Can economic and biological management objectives be achieved by the use of MSY-based reference points? A North Sea plaice (*Pleuronectes platessa*) and sole (*Solea solea*) case study

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We examined the biological and economic impact of changing from management based on single-species limit reference points to one based on alternative targets, using the multispecies multifleet North Sea flatfish fishery. The robustness of reference points was tested against identified changes in plaice and sole biology. Current ICES single-species limit and precautionary biomass and fishing mortality reference points were seldom consistent with each other. Although they were generally robust to biological uncertainty, fishing at F_{pa} for sole could lead to stock collapse under one biological scenario. Adoption of alternative targets would reduce reliance on current reference points as stocks moved to a more sustainable state. Maximum sustainable yield (MSY), maximum economic yield (MEY), and maximum employment conditions implied different effort levels in the two fleets modelled, and different profits. F_{target} could be achieved with equal effort reductions in both fleets. Changes in stock biology affected the fishing effort required to maximize employment within the fishery, whereas MSY, F_{max} and MEY targets were robust to this uncertainty. Resulting profits and yields did vary widely, however. The selection of target reference points therefore requires stakeholders to define fishery objectives explicitly, against which targets can be evaluated for the resulting trade-offs between risk to stocks, yield, employment, and other social objectives.

Keywords: flatfish, limit and target reference points, maximum sustainable yield, North Sea.

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Introduction

An important driver for future fisheries policy is the World Summit on Sustainable Development (WSSD; COFI, 2003), under which signatories are committed to maintain or restore stocks to levels that can produce the maximum sustainable yield (MSY) by 2015. This commitment is derived from the UN Convention on the Law of the Sea (UNCLOS; UN, 1982), under which the objective was qualified by environmental and economic factors, i.e. "taking into account ... fishing patterns, the interdependence of stocks and any generally recommended international minimum standards".

MSY combines biological and economic concepts (biomass, mortality, yield, and fishing effort by fleet) into a single point, providing a common reference to assess the current status of a stock and to provide a target for management. However, fisheries are complex systems to understand and to manage, because of the mix of biological, ecological, economic, social, and institutional processes. These processes are dynamic and interact with each other. Fish stocks can also fluctuate extensively over a large range of spatial and temporal scales, independently of human exploitation (Cushing, 1995). These fluctuations are often ascribed to stochastic variations in key processes, such as recruitment, predation or migration, in relation to environmental change (Lehodey *et al.*, 1997; Köster *et al.*, 2005). In turn, even moderate exploitation can induce complex and important changes in population processes through, for example, changes in habitat, population or genetic structure, and trophic interactions. Moreover, management systems that encourage the pursuit of short-term gain can result in a lack of interest in long-term sustainability. The flexibility and complexity of systems makes it difficult to generalize in the manner that MSY concepts require, meaning that MSY cannot be defined uniquely. As a result, MSY may not provide a robust objective in the face of this uncertainty.

Despite these difficulties, MSY has already been enshrined within fisheries objectives. The US Magnuson–Stevens Fishery Conservation and Management Act mandates precautionary management to attain optimum yield (the technical guidelines for implementation of the Act refer specifically to MSY). Also, some international management bodies, e.g. the International Commission for the Conservation of Atlantic Tunas (ICCAT), have MSY as a management objective (ICCAT, 2003).

As a result of commitments to WSSD, the European Commission proposed long-term fishery-based plans to bring all major fish stocks under their jurisdiction to rates of fishing at which MSY can be achieved. This implies moving away from a reactionary framework of limit and precautionary reference points, towards proactively seeking to reach target reference points. Scientific advice is currently provided by the International Council for the Exploration of the Seas (ICES), primarily on a single-species basis. The previous advice framework aimed to preclude spawning-stock biomass (SSB) falling below a threshold value (B_{\lim}) at which either recruitment is impaired or the dynamics are unknown, and fishing mortality exceeding a threshold (F_{lim}) that would drive the stock to B_{lim} . Precautionary reference points $(B_{pa} \text{ and } F_{pa})$ that take into account uncertainty were used to trigger management action. These reference points were derived in a variety of ways under different, often arbitrary, assumptions about uncertainty based on assessment estimates. Kell et al. (2005a, b) showed that ICES reference points are not always appropriate and not precautionary in practice. Indeed, European fisheries management often focuses on supporting the "TAC machine" (Holm and Nielsen, 2004) rather than a consideration of the uncertainty in stock biology, or in the driving forces behind fisheries prosecuting them. Moreover, the performance of single-species reference points may be inadequate when applied in a mixed fishery context (Piet and Rice, 2004).

Plaice (Pleuronectes platessa) and sole (Solea solea) in the North Sea are caught principally in a mixed flatfish beam trawl fishery, a fishery that accounts for \sim 40% of the total value of North Sea fish landings. Landings of plaice by weight are about fives times greater than those of sole, but because sole are considerably more valuable, landings of the two species are about of equal value. Landings of sole are greatest from the southern North Sea, those of plaice greatest from the central and northern North Sea. Current ICES reference points for the two species are fixed (i.e. are not adjusted as additional data are collected), so explicitly assume no change in productivity over time. However, reference points are proxies for biological processes, including maturity and productivity, which in flatfish species have fluctuated over a range of spatial and temporal scales, independent of human exploitation (Rijnsdorp, 1993; Millner et al., 1996), and in response to environmental change (Rijnsdorp and van Leeuwen, 1996). Additionally, long-term shifts in the distribution of these species in the North Sea have been identified (Perry et al., 2005), along with strong seasonal migrations (Hunter et al., 2003). Plaice and sole therefore show considerable biological complexity that is not currently considered when setting biological reference points, and this complexity interacts with the behaviour of fishing fleets, and the management measures put in place to control them.

Here, we evaluate the impacts of biological variability in spatial distribution, recruitment, growth, and maturity on biological and economic management objectives, using the North Sea flatfish fishery as a case study. The consequences of moving from a limit-based system of single-species reference points to a multispecies one, based on alternative target levels including MSY, are explored.

Material and methods

The definition of stocks used by ICES to provide management advice is an operational definition rather than an ecological or evolutionary one (Waples and Gaggiotti, 2006). It was therefore assumed that there was no immigration or emigration between the North Sea and other areas, and that stocks were homogeneous.

We first examined biological data available for plaice and sole in the North Sea to identify trends in stock distribution and biological parameters, then based on this analysis, two periods were selected to represent periods of high and low stock productivity. Additionally, stock-recruitment analysis suggested two plausible hypotheses for stock resilience to exploitation. This provided four scenarios for a subsequent equilibrium analysis.

