

# Lumpers or splitters? Evaluating recovery and management plans for metapopulations of herring

Laurence T. Kell, Mark Dickey-Collas, Niels T. Hintzen, Richard D. M. Nash, Graham M. Pilling and Beatriz A. Roel

Kell, L. T., Dickey-Collas, M., Hintzen, N. T., Nash, R. D. M., Pilling, G. M., and Roel, B. A. 2009. Lumpers or splitters? Evaluating recovery and management plans for metapopulations of herring. – *ICES Journal of Marine Science*, 66: 1776–1783.

The long-term management of a stock representing a metapopulation has been simulated in a case study loosely based upon herring to the west of the British isles, where stocks are currently assessed and managed by management area, although there is evidence of mixing between stocks (in terms of connectivity, migrations, and exploitation). The simulations evaluate scientific advice (based on virtual population analysis, VPA) and the sustainability of fishing under two population-structure scenarios, corresponding either to discrete stocks, which only mix on the feeding grounds, or where diffusion between stocks takes place. The ability of stock assessment to monitor stock status and exploitation levels was evaluated for defining stocks based on fishing areas and for stocks that combined fishing areas. The study showed that assessment based on VPA of the metapopulation could fail to detect overexploitation of stocks and fail to detect and distinguish between the effects of exploitation and regime shifts.

**Keywords:** diffusion, evaluation, fishery, FLR, herring, management, metapopulations, mixing, populations, regime shifts, stock definition, virtual population analysis.

Received 4 September 2008; accepted 12 April 2009; advance access publication 9 July 2009.

L. T. Kell, G. M. Pilling, and B. A. Roel: *Cefas, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK.* L. T. Kell current address: *International Commission for the Conservation of Atlantic Tunas (ICCAT), Corazón de Maria 8, Planta 6, 28002 Madrid, Spain.* M. Dickey-Collas and N. T. Hintzen: *Wageningen Institute for Marine Resources and Ecosystem Studies (IMARES), PO Box 68, 1970 AB IJmuiden, The Netherlands.* R. D. M. Nash: *Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway.* Correspondence to L. T. Kell: tel: +34 914 165 600; fax: +34 914 152 612; e-mail: laurie.kell@iccat.int.

## Introduction

A key concept in fishery science and management is the unit stock, defined as a population aggregate that can be managed as a discrete unit (Quinn and Deriso, 1999). Such a definition implies that stocks of the same species are largely isolated from each other and are self-sustaining, that fisheries do not take mixed catches from different stocks, and that management regulations can be enforced by stock. However, Waples and Gaggiotti (2006), in their review entitled “What is a population?”, conclude that no consensus has yet emerged regarding a quantitative definition of a stock or a population. Instead, one has to rely on qualitative descriptions, such as “a group of organisms of the same species occupying a particular space at a particular time” (Krebs, 1994). If fisheries catch fish from aggregations of mixed origin and these catches are assigned to a specific stock, the results of assessments using classical methods are confounded for all stocks involved. Furthermore, management advice in terms of total allowable catches (TACs) from a stock that is defined operationally (e.g. by the area within which a fishery operates), rather than in terms of biological understanding of population structure (Reiss *et al.*, 2009), may have unforeseen ecological and evolutionary impacts. To avoid confusion, the term “population” will be used here to

refer to more-or-less reproductively isolated spawning components within a metapopulation (Levins, 1969), and “stock” to the management unit as defined by catches from the fisheries.

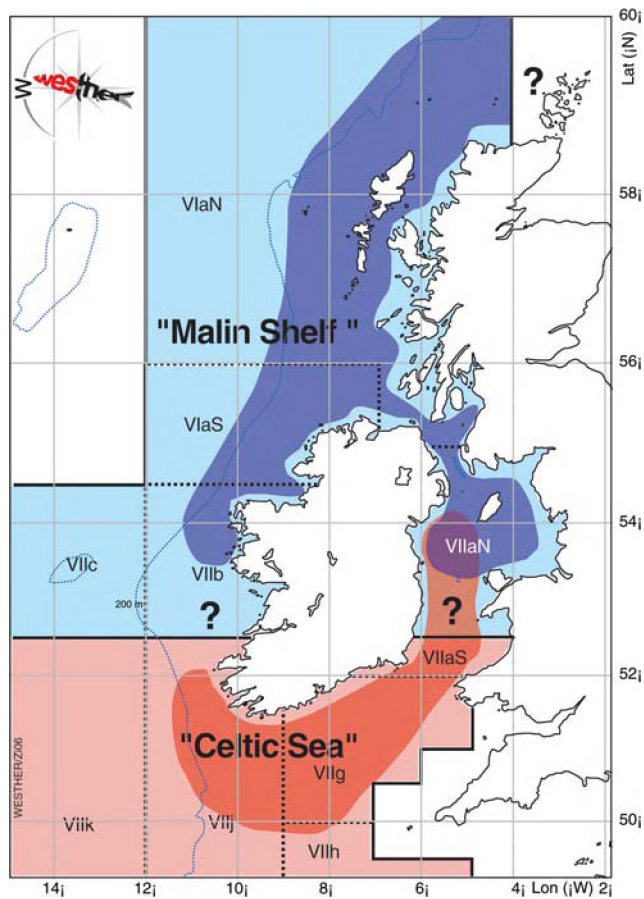
There is an ever-expanding suite of techniques available to define populations. Waldman (1999) therefore suggested that any choice of stock definition must balance costs, sampling needs, the likelihood of detecting multiple populations within or among stocks, and persistence, and should fit the particular management context. We address the consequences for assessment of defining stocks on fisheries, rather than on reproductive isolation (i.e. real populations), through a case study loosely based on what is known about herring populations to the west of the British Isles. Herring in this area are currently assessed and managed as four separate stocks (ICES, 2008; Figure 1): west of Scotland (VIaN), west of Ireland (VIaS), Irish Sea (VIIaN), and Celtic Sea (VIIaS, VIIg, VIIh, VIIj, VIIk). There are also smaller spawning stocks, such as the Clyde, which are not regularly assessed, although they have supported important fisheries in the past.

