2010) collate data for different herring stocks, and compare life history traits within and across stocks; similar datasets for a range of species would be necessary to accomplish this task.

The suitability and value of life history-based approaches for estimating sustainable fishing rates will depend on the risk aversion of the manager. Adopting the lower uncertainty interval of a RP from a calculation using life history relationships (levels I–III) would place a relatively small proportion of stocks at risk, but would also likely underestimate sustainable rates of fishing: the values of RP are over twice as likely to be below the lower uncertainty interval at level V than they are to be above the upper limit. This means using life history relationships to establish RP, without increasing risk, would entail a trade-off where yield would be lost in relation to the yield available when RP were based on more comprehensive data (levels IV and V, growth and maturity data). Maintaining the same level of risk aversion when setting RP based on different levels of data would provide an incentive to gather growth data. This is because our analyses show that the inclusion of growth and maturity data will usually lead to RP that allow higher yields to be taken for a given risk. One-off collections of growth and maturity data are unsatisfactory, however, as risk can be increased when RP change over time. Finally, our results emphasize the importance of correctly characterizing selectivity. Investing in biological data collection may not produce reliable RP estimates unless selectivities are well described.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

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