Management of the mixed flatfish fishery in the North Sea includes the use of gear restrictions. Minimum codend mesh sizes have been set at 80 mm in the south (the boundary defined by 55° N west of 5° E, and by 56° N to the east; Figure 1) and 100 mm in the north. Therefore, within the analysis, two fleets represent the fishery. The first comprises a large-mesh (100 mm) fleet in the north, the second a small-mesh (80 mm) fleet in the south. The two fleets target plaice and sole, respectively (see 'Fleet' section below).

Our analysis used an age-structured equilibrium model that combined SSB- and yield-per-recruit, and stock-recruitment analyses. The robustness of candidate biological, economic, and social reference points to changes in flatfish stock productivity and resilience was examined for the four stock scenarios identified. As current management relies on area-based mesh regulations and single-species reference points, changes in stock biology will, for example, impact on selectivity and hence partial fishing mortality in the fisheries. Within each scenario, biological parameters [massand maturity-at-age, stock-recruitment parameters (carrying capacity for a given steepness), and stock distributions relative to the management division] were taken as averages across the relevant identified period (representing high or low stock productivity). This ensured that correlations between all these biological processes were maintained.



Figure 1. Chart showing the gear mesh-size management line in the North Sea and the ICES Divisions.

Biology

Analyses were conducted on biological variability in spatial distribution, mass- and maturity-at-age, and the carrying capacity and resilience (maintenance of recruitment at low population size) of plaice and sole stocks. Plaice analyses were performed separately by sex because of the prevalence of size-specific discarding.

Spatial distribution

The proportion of plaice and sole by age available to the northern and southern fleets was estimated by general linear modelling (GLM), using International Bottom Trawl Survey (IBTS) data. The number-at-age of each species in the northern area (for the area north of the 55/56°N line from the gear regulation; Figure 1) was examined with a normal error model of the form $N_{a,N} \sim$ Factor(age) * Factor(year) * Factor(sex) * Latitude. Longitude, quarter, and country were also included in the model to standardize for changes in these covariates. The model was also fitted with an interaction between year and country, to examine whether there were changes in the survey over time that were not accounted for by the inclusion of country and year separately. The inclusion of this interaction did not result in a significant improvement in model performance, based on the additional explained variance against the loss of degrees of freedom (as identified by ANOVA; p = 0.35).

Maturity- and mass-at-age

Data used by the ICES North Sea Demersal Working Group (ICES, 2004) do not allow a full description of biological processes. For example, maturity-at-age is held constant throughout the timeseries. Therefore, biological data from more than 636 000 individual fish available from English and Dutch research surveys and commercial market sampling were combined into a single database for analysis. The biological data were originally collected on a length-stratified basis to construct age/length keys, which means that they are not representative of the frequency at age. The raw data were corrected therefore by the age–length distributions.

Individual maturity-at-age data for females of each species in quarter 1 of the year were examined through logistic regression, using a logit-link function. The probability of maturity was related to age and year (as factors). Factors for country, gear type, and data type (survey and market sampling) were included to standardize for these.

Mass-at-age in a given year was investigated for each species using a basic model which followed that of Shepherd and Nicholson (1991), i.e. $W_{a,t} \sim f(age, quarter)$. Year class was not included because preliminary modelling indicated that this factor was not significant. Factors for country, gear type, and data type (survey and market sampling) were included to standardize for these. The normal quantiles of mass-at-age showed that mass was not normally or lognormally distributed. A gamma error and log-link was therefore selected for the model (Shepherd and Nicholson, 1991).

For both the maturity and mass models, intercepts were not included. Large numbers of degrees of freedom were a concern, so the analysis was repeated on 5000 random samples (3% of the dataset) drawn with replacement from the whole dataset. This was repeated 1000 times. Overall coefficient and *t*-values were determined from the mean of individual fits.

Stock-recruitment relationship

Temporal coverage of the IBTS data was limited when compared with the ICES assessment datasets. ICES assessment data were therefore used to estimate the stock-recruitment relationships for sole. For plaice, however, catch numbers-at-age (Kell and Bromley, 2004), and catch per unit effort (cpue) for the Dutch Beam Trawl and Sole Net Surveys disaggregated by sex were available, allowing population estimates and fishing mortalities to be estimated by virtual population analysis (VPA) for both sexes. In addition, catch numbers-at-age for plaice were corrected for discarding (see below).

Sole recruitment was modelled at age 1, as per the recommendation of the ICES Working Group. Recruitment of plaice was modelled for females at age 2 (because no catches were reported at age 1 early in the dataset) as a function of female-only SSB. A Beverton and Holt (1957) stock-recruitment relationship was assumed:

$$R = \frac{\alpha \text{SSB}}{\text{SSB} + \beta},\tag{1}$$

where *R* is the level of recruitment, and α and β are the estimated parameters assuming a lognormal distribution in the data. The Beverton and Holt model is commonly used for North Sea flatfish (e.g. Kell *et al.*, 2005a). The formulation of Francis (1992) was used to reparameterize the relationship (for given natural mortality, mass- and maturity-at-age) in terms of steepness (τ) and virgin biomass (γ). Steepness is the fraction of the virgin recruitment (R_0) expected when SSB has been reduced to 20% of its maximum (i.e. $R = \tau R_0$ when SSB = $\gamma/5$), and represents the resilience of the stock to exploitation:

$$\alpha = 4\gamma \frac{\tau}{(\text{SSB}/R)_{F=0}(5\tau - 1)}$$
(2)

and

$$\beta = \frac{\alpha(\text{SSB}/R)_{F=0}(\tau^{-1} - 1)}{4}.$$
(3)

Fleet

Catchabilities

Realistic fleet-specific catchabilities were developed for the two fleets modelled (north and south). Age-aggregated partial catches by species were estimated using the MTAC database (Vinther *et al.*, 2004) for 2002, for four fleets, based on the meshsize management regulations in the North Sea:

- (i) Dutch beam trawlers (80 mm mesh);
- (ii) Dutch beam trawlers (100 mm mesh);
- (iii) English beam trawlers (80 mm mesh English flag vessels);
- (iv) English beam trawlers (100 mm mesh English flag vessels).