Based on historical information, these stocks have been defined by geographical areas and have been assigned a “spawner type” (i.e. spawning in autumn, winter, or spring), although, within an area, different populations may spawn in different seasons

© Crown Copyright 2009. Reproduced with the permission of the Controller of Her Majesty’s Stationery Office.

For Permissions, please email: journals.permissions@oxfordjournals.org

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/2.0/uk/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.



**Figure 1.** Fisheries and populations to the west of the British Isles. Supplied by C. Zimmermann through the WESTHER project.

(Mitchell, 1864; Samuel, 1918; Parrish and Saville, 1965). The main summer feeding aggregations are on the Malin Shelf and in the Celtic Sea (Parrish and Saville, 1965; Figure 1) and are thought to comprise fish from a number of populations. Fisheries target these aggregations of feeding fish, and the catches are apportioned to stocks based on the boundaries of the management unit in which they are taken, rather than based on the population to which they belong.

Since the early 1990s, conflicting trends have been seen not only in the catch data for the four stocks, but also between catch and survey data. The problems have been exacerbated by apparent changes in their productivity (Simmonds and Keltz, 2007). In turn, management measures have failed to prevent overexploitation (ICES, 1994, 2008; Molloy, 2006), and the definitions of assessment and management units (i.e. the stocks) have changed repeatedly since routine assessments started (ICES, 1994; Molloy, 2006). Recent studies and the results of an EU-funded project (WESTHER) indicate that the population structure within the whole area is complex and that fisheries and management are apparently not always linked to discrete populations (Mackenzie, 1985; Brophy *et al.*, 2006; Campbell *et al.*, 2007).

Stephenson (1999) noted difficult management problems caused by the complex population structure of herring in the western Atlantic and argued that persistence of the full diversity of spawning components within each management unit should become a principle of management under the “precautionary approach”. This would represent a default position (e.g. a reversal

of the burden of proof) different from that used for most stocks to date. In other words, we should expect a complex population structure and ensure the management of stocks at appropriate scales to preserve population complexity (cf. McPherson *et al.*, 2001; Ruzzante *et al.*, 2006; Secor *et al.*, 2009). Therefore, the development of appropriate assessment and management procedures to maintain separate spawning components in a healthy state where fisheries exploit multiple components is a major challenge. The answer to the conundrum of lumping or splitting stocks depends on the ability of assessment methods to estimate the status of, and fishing pressure on, each of these in relation to the target and limit reference points required by the precautionary approach (FAO, 1996).

We evaluate other practical options related to the assessment process, such as survey timing and identification of catch by spawning population, in terms of their impact on the estimates of spawning-stock biomass ( $S$ ), exploitation rate ( $H$ ), and appropriate reference points for management. To this end, we develop a simulation framework that can be used to investigate the consequences of taking into account (splitting) or ignoring (lumping) the known underlying population demography. Specifically, we test our ability to provide robust advice on  $S$  and  $H$ . In addition, we evaluate the potential impact of regime shifts on our perception of the metapopulation structure and the consequences of differential levels of exploitation across populations.