The relationship between mean fishing mortality (0.46 and 0.70 for sole and plaice, respectively, calculated for ages fully recruited to the fishery; ICES, 2004) and effort, i.e. catchability, was used to calculate fishing mortality by fleet and area. Data were then combined to model the two fleets within the analysis. The English

100 mm fleet and Dutch 100 mm fleet were combined to represent the northern North Sea fleet, and the Dutch 80 mm fleet and English 80 mm fleet combined to represent the southern North Sea fleet. Corresponding estimates of total effort for 2002 were 53.7 Mhp-days (Dutch) and 30.6 Mhp-fishing hours (English). The data for effort were obtained from Kraak *et al.* (2008) for the Dutch fleets and from STECF (2003) for the English fleets, and converted to the same units, because the English effort is normally in Mhp-fishing hours (see below).

Discarding

The assumption was made that sole would not be discarded in the fishery, because of its high value. The proportion of plaice discarded at age (D_a) was estimated based on the distribution-at-age (north and south, calculated above) and the probability of discarding $[P(D_a)]$. The latter was modelled based on the distribution of lengths-at-age, the minimum landing size (MLS; 27 cm for plaice), theoretical asymptotic length (L_{∞}) and the probability of capture by the gear (100 mm in the north, 80 mm in the south), e.g. for each age:

$$P(D_a) = \frac{\int_{x=0}^{\text{MLS}} \left(1/\sqrt{2\pi\sigma^2} \right) e^{\left[-1/2(x-\mu/\sigma_a)^2 \right]} \left(1/\left[1 - \exp(x-m/sc) \right] \right) dx}{\int_{x=0}^{L_{\infty}} \left(1/\sqrt{2\pi\sigma^2} \right) e^{\left[-1/2(x-\mu/\sigma_a)^2 \right]} \left(1/\left[1 - \exp(x-m/sc) \right] \right) dx},$$
(4)

where x is length, μ mean length, σ the standard deviation of an age (*a*), and *m* and sc the mean and scale of the cumulative distribution function of the exponential probability distribution of retention by the gear.

The actual catch (C) can then be derived from the landings (L) by age (a), sex (s), and area (l):

$$C_{a,s,l} = \frac{L_{a,s,l}}{1 - P(D_{a,s,l})},$$
(5)

where landings were derived from those reported to the ICES WG, but sex-disaggregated (Kell and Bromley, 2004). Landings by age and sex were then disaggregated by area using the proportion of each stock in the north and the south by age, as calculated above. Total catches (across areas) can then be estimated from landings by age and sex:

$$C_{a,s} = \left(\frac{L_{a,s,N}}{1 - P(D_{a,s,N})}\right) + \left(\frac{L_{a,s,S}}{1 - P(D_{a,s,S})}\right).$$
 (6)

Economy

Prices-at-age for each stock (plaice and sole) were estimated using the values for 2002, based on converting market-sized categories to age. Values were based on market prices for Urk in the Netherlands (a key processing and market site), and averaged over the last 6 months of that year. The relationship between effort and cost was calculated using the method of Kraak *et al.* (2008): variable $cost = \theta + \rho E \times 10^6$, where *E* is effort in Mhp-days (see Appendix). As most of the English fleet now fishes out of Dutch ports, costs were assumed to be comparable with those of the Dutch fleet, and the English measure of effort was converted into the same units as the Dutch. The assumption was made that vessels fish for 18 h d⁻¹ (the number of hauls per day varies between 8 and 10, and the haul duration is ~ 2 h). The English effort in Mhp-hours was therefore converted to Mhp-days as: effort(Mhp-hours) $\times 1/18$. After adjusting for effort by fleet in each area, and combining the fleets into the northern and southern fleets, our estimates for effort were 55.92 Mhp-days for the south, and 14.65 Mhp-days for the north.

Fixed costs were not considered within the analysis. The simplifying assumption was made therefore that changes in effort did not affect the fleet structure.

Equilibrium analysis

Partial fishing mortality $F_{a,s,l}$ was calculated as:

$$F_{a,s,l} = E_l q_{a,l} \mathrm{Sel}_{a,s,l},\tag{7}$$

where Sel is the selection pattern at age in each area (l), age (a), and sex (s), and q is catchability, i.e. the constant of proportionality that allows effort (E) to be scaled to F, taking into account the catchability by area and availability by age in each area (see above).

Expected stock dynamics were evaluated using an age-structured equilibrium model that combined SSB-per-recruit, yield-per-recruit, and stock-recruitment analyses, using partial fishing mortality-at-age (F_a) , natural mortality-at age (M_a) , and mass-at-age (W_a) data, with a stock-recruitment relationship. If all individuals die at age n, then the SSB-per-recruit (SSB/R) is given by

$$SSB/R = \sum_{a=r}^{n-1} e^{-\sum_{i=r}^{a-1} F_i + M_i} W_a Q_a + e^{-\sum_{i=r}^{n-1} F_i + M_i} \frac{W_n Q_n}{1 - e^{-F_n + M_n}},$$
(8)

where the second term is the plus-group (i.e. summation of all ages from the last age to infinity). Likewise, for yield-per-recruit (Y/R), if all individuals die at age *n*, then:

$$Y/R = \sum_{a=r}^{n-1} e^{-\sum_{i=r}^{a-1} F_i + M_i} W_i \frac{F_i}{F_i + M_i} (1 - e^{-F_i - M_i}) + e^{-\sum_{i=r}^{n-1} F_i + M_i} W_n \frac{F_n}{F_n + M_n},$$
(9)

where *a* is the age, *n* the oldest age, *r* the age at recruitment, W_a the mass-at-age in the catch, and Q_a the proportion mature-at-age.

The SSB is expressed as a function of the spawner-per-recruit ratio by rearranging the stock-recruitment model so that recruitment is a function of SSB/R. For a Beverton and Holt stock-recruitment model,

$$R = \alpha - \frac{\beta}{(\text{SSB}/R)}.$$
 (10)

SSB can then be found as a function of F from the product of Equations (8) and (10), and yield is calculated from the product of Equations (9) and (10).

All modelling was performed in R using the FLR framework (Kell *et al.*, 2007). For given levels of effort in the northern and southern fleets relative to 2002 levels (i.e. $F_{2002} * F_{mult}$), the level of recruitment (relative to that at virgin biomass) and expected profit (in this case, gross surplus) from the fleets combined were

calculated. Parameter values are presented in the Appendix. Other parameter values were taken from the ICES Working Group (ICES, 2004) or the sex-specific VPA (see above).