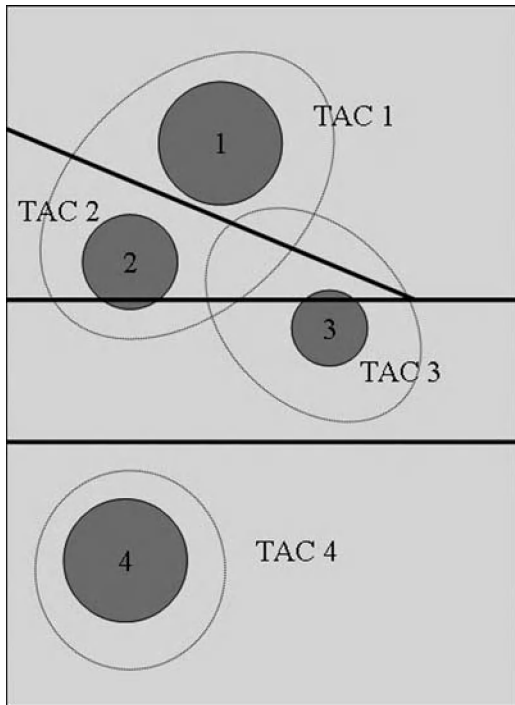
## Material and methods

### Framework

The “Fisheries Library in R” (FLR) framework (Kell *et al.*, 2007; www.flr-project.org) for management strategy evaluation was used to build an operating model (OM) that can represent alternative hypotheses about stock and fishery dynamics, allowing a higher level of complexity and assumptions than used by standard stock-assessment models. An observation-error model is used to sample pseudo-data from the OM, and a stock-assessment and management procedure to derive estimates of stock status from the pseudo-data and to provide management advice.

Four populations were constructed, corresponding to the west of Scotland (population 1), west of Ireland (population 2), Irish Sea (population 3), and Celtic Sea (population 4) stocks (i.e. based on where and when they spawn), and four fisheries, based on their feeding migrations, were distinguished by sharp geographical boundaries (Figure 2). These fisheries define the fish as belonging to four stocks, which are managed by individual TACs, and only in one case—population 4—does the stock correspond exactly to a population. This generic scheme roughly mimics the population structure seen in Figure 1; this is not meant to add complete realism to our simulation, but rather to facilitate realistic input parameters for herring stocks in a general way. Although the biological parameters and historical estimates of stock status were taken from the ICES assessments for the herring stocks west of the British Isles, these have all been biased about the “biological” populations in our scheme because the estimates assumed no mixing among stocks. Also, the availability of each spawning population to the fishery in each area is unknown. Nevertheless, this configuration allows us to contrast, within a stock-assessment context, an isolated population with others that have varying degrees of connectivity.

The four fisheries, operating in the four areas during the feeding season, determine the availability of each population to



**Figure 2.** Diagrammatic representation of the mixing hypotheses (dark grey circles, spawning aggregations of the four “populations”; dotted circles, their distribution area during the feeding season; straight lines, the borders of the assessment/management units or “stocks”).

**Table 1.** Percentage availability of all age groups in each population (1–4) to each fishery (1–4).

Fishery	Population (%)			
	1	2	3	4
1	75	25	25	0
2	25	75	25	0
3	0	0	50	0
4	0	0	0	100

**Table 2.** Fidelity of populations under the diffusion hypothesis.

Population	Age of fish	Diffusion between populations (%)			
		1	2	3	4
1	1	95	2.5	2.5	0
	2	95	2.5	2.5	0
	3 <sup>+</sup>	95	2.5	2.5	0
2	1	2.5	95	2.5	0
	2	2.5	95	2.5	0
	3 <sup>+</sup>	2.5	95	2.5	0
3	1	2.5	2.5	75	20
	2	2.5	2.5	85	10
	3 <sup>+</sup>	2.5	2.5	95	0
4	1	0	0	20	80
	2	0	0	10	90
	3 <sup>+</sup>	0	0	0	100

each fishery (Table 1). Population fidelity is assumed to be 100%, so the only interaction is through mixing in the feeding areas. An alternative hypothesis, of limited diffusion, has been implemented (in addition to mixing) by allowing a fixed proportion by age group and population to move annually to other populations (Table 2). However, detailed results are only presented for the option based on 100% fidelity because the effects of diffusion were subordinate to those of mixing.

Time-series of catch, stock numbers, and fishing mortality-at-age ( $F_a$ ) for populations 1–4 are taken from the current assessments for herring in areas west of Scotland, west of Ireland, Irish Sea, and Celtic Sea, respectively (ICES, 2008). Life-history traits are only loosely based on the available information for the four stocks:

- annual spawning (one cohort per year), with populations 1 and 3 spawning in autumn, and populations 2 and 4 spawning in winter/spring;
- maturity-at-age schemes for ages 1, 2, 3, and >4 were 0.1, 0.5, 0.8, and 1.0, respectively, for populations 1 and 2; and 0.2, 0.7, 0.8, and 1.0, respectively, for populations 3 and 4;
- fecundity, assumed to be proportional to weight;
- weight-at-age, as used in the assessments (ICES, 2008);
- 7-year lifespan;
- time-invariant but age-specific natural mortality:  $M = 1.0, 0.3, 0.2,$  and  $0.1$  for ages 1, 2, 3, and >4, respectively (ICES, 2008).

Given the selection pattern ( $s$ ) of a fishery and the catchability ( $q$ ) of a population for a given effort ( $E$ ), the fishing mortality rate ( $F_{a,y,i,j}$ ) for age  $a$ , year  $y$ , fishery  $i$ , and population  $j$  is given by

$$F_{a,y,i,j} = E_{y,i} q_{y,j} s_{a,i,j} A_{a,i,j} \tag{1}$$

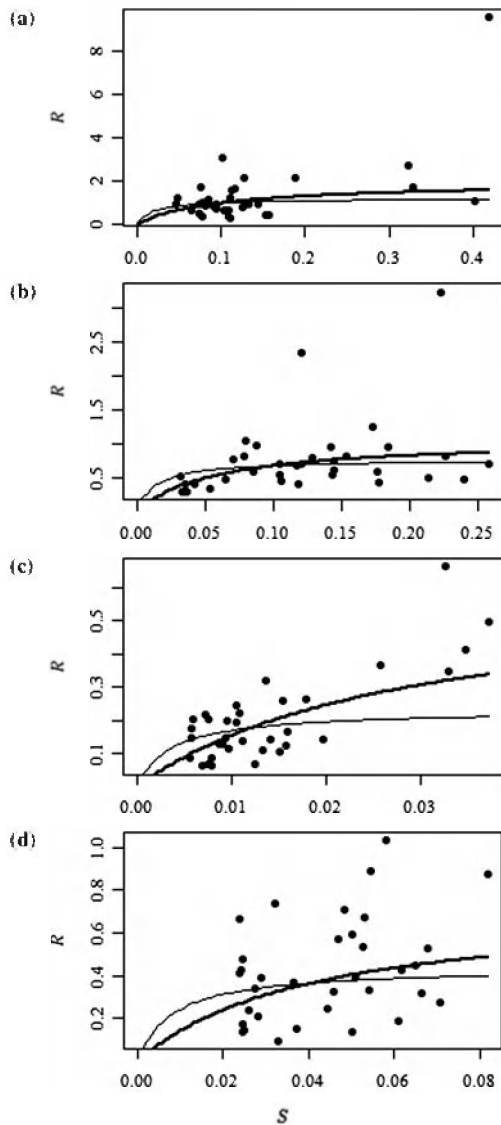
where  $A_{a,i,j}$  represents the availability to a fishery (Table 1).

The population abundance ( $N$ ) at age  $a + 1$ , at the start of year  $y + 1$ , in population  $j$  is given by

$$N_{a+1,y+1,j} = \sum_{k \neq j} N_{a,y,k} e^{-Z_{a,y,k}} D_{a,k \rightarrow j} + N_{a,y,j} e^{-Z_{a,y,j}} \left( 1 - \sum_{k \neq j} D_{a,j \rightarrow k} \right), \tag{2}$$

where  $k$  is the source population of immigrants,  $Z = F + M$ ,  $D_{a, k \rightarrow j}$  corresponds to the diffusion proportion of population  $k$  into population  $j$  at age  $a$ , and  $D_{a, j \rightarrow k}$  is the equivalent from population  $j$  into population  $k$ . We assume that diffusion takes place just after the start of the year, followed by mortality.

We assume a Beverton and Holt (1957) stock–recruitment relationship ( $S$ , spawning-stock biomass;  $R$ , recruitment), but use the formulation of Francis (1992) to reparameterize the relationship (for given  $M$ -, weight-, and maturity-at-age) in terms of steepness ( $\tau$ ) and virgin biomass ( $\gamma$ ). Steepness is the fraction of the virgin recruitment ( $R_0$ ) expected when the  $S$  has been reduced to 20% of its maximum (i.e.  $R = \tau R_0$  when  $S = \gamma/5$ ) and represents the resilience of the stock to exploitation. Defining the spawning-stock biomass-per-recruit ( $S/R$ ) at zero fishing mortality as  $\Psi_{F=0}$ , the Beverton–Holt parameters  $\alpha$  and  $\beta$  may be



**Figure 3.** Stock–recruitment data for the four populations (a–d), with Beverton–Holt functional forms for steepness values of 0.75 (thick line) and 0.9 (thin line).

derived from:

$$\alpha = \frac{4\gamma\tau}{\Psi_{F=0}(5\tau - 1)} \tag{3}$$

$$\beta = \frac{\alpha\Psi_{F=0}(\tau^{-1} - 1)}{4} \tag{4}$$

Parameters were estimated from the  $S$  and  $R$  data for each population (Figure 3). Unconstrained fits of both Beverton–Holt and Ricker functional forms were similar but implausible, because recruits kept increasing with stock biomass. Therefore, a Beverton–Holt relationship was fitted assuming a fixed but plausible value of steepness (0.75). Sensitivity analyses assuming an alternative value of 0.9 indicated that simulation results were qualitatively the same, the only difference being in the absolute  $F_s$  at which the maximum sustainable yield (MSY) was achieved ( $F_{MSY}$ ) and at which the stock was driven to extinction ( $F_{Crash}$ ).

**Table 3.** Reference points by population (steepness parameter = 0.75).

Population	$F_{MSY}$	MSY	$B_{MSY}$	$F_{Crash}$
1	0.15	0.05	0.27	0.49
2	0.21	0.03	0.16	1.23
3	0.16	0.02	0.08	0.65
4	0.22	0.02	0.11	1.46

Therefore, only results corresponding to a steepness of 0.75 are presented. The target reference points (MSY; the corresponding total-stock biomass,  $B_{MSY}$  and  $F_{MSY}$ ) and limit reference points ( $F_{Crash}$ ) for the four populations and a steepness value of 0.75 are presented in Table 3.