The results for recruitment and profit were compared with the relative positions of the current limit and precautionary biological reference points for plaice and sole (ICES, 2004; Table 1). Several alternative target reference points were also examined. In 2006, the European Commission adopted a proposal to establish a management plan for fisheries exploiting stocks of plaice and sole in the North Sea (Council Regulation no 2371/2002, OJ L 358, 31 December 2002) based on target fishing mortality (F_{target}) reference points of 0.3 and 0.2 for plaice and sole [SEC(2004) 1209 of 1 October 2004], respectively, values expected to result in optimum yields (but not necessarily MSY). Single-species MSY levels were examined to identify the changes necessary to fulfil obligations under the WSSD. For mixed fisheries, however, there are advantages in also considering fishery-related targets based on effort and yield. Therefore, the performance of the target reference points maximum economic yield (MEY) and maximum social yield (MSocY; see http://www.scotland.gov.uk/Topics/Fisheries/ Sea-Fisheries/Strategy/Advisory/SWG060123-NSRACMSYPaper) were also evaluated with respect to the financial implications for the fisheries. MSocY here is simplistically defined as the break-even or zero profit point, where effort is maximized in a non-lossmaking fishery, and hence is used as a proxy for maximum employment.

Results

Biological variability

Spatial distribution

The changes in distribution of sole and place relative to the mesh regulation line are shown in Figures 2a and 2b, respectively, for ages 3, 4, and 5 years. The proportion of place in the north is notably higher than that of sole, confirming its more northern

Table 1. Precautionary and limit biological reference points for plaice and sole in the North Sea.

Reference point	Plaice	Sole	
F _{lim}	0.74	_	
F _{pa}	0.60	0.40	
, F _{target}	0.3	0.2	
F ₂₀₀₂	0.7	0.46	
B _{lim (t)}	160 000	25 000	
B _{pa (t)}	230 000	35 000	

distribution. The proportion of both species in the north increased between 1983 and 2002, particularly for plaice aged 3 years.

Maturity- and mass-at-age

For sole, the maturity ogives developed from the logistic model parameters were comparable for the two periods (Figure 3a). In contrast, the maturity ogives of plaice suggested that females were maturing at a younger age in the late 1990s than in the late 1980s (Figure 3b). Note that the first quarter of the year represents the start of the spawning period for sole, and samples taken during the peak of spawning might have provided a different signal.

Using the GLM model, mass-at-age for each species in each year was predicted for quarter 1. Data limitations and the restriction to quarter 1 meant that predictions could only be made back to 1983. To illustrate trends in the predictions (rather than specific by-year estimates), a lowess smoother with span 0.5 was fitted to the data (Figure 4). Mass of age-5 female plaice decreased from the early 1980s to the early 1990s, then increased slightly. Female sole mass-at-age 5 mirrored these trends. The slight increase began later in sole than in plaice. Comparable temporal trends were seen within each species for ages 3 and above.

Stock-recruitment relationship

Initially, parameters for both steepness and virgin biomass were estimated for plaice and sole when fitting Beverton and Holt stock-recruitment relationships. However, unconstrained model fits to the plaice stock-recruit data resulted in implausible estimates (i.e. steepness > 1.0), because of a lack of data points at relatively low spawning-stock sizes and a general trend of declining recruitment at higher levels of SSB (Figure 5a). Therefore, steepness was fixed at 0.9 or 0.75, plausible values that made sense biologically (Kell et al., 2005a), and virgin biomass was then estimated at 12 600 and 15 300 kt, respectively. For sole, estimates of steepness of 0.9 and virgin biomass of 750 kt were obtained when freely fitting both parameters to the data (Figure 6a). However, the estimated standard error indicated that there was little information in the data with respect to steepness. Therefore, virgin biomass for sole was also estimated for a steepness set at 0.75, in which case virgin sole biomass was estimated as 1500 kt. The two values of steepness represent alternative hypotheses on the resilience of the stocks (i.e. high and low resilience) at low spawning-stock size.

Residuals from the stock-recruitment fits (Figures 5b and 6b) were standardized and smoothed using a lowess smoother (span = 0.5). The residuals showed considerable temporal variation. For plaice, the smoother indicated clear positive residuals, with







Figure 3. Maturity ogives estimated for female (a) sole, and (b) plaice in quarter 1, in the years 1985-1989 and 1995-1999.



Figure 4. Smoothed predicted quarter 1 mass-at-age 5 years for sole (open squares) and female plaice (filled diamonds) over the period 1983 – 2002.

increased residual variation, in the late 1980s, with generally negative residuals before the 1980s and in the late 1990s. Residual variance for sole also increased during the late 1980s. Although the smoother showed relatively little variation, residuals also tended to be generally negative in the 1990s and before the 1980s.

Biological scenarios

Temporal patterns in the stock-recruitment relationship residuals for plaice, and to a lesser extent for sole, varied between a relative high in the period 1985–1989 and a low from 1995 to 1999. These variations were mirrored by the trends in growth (higher for both sole and plaice in the late 1980s than in the late 1990s). In turn, maturity-at-age and the geographic distribution of plaice in particular also varied between these two periods. Whatever the causal factors for these decadal changes in biological parameters, they have implications for fisheries management.

In the subsequent equilibrium analyses, four biological scenarios were evaluated (Table 2). These scenarios corresponded to periods of high and low stock resilience (stock-recruitment steepness equal to 0.9 and 0.75, respectively) and high and low stock productivity (periods 1985–1989 and 1995–1999, respectively), and were used to evaluate the robustness of scientific advice and reference points to variations in stock dynamics.

Equilibrium analysis

Single-stock limit and precautionary reference points

The effect of biological changes on limit reference points is shown in Figure 7, where the ratio of recruitment to virgin recruitment, i.e. an index of the extent of recruitment-overfishing, is plotted as a function of effort relative to 2002 levels in the southern and



Figure 5. (a) Stock-recruitment data for plaice, and the Beverton and Holt relationship where steepness is 0.9 (dotted line) and 0.75 (solid line). (b) Standardized residuals (points) and smoothed standardized residuals (line) from a fit where steepness is 0.9.



Figure 6. (a) Stock-recruitment data for sole, and the Beverton and Holt relationship where steepness is 0.9 (dotted line) and 0.75 (solid line). (b) Standardized residuals (points) and smoothed standardized residuals (line) from a fit where steepness is 0.9.

northern North Sea. Effort corresponding to the target fishing mortality, $F_{\rm pa}$, and $F_{\rm lim}$, as well as to biomass corresponding to $B_{\rm pa}$, $B_{\rm lim}$, and the level at which the stock would collapse are indicated.