In the presentation of the results, we use the exploitation rate ( $H$ ), which we define as the ratio between yield and stock biomass, rather than fishing mortality, because the populations were modelled assuming different distributions during two seasons, whereas the stocks are modelled yearly. Therefore, fishing mortalities are not equivalent.

### The stock-assessment procedure

The stock-assessment procedure combined a particular sampling regime and stock-assessment technique. The sampling regime is simulated by the observation-error model, which generates a total catch-at-age array and indices of abundance from the fisheries and populations. The indices of abundance were derived either during the spawning season or during the fishing season. The former index represents an unbiased estimate of the spawning population, whereas the latter represents an index of abundance of all stocks caught in each of the fishing areas combined (i.e. at the time of mixing). In both cases, a single series that covered the age range in the population was constructed assuming a lognormal observation error with a  $CV$  of 30%, corresponding to the typical error seen in herring assessments. Detailed results are only presented for the assessment based on indices obtained during the feeding season.

Using the indices of abundance for calibration, a single extended survivor analysis (XSA; Shepherd, 1999) is performed at the end of the projection period to estimate  $F$ -at-age and  $N$ -at-age in the population, conditional on the assumed values of  $M$  and reported catch-at-age. In estimating the terminal  $F_s$ , the relationship between number-at-age and the index of abundance is assumed to include measurement and process error, whereas the catch-at-age is assumed to be exact. This means that the estimation errors are largest for the older age groups and smallest for the recruiting age class. Estimates of spawning-stock biomass are dominated by ages 2–4 because of the selection pattern, which results in a higher  $F$  for the older ages, and by the weight-at-age.

### Scenarios

A set of five scenarios was run to compare the XSA estimates by stock, as defined by the fisheries, with the “true” values for the spawning populations in these areas. Moreover, we evaluate whether lumping data for two or three of the stocks/populations lead to closer agreement between estimated stocks and true populations. The scenarios reflected different developments in the fisheries and changes in the productivity for one of the populations, thereby testing the ability to monitor stocks and fisheries.

Scenario I: constant effort in all the fisheries, equivalent to the  $F_{MSY}$  in areas 2, 3, and 4, and to twice this value in area 1;

Scenario II: a doubling of effort in fishery 1 after 20 years;

Scenario III: a doubling of catchability in the fishery for population 1 after 20 years;

Scenario IV: a 60% decrease in productivity (MSY) of population 1 after 20 years, caused by a change in  $F_{MSY}$ ;

Scenario V: a 60% decrease in productivity (MSY) of population 1 after 20 years, caused by a change in  $B_{MSY}$ .

All scenarios are based on constant effort in all the fisheries (equivalent to  $F_{MSY}$ ), unless otherwise indicated.

## Results

The results presented are meant to illustrate factors that influence our ability to estimate population status and fishing pressure, rather than to provide an exhaustive interpretation or to make management recommendations. The mean spawning-stock biomass ( $S$ ; Figure 4a) and the exploitation rate ( $H$ ; Figure 4b), as estimated for each stock (or combination of stocks), are contrasted with the true values for each population (or combination of populations). These means (and the interquartiles of the distributions) are plotted relative to the values of  $B_{MSY}$  and  $F_{MSY}$ , respectively, by scenario (rows). Columns represent either single stocks/populations (1–4) or combinations of different stocks/populations (as indicated), where stock estimates are based on catches taken within the boundaries of the management units.

All results refer to assessments calibrated with a survey index obtained during the fishing season. Although the estimates are mainly driven by the catch-at-age distribution, survey timing did affect the assessment. The survey index obtained during the fishing season added a slight negative bias to the estimates of spawning-stock biomass under some scenarios. Diffusion had a limited impact compared with mixing, so only results from the mixing option are presented.

In trying to understand the behaviour of the simulations, the relatively simple but implausible constant-effort scenario (scenario I) raises several points of interest. The interquartile ranges of the estimates of  $S$  are narrower than the corresponding population values. The explanation is that XSA estimates are partly based on weighted averages, which reduce the variance at the expense of bias. Estimates based on split stocks are biased positively for population 1 and negatively for populations 2 and 3; this is because population 1 suffers a lower mortality than suggested by the age composition of the catches, because not all individuals are available to the fishery; the reverse is true for populations 2 and 3. Lumping two or three stocks results in a markedly reduced bias in the estimates. For the exploitation rate, the precision in the stock estimates (as reflected in the interquartile range) is similar to the population values, whereas the means are unbiased (except for a positive bias in the most recent year), irrespective of splitting or lumping.