For plaice (Figure 7a-d), the isobars are diagonal, indicating that effort in both the northern and southern fleets influenced recruitment levels. Changes in resilience (rows) have a greater effect than changes in productivity (columns). Under the highresilience scenarios, both B_{lim} and B_{pa} correspond to recruitment >85% of virgin, whereas for low resilience, they correspond to a level >65%. The biomass reference points for plaice therefore appear robust to changes in stock productivity and resilience. However, given its proximity to Blim, Bpa would appear to provide only a small buffer to that limit reference point when considering the impact on recruitment, because a relatively small increase in effort will result in B_{lim} being breached when at B_{pa} . For plaice, F_{lim} and F_{pa} correspond to recruitment at levels of 80% of virgin when resilience is high. When resilience is low, however, Flim corresponds to 43% and 63% of virgin recruitment, and F_{pa} to 62% and 77%, when productivity is low and high, respectively (Table 3). Fishing at F_{target} implies recruitment levels close to virgin (>85% of virgin levels under all conditions). The fishing mortality and biomass reference points are consistent (i.e. precautionary reference points do not imply breaching limit levels) when productivity or resilience is high. However, fishing mortality reference points imply lower relative recruitment than their biomass counterparts when productivity is low, and in particular when both stock productivity and resilience are low. In all scenarios, the precautionary and limit reference points appear to offer a buffer to plaice stock collapse.

Table	2.	Scenarios	for	equilibrium	analyses.
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Resilience	Productivity			
	Low	High		
High	Years = 1995 – 1999,	Years = 1985 – 1989,		
	steepness = 0.9	steepness = 0.9		
Low	Years = 1995 – 1999,	Years = 1985 - 1989,		
	steepness = 0.75	steepness = 0.75		

In contrast to plaice, the recruitment isobars for sole are vertical, indicating that only effort in the south has an effect on sole recruitment (Figure 7e-h). This reflects the small numbers of sole in the north and the larger mesh size used there. As for plaice, the clearest impacts are seen under the different resilience scenarios. Under the high and low resilience scenarios, Blim corresponds to a level of recruitment around 63% and 36% of virgin, respectively, and B_{pa} to ~71% and 45%. Those percentages hold under either productivity scenario (Table 3). Although B_{pa} provides a buffer to B_{lim} , as for plaice, this buffer is relatively small, particularly under the low-resilience scenario. F_{pa} (F_{lim} is not defined for sole) corresponds to fishing mortality at 2002 levels of effort, whereas F_{target} corresponds to ~80% of virgin recruitment if resilience is high, but only 35-50% if resilience is low. Fishing at F_{pa} has the potential to drive the stock to extinction where resilience and productivity are low, suggesting it is not robust to biological uncertainty. The F_{pa} level is only consistent with the B_{pa} level where productivity and resilience are high.

Across the species, the biggest impact on the limit reference points is the assumed resilience of the stock at low SSBs, rather than its productivity. However, consideration of stock productivity can be critical at levels close to that of stock collapse, particularly for sole.

Target and mixed-stock reference points

Figure 8 presents profit (as a percentage of the maximum profit across all scenarios) combining stocks and fleets, as a function of effort in the north and the south (relative to the 2002 levels) for the resilience (rows) and productivity (columns) scenarios.

The general vertical orientation of the isobars show that reducing effort in the south has a much greater effect on profit than reducing effort in the north. Highest profit is seen in the bottom right hand panel, representing high productivity and low resilience; at high SSB levels under low fishing mortality, a greater level of recruitment results than with the other productivity and resilience combinations.

The maximum profit or MEY, indicated by the plus sign, is found at \sim 50% of 2002 effort in the north, but at much lower than 2002 effort in the south, for all scenarios. MEY is strongly affected by productivity, with MEY under low productivity being around 45% of the maximum profit across scenarios (Table 4).



Figure 7. (Top) Plaice and (bottom) sole recruitment relative to recruitment at virgin biomass, as a function of effort (relative to 2002 levels) in the northern and southern North Sea. The top row of each block represents high resilience, and the left column low productivity. Isopleths show graduations in relative recruitment, i.e. the lightest shade corresponds to 100% of virgin recruitment, and red to zero. Lines represent the effort level corresponding to stock collapse (solid blue line), $B_{\rm linn}$ and $B_{\rm pa}$ (medium and thin blue lines). Effort levels corresponding to the target fishing mortality ($F_{\rm target}$), $F_{\rm par}$ and $F_{\rm lim}$ are shown by the star, and open and closed triangles, respectively. Note that $F_{\rm lim}$ has not been set for sole.

The effort levels corresponding to MSY (blue and green circles for plaice and sole, respectively) also show that a decrease in southern fleet effort has a much greater effect than a reduction in northern effort. Indeed, effort in the north can be increased from 2002 levels to achieve MSY for both species. The underlying profit at MSY is

Table 3.	Recruitment as a	percentage	of recruitment	at virgin
biomass	at each reference	point.		

Stock	Resilience	Productivity	B _{lim} (%)	B _{pa} (%)	F _{lim} (%)	F _{pa} (%)	F _{target} (%)
Plaice	High	Low	87	91	82	88	96
		High	87	90	88	92	97
	Low	Low	68	76	43	62	88
		High	67	75	63	77	94
Sole	High	Low	63	71	-	62	79
		High	63	71	-	69	84
	Low	Low	37	45	-	0	34
		High	36	44	-	8	50

Percentage calculated within scenarios.

affected by the productivity and resilience scenarios, for plaice by between 22% and 69%, and for sole by between 6% and 19% of the maximum overall profit (Table 4).

 $F_{\rm target}$ levels (blue and green star for plaice and sole, respectively) are consistent, and imply a 50% reduction in effort in both southern and northern fleets. They lie between the breakeven line and MEY. Resulting profits range from 18% to 58% of the maximum overall profit, dependent on the biological scenario (Table 4).

At the break-even point, combined profits are zero, but effort and hence employment is greater than at either MEY or MSY. In a mixed fishery with more than one fleet, however, the break-even



Figure 8. Expected profit, for plaice and sole and both fleets combined, as a function of effort (relative to 2002 levels) in the northern and southern North Sea. The top row represents high resilience, and the left column low productivity. Isopleths represent increments of profit, relative to the break-even point (no profit, black line). Lighter colours represent greater profit, with the plus sign indicating the location of maximum profit. Other lines represent the effort level corresponding to the collapse of plaice (blue line) and of sole (green line). Target effort levels (F_{target} ; blue and green stars for plaice and sole, respectively) and MSY levels (blue and green circles for plaice and sole, respectively) are also shown.