In scenario II, the effort in fishery 1 doubles after 20 years. Bias and precision are comparable with scenario 1, although the estimated  $H$  for stock 2 incorrectly suggests an increase in mortality even before it occurred. This is due to the same bias noted above. Estimates after lumping are similar to those obtained for population 1, again because this stock contributes most of the biomass.

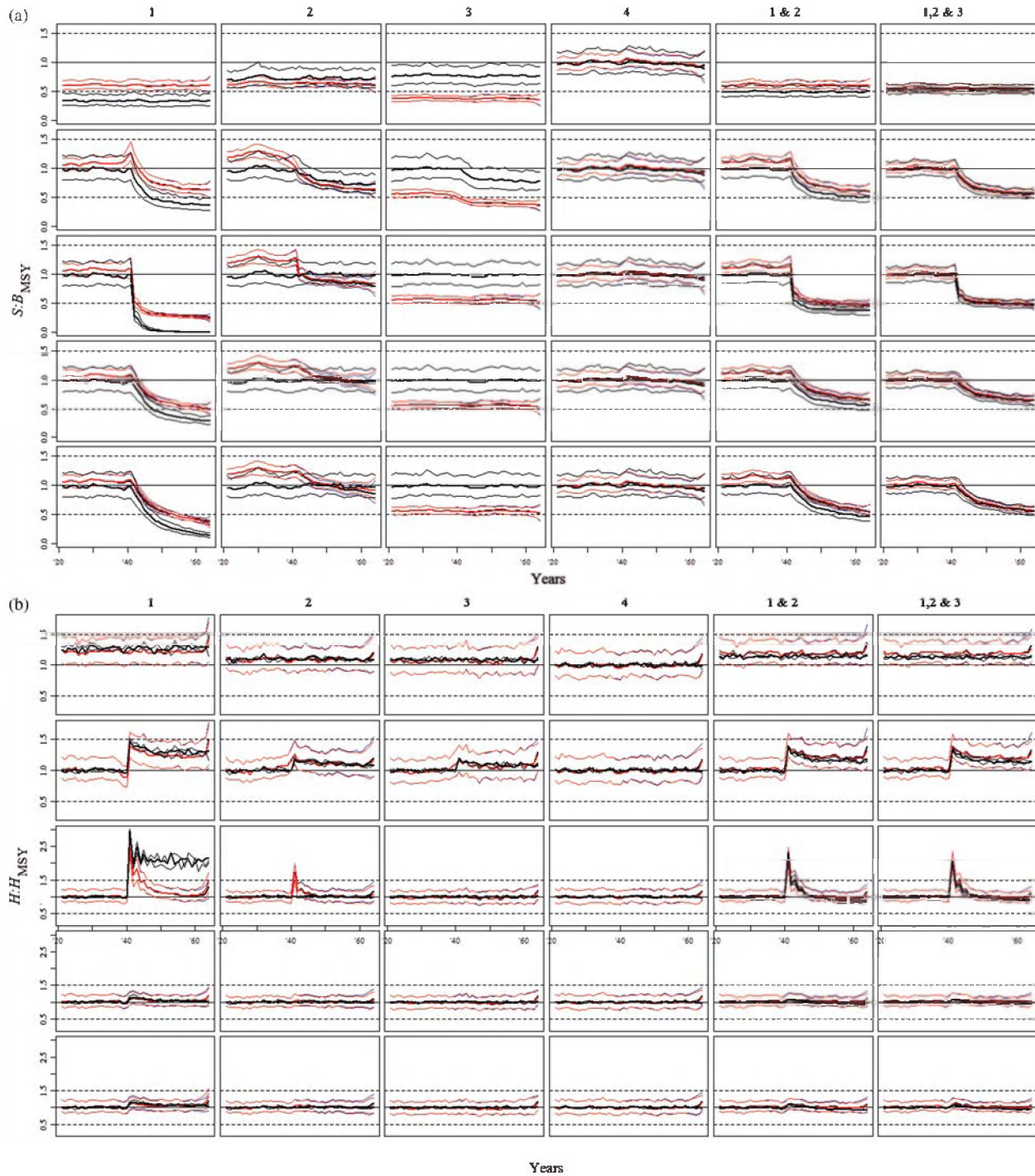
In scenario III, it is the catchability in the fishery for population 1 that is doubled rather than the effort (e.g. because the populations are not evenly mixed within the fishery). However, more important, the fishing mortality for population 1 becomes greater than  $F_{Crash}$  and consequently population 1 collapses. The reason a high exploitation rate can appear to be maintained after the population has collapsed is because the  $F$ s are not partial  $F$ s. For example, if in each year, half of the population goes to fishery 1 (with an infinite fishing mortality) and half goes to fishery 2 (with a sustainable fishing mortality), there will always be some survivors to spawn. However, because catches from population 2 continue within the geographical area exploited by fishery 1, population 1 appears to persist, and the total collapse of the local population is not detected. In this case,  $H$  responds quite differently from  $S$ . For example, although  $H$  for population 1 is constant after the increase, the XSA indicates a decline to the  $H_{MSY}$  level. In population 2, and to a lesser extent in the lumped assessment for populations 1 and 2, there is an apparent decline in both spawning-stock biomass and  $H$ . The assessment after lumping populations 1 and 2 (and also 1, 2, and 3) matches the trend in the combined stocks. However, importantly, the extirpation of population 1 is not detected by the assessment when stocks are lumped. There appears to be a long-term drop in total  $S$  after a short-term increase in  $H$ . Moreover, the trend in  $H$  suggests that the stocks are ultimately being exploited sustainably. A possible explanation of these trends, based on stock assessment, is that a regime shift has occurred, rather than the overexploitation of one population.