Resilience	Productivity	MSY _{plaice} (%)	MSY _{sole} (%)	MEY (%)	MSocY (%)	F _{target} (%)
High	Low	22	6	45	0	24
	High	44	17	82	0	53
Low	Low	23	10	44	0	18
	High	69	19	100	0	58

Table 4. Combined profit achieved at each target reference point examined under each biological scenario, as a percentage of maximum profit across the scenarios.

point corresponds to a line rather than a point. The break-even line is reasonably vertical, showing again that it is more important to manage the southern fleet than the northern. It is therefore potentially profitable to fish in the north even at increased levels of effort over those in 2002, if effort in the south is controlled. Break-even conditions are affected by changes in both resilience and productivity. Under low resilience and low productivity, 2002 effort levels would result in the two fisheries making a loss, whereas under the other scenarios, the fleets could operate at a profit; i.e. under those conditions, more effort could be financially sustainable. When stock resilience and productivity are low, fishing at 2002 effort levels may be sufficient to collapse the sole stock. In turn, the fact that when resilience is low, fleets can breakeven at southern effort levels greater than that required to collapse the sole stock, implies that there could be an incentive to overfish sole.

Discussion

This analysis of historical North Sea plaice and sole biological characteristics has shown that there have been large changes in the productivity of these stocks over recent decades. There is uncertainty about both the causes of these changes, and the ability of the two stocks to withstand fishing. Rijnsdorp (1993) and Grift et al. (2007) suggest that changes in maturation can result from exploitation. Perceived shifts in plaice distribution could be linked to fishing pressure, resulting from the use of smaller-mesh gear in the southern North Sea and differential depletion of spatially segregated substocks (e.g. Wright et al., 2006), whereas overall reductions in population size may result in stock contraction into optimal habitats (Blanchard et al., 2005). Changes in flatfish distribution have also been linked to climate change and variations in competition and predation levels (Perry et al., 2005; van Keeken et al., 2007). A major question with respect to scientific management advice is therefore: given such biological variation and uncertainty, how do current management approaches perform, and how can we successfully move to a target-based system consistent with commitments under the WSSD within mixed fisheries?

Within the traditional ICES management system, this study suggests that current mortality limit and precautionary reference points for plaice are generally robust to variation in and uncertainty about biological parameters, but they may not be consistent with each other under all conditions. In turn, while the biomass reference points for sole appear to be relatively robust to biological uncertainty, the F_{pa} level does not; fishing at that level could result in stock collapse under certain scenarios. With a properly applied and managed move towards target reference points, however, the current limit reference points should become less critical as the stock moves to a more sustainable state.

There are well-documented issues with the definition and performance of MSY targets in fisheries where there are natural

fluctuations in the resource (Sissenwine, 1978; Rosenberg and Restrepo, 1994; Mace, 2001; Powers, 2005). The movement towards an MSY target is further complicated where fish stocks are caught in a multispecies, multifleet fishery such as that for North Sea flatfish. In addition to these problems, as Maunder (2002) and Powers (2005) stress, determination of reference points depends on the selectivity of fleets, the relative mix of fleets that management desires, and any bycatch of non-target fisheries. As a result, when applied to the North Sea flatfish fishery, the use of single-species MSY values as targets for either stock implies quite different consequences for the fleets. The position of MSY for plaice is obtained at levels of effort in the northern fleet much greater than 2002 levels. In contrast, the southern fleet would have to fish at much reduced levels, if at all. This is because of the selectivity of the gear for younger plaice and the greater availability of young plaice in the southern area before they move north with age. As a result, plaice are susceptible to growth-overfishing in the south. Discarding undersized plaice means that they do not contribute to catch or revenue. Southern effort at MSY for sole is much lower than 2002 levels, implying that a large reduction in effort (and hence employment) would be required. Effort in the north could be very high, although little sole revenue comes from that fishery-the catchability of sole (availability and selectivity) in the northern fleet is very low, and catches are limited to the larger, older fish. Obviously, this statement ignores the influence of markets and prices on fleet behaviour.

Achieving MEY required considerable reductions in the effort of both fleets, although like MSY, those reductions fall disproportionately on the southern fleet. Clearly, consideration must be given to whether MEY is an appropriate management target, because at that point the ratio of revenue to cost is large. This could mean that only a few vessels prosecute the fishery, making a large profit on a shared resource. Increased profitability could also mean that investment can be increased, leading to increased efficiency and catchability. This could support calls to increase fishing mortality and pressure to ignore downward revisions in quotas.

An alternative management goal of maximizing employment opportunities in a fishery was examined. In our analysis, we made the simplistic assumption that this related to those effort levels that are just economically sustainable. In a mixed fishery, this break-even point does not relate to a single point (e.g. MSocY), but to a line. Decisions on the relative effort and catches of different fleets are therefore required. Such a barely economically sustainable level of effort is affected by both productivity and resilience. Under the assumptions made within our analysis, where there are conditions of low productivity and low resilience, fleets would not break-even at 2002 effort levels, and there is also the potential to collapse the sole stock. Although fixed costs were not considered, their inclusion would be expected to increase the profit gradient across the effort surface; at higher effort, fixed costs would be greater (and hence combined profit lower), whereas at low effort, fixed costs would likely be lower, but not to the same degree. The break-even line would therefore shift to lower effort levels (i.e. towards the origin), particularly for the southern fleet. Given the expected non-linear effect of including fixed costs, the effort levels required to achieve maximum profit (which is at low effort levels) should be less affected. Additionally, some 20% of the revenue in the North Sea flatfish fishery is known to come from the sale of bycatch species (Ulrich *et al.*, 2002), which is also not considered in this analysis. When taking potential bycatch revenue into account, the fishery could be viable in the long term at 2002 effort levels under all scenarios, but the potential to collapse the sole stock would remain.

 F_{target} lies between MEY and the break-even line, so may represent a trade-off between goals of maximizing profit, and maximizing employment. The F_{target} levels for both species are consistent, and allow effort to be reduced equally between the two fleets. Indeed, the efforts required to achieve target reference points MSY, F_{target} , and MEY were robust to uncertainty about the biological productivity and resilience of the stocks, because they varied little between scenarios. However, profits, yields, and underlying recruitment resulting from these effort levels did vary widely with system productivity. For example, the performance of F_{target} for sole suffered where stock resilience was low, resulting in reduced recruitment. This has obvious socio-economic consequences, because management might be able to set appropriate effort levels (e.g. cost), but not yields (e.g. revenue).

To be achieved, many of the target reference points examined require disproportionate changes in effort for the southern fleet. This unequal division of effort between fleets (particularly if they are from different nations) has the potential to go against one of the basic principles of the Common Fisheries Policy of the European Union, "relative stability" (Articles 32–37 of the EC Treaty; Holden, 1994). The situation is further complicated by the need to balance issues including the levels of historical fishing by given fleets, the availability of other fishing opportunities, the relative importance of fleets, target, and bycatch species, and the need for jobs vs. greater profits for some. Decisions on the relative effort and catches of fleets therefore have to be decided on a social, institutional, and/or economic basis rather than a purely biological basis, and will depend on specific circumstances.

We therefore suggest that a more holistic view of management objectives is required when setting reference points. Biological management objectives need to be combined with economic analyses, so that trade-offs between risk to stocks, yield levels, employment opportunities, and other social objectives such as extracting rent from profitable fisheries can be fully evaluated across fleet sectors. Before an appropriate advice and management framework can be developed, however, the relative importance of each of these objectives needs to be explicitly stated and assigned priority. These priorities, with the corresponding definition of trade-offs and acceptable risk levels, and the prioritization of fleet-specific goals, are a management decision.

Once this is defined, the performance of reference points should be examined using management strategy evaluation, computer-based experiments that embody how the whole system reacts to a variety of possible management actions (Kirkwood and Smith, 1996; Punt, 2006; De Oliveira et al., 2008). The robustness of management strategies and their associated reference points to uncertainty about the "true" system dynamics, and their ability to meet the requirements of the precautionary approach to fisheries management advocated by the FAO (1996) can then be evaluated as a part of data-collection regimes, fleetbased economic considerations, stock assessment procedures, and harvest control rules, and against the pre-agreed priorities in collaboration with managers and others (Deas, 2000). As in this study, population dynamics should be deduced from a range of plausible hypotheses and available datasets, rather than being based on a single set of assumptions. In this way, uncertainty in our ability to estimate stock status and reference points and to implement management can be accounted for when investigating the next step on from the equilibrium approach used here: how target reference points can be reached when starting from our current situation.

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References

- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fishery Investigations, London, Series II, 19. 533 pp.
- Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., and O'Brien, C. M. 2005. Distribution-abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. Canadian Journal of Fisheries and Aquatic Sciences, 62: 2001–2009.
- COFI. 2003. World Summit on Sustainable Development 2002 and its implications for fisheries. Committee on Fisheries, 25th session, Rome, Italy, 24–28 February 2002. COFI/2003/Inf.14.
- Cushing, D. H. 1995. The long-term relationship between plankton and fish. ICES Journal of Marine Science, 52: 611–626.
- De Oliveira, J. A. A., Kell, L. T., Punt, A. E., Roel, B. A., and Butterworth, D. S. 2008. Managing without best predictions: the management strategy evaluation framework. *In* Advances in Marine Science. 50 Years on from Beverton and Holt, pp. 104–134. Ed. by A. Payne, J. Cotter, and T. Potter. Blackwell Publishing, Oxford. xxi+546 pp.
- Deas, B. 2000. Fisherman and scientists: collaboration as the basis for stock recovery. ICES Document CM 2000/X: 03.
- FAO. 1996. Precautionary approach to capture fisheries and species introductions. Elaborated by the Technical Consultation on the Precautionary Approach to Capture Fisheries (including Species Introductions). Lysekil, Sweden, 6–13 June 1995. FAO Technical Guidelines for Responsible Fisheries, 2. 54 pp.
- Francis, R. I. C. C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus*

atlanticus) on the Chatham Rise, New Zealand. Canadian Journal of Fisheries and Aquatic Sciences, 49: 922–930.

- Grift, R. E., Heino, M., Rijnsdorp, A. D., Kraak, S. B. M., and Dieckmann, U. 2007. Three-dimensional maturation reaction norms for North Sea plaice. Marine Ecology Progress Series, 334: 213–224.
- Holden, M. 1994. The Common Fisheries Policy. Origin, Evaluation and Future. Fishing News Books, Oxford.
- Holm, P., and Nielsen, K. N. 2004. The TAC Machine. Appendix B, Working Document 1 in ICES, 2004, Report of the Working Group for Fisheries Systems (WGFS). Annual Report.
- Hunter, E., Metcalfe, J. D., and Reynolds, J. D. 2003. Migration route and spawning fidelity by North Sea plaice. Proceedings of the Royal Society of London, Series B—Biological Sciences, 270: 2097–2103.
- ICCAT. 2003. Basic Texts. International Commission for the Conservation of Atlantic Tuna, 3rd edn. ICCAT Publication, Madrid.
- ICES. 2004. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2004/ACFM: 07.
- Kell, L. T., and Bromley, P. J. 2004. Implications for current management advice for North Sea plaice (*Pleuronectes platessa* L.). 2. Increased biological realism in recruitment, growth, density dependent sexual maturation and the impact of sexual dimorphism and fishery discards. Journal of Sea Research, 51: 301–312.
- Kell, L. T., Mosqueira, I., Grosjean, P., Fromentin, J-M., Garcia, D., Hillary, R., Jardim, E., *et al.* 2007. FLR: an open-source framework for the evaluation and development of management strategies. ICES Journal of Marine Science, 64: 640–646.
- Kell, L. T., Pastoors, M., Scott, R., Smith, M., Van Beek, F., O'Brien, C. M., and Pilling, G. M. 2005a. Evaluation of multiple management objectives for Northeast Atlantic flatfish stocks: sustainability vs. stability of yield. ICES Journal of Marine Science, 62: 1104–1117.
- Kell, L. T., Pilling, G. M., Kirkwood, G. P., Pastoors, M., Mesnil, B., Korsbrekke, K., Abaunza, P., *et al.* 2005b. An evaluation of the implicit management procedure used for some ICES roundfish stocks. ICES Journal of Marine Science, 62: 750–759.
- Kirkwood, G. P., and Smith, A. D. M. 1996. Assessing the precautionary nature of fishery management strategies. *In* Precautionary Approach to Fisheries. 2. Scientific Papers. Prepared for the Technical Consultation on the Precautionary Approach to Capture Fisheries (including Species Introductions). Lysekil, Sweden, 6–13 June 1995 (a scientific meeting organized by the Government of Sweden in cooperation with FAO). FAO Fisheries Technical Paper, 350, Part 2.
- Köster, F. W., Mollmann, C., Hinrichsen, H-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment—the impact of climate variability on key processes. ICES Journal of Marine Science, 62: 1408–1425.
- Kraak, S. B. M., Buisman, F. C., Dickey-Collas, M., Poos, J. J., Pastoors, M. A., Smit, J. G. P., van Oostengbrugge, J. A. E., *et al.* 2008. The effect of management choices on the sustainability and economic performance of a mixed fishery: a simulation study. ICES Journal of Marine Science, 65: 697–712.
- Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., and Picaut, J. 1997. *El Niño* Southern Oscillation and tuna in the western Pacific. Nature, 389: 715–718.
- Mace, P. M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish and Fisheries, 2: 2–32.