Scenarios IV and V address the potential for correctly estimating the changes in productivity for population 1, caused by a decrease in survival of recruits (i.e.  $F_{MSY}$ ) and by a change in carrying capacity (i.e.  $B_{MSY}$ ), respectively. As these two scenarios lead to indistinguishable results, the process that caused a change in productivity is unlikely to be deduced from stock assessment alone. As any management advice should depend on changes in specific reference points, this means that without additional information, it will be difficult to provide advice on appropriate actions in terms of harvest control rules based on reference points.

## Discussion

The original question posed was whether to lump or split. Splitting is of course conditional on our ability to assess and manage populations that are defined on biological grounds, whereas lumping might be appropriate when populations cannot be assessed separately because fisheries exploit mixed populations and the catches cannot be split into different components. Our simulation (although admittedly simpler than the reality) raises some important issues related to the maintenance of population structure within a stock that is currently considered to represent a single population, even if it is known to comprise several spawning components (e.g. North Sea herring), as well as to the quality of the advice for stocks that are known to cross the management areas (such as the herring stocks west of the British Isles).

Clearly, lumping catches from mixed populations may provide biased estimates of stock status and exploitation of the individual components. For a stock made up of two populations with the same productivity, catches will be greater from the stock fished closest to  $F_{MSY}$ . Because  $F$  is estimated from the overall catch-at-age ratios, estimates of  $F$  from virtual population analysis (VPA) will be biased downwards. If one population is being fished unsustainably and collapses,  $F$  will appear to decline (as the catch



**Figure 4.** Plots of (a) spawning-stock biomass ( $S$ ) and (b) exploitation rate ( $H$ ) relative to the target reference points  $B_{MSY}$  and  $F_{MSY}$ , respectively (solid horizontal lines; dashed lines, 0.5 and 1.5 times the MSY reference level), by scenarios (I–V; rows) and by the levels of aggregation of stocks/populations (1–4 separately and in two combinations, 1 and 2, and 1, 2, and 3; columns). The XSA “stock” estimates (red lines), based on total catches from the fisheries, are contrasted with the “true” populations (black lines), with thinner lines indicating the respective interquartile and median values.

data will be based increasingly on the population fished at the lower  $F$ ). Although the  $F$  may be perceived as sustainable, recovery may be impaired because there is now only one population where previously there were two. Therefore, lumping will underestimate the risk of stock collapse and overestimate the probability of recovery, although lumping of stocks generally provides a

less biased estimate of overall abundance than the individual assessments.

While mixing between management units is often recognized as a problem affecting the accuracy of an assessment, ignoring that a stock may, in fact, represent a metapopulation with several spawning components may be an even more serious problem. Preserving

the spatial population structure can be important for a metapopulation in terms of maintaining its ability to sustain variable environmental conditions (Hilborn, 2003) because a broad spectrum of spawning behaviour and conditions for early survival is at least as important as spawning biomass in ensuring long-term sustainability of the fisheries (Berkeley *et al.*, 2004). Failure to recognize and account for complexity in population structure may lead to erosion of spawning components and have unexpected ecological consequences, although management at appropriate scales to preserve this complexity remains a major challenge (Stephenson, 1999). Within an ecosystem-based approach to fisheries management, maintenance of the full diversity of spawning locations and times is an important aspect of topical discussions on Marine Protected Areas, and greater emphasis on population structure will be required.

Ideally, for stock assessment, catches should be split by population, and the survey index should provide an unbiased estimate of the abundance of the spawning populations. If fisheries exploit mixed aggregations during the feeding season, resulting in the lumping of catches from different populations, the simulations show that XSA does not accurately detect high exploitation rates and depletion of individual populations. In this case, additional data are required, either to separate catches or to estimate mixing rates (Porch, 1997). However, Powers and Porch (2004) showed that the bias caused by incorrect assumptions about mixing rates can be greater than that caused by ignoring mixing entirely. To deserve the epithet “precautionary” and ensure that the associated risks are acceptable [<http://www.ipcc.ch/pdf/supporting-material/uncertainty-guidance-note.pdf>], management of population mixes will have to be based on models that incorporate structural uncertainty (i.e. accept that important processes may be specified incorrectly or not considered and that there may even be disagreement about which model is correct). As a consequence, for a given level of risk, the level of exploitation of a stock representing a population mix should always be lower than a stock representing an isolated population.