- Maunder, M. N. 2002. The relationship between fishing methods, fisheries management and the estimation of maximum sustainable yield. Fish and Fisheries, 3: 251–260.
- Millner, R., Flatman, S., Rijnsdorp, A. D., van Beek, F. A., De Clerck, R., Damm, U., Tetard, A., *et al.* 1996. Comparison of long-term trends in growth of sole and plaice populations. ICES Journal of Marine Science, 53: 1196–1198.
- Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Climate change and distributional shifts in marine fishes. Science, 308: 1912–1915.
- Piet, G. J., and Rice, J. C. 2004. Performance of precautionary reference points in providing management advice on North Sea fish stocks. ICES Journal of Marine Science, 61: 1305–1312.
- Powers, J. E. 2005. Maximum sustainable yield and bycatch minimization "to the extent practicable". North American Journal of Fisheries Management, 25: 785–790.
- Punt, A. E. 2006. The FAO precautionary approach after almost 10 years: have we progressed towards implementing simulation-tested feedback-control management systems for fisheries management? Natural Resource Modelling, 19: 441–464.
- Rijnsdorp, A. D. 1993. Fisheries as a large-scale experiment on lifehistory evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice *Pleuronectes platessa* L. Oecologia, 96: 391–401.
- Rijnsdorp, A. D., and van Leeuwen, P. I. 1996. Changes in growth of North Sea plaice since 1950 in relation to density, eutrophication, beam-trawl effort, and temperature. ICES Journal of Marine Science, 53: 1199–1213.
- Rosenberg, A. A., and Restrepo, V. R. 1994. Uncertainty and risk evaluation in stock assessment advice for US marine fisheries. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2715–2720.
- Shepherd, J. G., and Nicholson, M. D. 1991. Multiplicative modelling of catch-at-age data and its application to catch forecasts. ICES Journal of Marine Science, 47: 284–294.
- Sissenwine, M. P. 1978. Is MSY an adequate foundation for optimum yield? Fisheries, 3: 22–42.
- STECF (Scientific, Technical and Economic Committee for Fisheries). 2003. Report of the *Ad Hoc* Working Group on Mixed Fisheries, Brussels, 21–24 October 2003. 78 pp.
- Ulrich, C., Sparre, P. J., and Marchal, P. 2002. Influence of trends in fishing power on bioeconomics in the North Sea flatfish fishery regulated by catches or by effort quotas. Canadian Journal of Fisheries and Aquatic Sciences, 59: 829–843.
- UN. 1982. United Nations Convention on the Law of the Sea (UNCLOS). United Nations, New York. 208 pp.
- van Keeken, O. A., van Hoppe, M., Grift, R. E., and Rijnsdorp, A. D. 2007. Changes in the spatial distribution of North Sea plaice (*Pleuronectes platessa*) and implications for fisheries management. Journal of Sea Research, 57: 187–197.
- Vinther, M., Reeves, S. A., and Patterson, K. R. 2004. From single-species advice to mixed-species management: taking the next step. ICES Journal of Marine Science, 61: 1398–1409.
- Waples, R. S., and Gaggioti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Molecular Ecology, 15: 1419–1439.
- Wright, P. J., Neat, F. C., Gibb, F. M., and Gibb, I. M. 2006. Evidence for metapopulation structuring in cod from the West of Scotland and North Sea. Journal of Fish Biology, 69: 181–199.

Appendix: tables of parameter values used within models

Table A1. Biological parameters.

Biological parameter	Plaice		Sole	
	High productivity (1985–1989)	Low productivity (1995–1999)	High productivity (1985–1989)	Low productivity (1995 – 1999)
Maturity-at-age	Female/male	Female/male	Sexes combined	Sexes combined
2	0.00	0.11	0.41	0.49
3	0.11	0.25	0.79	0.72
4	0.50	0.66	0.97	0.96
5	1	0.92	1	0.98
6	1	0.98	1	1
7	1	1	1	1
Mass-at-age (kg)	Female/male	Female/male	Sexes combined	Sexes combined
2	0.20/0.20	0.19/0.20	0.12	0.12
3	0.24/0.21	0.26/0.22	0.21	0.20
4	0.33/0.25	0.35/0.26	0.32	0.30
5	0.46/0.31	0.44/0.30	0.43	0.38
6	0.55/0.36	0.52/0.34	0.51	0.45
7	0.63/0.38	0.61/0.35	0.56	0.53
8	0.69/0.41	0.64/0.36	0.60	0.57
Proportion in north by age	Female/male	Female/male	Sexes combined	Sexes combined
2	0.14/0.29	0.56/0.54	0.17	0.18
3	0.44/0.52	0.67/0.69	0.18	0.21
4	0.66/0.70	0.72/0.70	0.19	0.23
5	0.66/0.70	0.74/0.73	0.21	0.21
6	0.71/0.69	0.73/0.72	0.21	0.21

Table A2. Selectivity parameters by gear and species.

Table A3. Economic parameters.

Selectivity	South (80 mm)		North (100 mm)	
	Plaice	Sole	Plaice	Sole
L ₂₅	15.3	24.0	20.5	27.5
L ₅₀	16.8	25.1	22.0	30.1

Age (years)	Price-at-age (€ kg ⁻¹)		
	Plaice	Sole	
1	1.81	7.18	
2	1.81	7.18	
3	1.81	8.82	
4	1.93	8.82	
5	1.93	11.14	
6	2.39	11.14	
7	2.39	14.46	
8	2.39	14.46	
9	2.39	14.46	
10	3.42	14.46	
11	3.42	15.23	
12	3.42	15.23	
13	3.42	15.23	
14	3.42	15.23	
15	3.42	15.23	
Parameter	Variable cost func	tion ^a	
θ	0.4715		
ρ	1.4021		

^aAfter Kraak *et al.* (2008).

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