International agreement on the precautionary approach (FAO, 1996) requires the setting of reference points based on both biomass and fishing mortality. By definition, a reference point implies a time-invariable, fixed value. However, several reviews on pelagic as well as demersal fish (Cushing and Dickson, 1976; Schwartzlose *et al.*, 1999; Lehodey *et al.*, 2006) have concluded that population processes are non-stationary, and therefore the conditions of sustainability (for which the reference points are proxies) may vary over time. Although several simulation studies (Kell and Fromentin, 2007; Kell *et al.*, 2007) have suggested that  $F$ -based reference points are more robust than biomass-based ones, our simulations show that it is not necessarily possible, based on stock assessment alone, to distinguish between the causes of changes in productivity and hence to identify which reference point should be modified.

An alternative to trying to improve assessments is to improve management directly by setting constraints on where or when to fish to minimize unpredictable effects. For instance, the revised management procedure developed for baleen whales by the International Whaling Commission (Punt and Donovan, 2007) only allows fisheries to operate in an area where the proportion of different species in the catch equals the proportion in the aggregate “stock” of baleen whales. This would ensure that all individual stocks were fished at the same  $F$ , which to be precautionary would have to be set to the lowest stock-specific sustainable  $F$ . If stock-

specific surveys are available, another option is to abandon VPA-based methods and to develop a management procedure based solely on surveys (De Oliveira and Butterworth, 2004). A benefit of the management-procedure approach is that data, assessment methods, reference points, and decision rules are considered explicitly as being interrelated. The approach emphasizes that a range of potential management procedures should be evaluated across a range of hypotheses about stock and fleet dynamics and should span a variety of plausible operating conditions and assessments, before the most appropriate procedure is selected.

Although our simulations have been based only loosely on western herring stocks, they raise a number of issues that are relevant for improving their management. Specifically, the different options for reducing uncertainty about mixing of stocks need to be evaluated: (i) improving biological knowledge by scientific study and hypothesis testing; (ii) improving data collection by conducting surveys and disaggregating catches on appropriate temporal and spatial scales; and (iii) developing robust management procedures that are less dependent on precise knowledge. The last option is a particularly important but difficult challenge. The framework used here may help in evaluating the robustness of current and alternative management measures designed to prevent overexploitation of stock components and to ensure that fisheries are managed in a manner that is consistent with commitments under agreements (e.g. the World Summit on Sustainable Development) to recover stocks to a level that can support MSY by 2015.

## Acknowledgements

This study was partly funded through the European Commission’s research, technological and demonstration (RTD) programme “Specific Support to Policies” (SSP-4-FISH-Area 8.1. B.1.3: Task 2. Understanding the mechanisms of Stock Recovery). It does not necessarily reflect its views and in no way anticipates the Commission’s future policy in this area. The programme also provided funding for the Open Access publication charges. Partial support for RDMN was provided through the North Sea Programme of the Institute for Marine Research (IMR), Bergen, and for LTK, GMP, and BAR, through the UK’s Department for Environment, Food and Rural Affairs (Defra; under contract MF1201). We also thank the editor, Niels Daan, for perhaps being more patient than he should have been.

## References

- Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29: 23–32.
- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. *Fisheries Investigations*, London (Series 2), 19. Ministry of Agriculture, Fisheries and Food, UK. 533 pp.
- Brophy, D., Danilowicz, B. S., and King, P. A. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 607–616.
- Campbell, N., Cross, M. A., Chubb, J. C., Cunningham, C. O., Hatfield, E. M. C., and MacKenzie, K. 2007. Spatial and temporal variations in parasite prevalence and infracommunity structure in herring (*Clupea harengus* L.) caught to the west of the British Isles and in the North and Baltic Seas: implications for fisheries science. *Journal of Helminthology*, 81: 137–146.

- Cushing, D. H., and Dickson, R. R. 1976. The biological response in the sea to climatic changes. *Advances in Marine Biology*, 14: 1–122.
- De Oliveira, J. A. A., and Butterworth, D. S. 2004. Developing and refining a joint management procedure for the multispecies South African pelagic fishery. *ICES Journal of Marine Science*, 61: 1432–1442.
- FAO. 1996. Precautionary approach to capture fisheries and species introductions. *FAO Technical Guidelines for Responsible Fisheries*, 2. FAO, Rome. 60 pp. <http://www.fao.org/> (last accessed 6 January 2006).
- 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.
- Hilborn, R. 2003. The state of the art in stock assessment: where we are and where we are going. *Scientia Marina*, 67(Suppl. 1): 15–20.
- ICES. 1994. Report of the Study Group on Herring Assessment and Biology in the Irish Sea and Adjacent Waters, Belfast, Northern Ireland, 22–15 February 1994. *ICES Document CM 1994/H: 05*. 69 pp.
- ICES. 2008. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG), 11–19 March, ICES Headquarters, Copenhagen. *ICES Document CM 2008/ACOM: 02*. 601 pp.
- Kell, L. T., and Fromentin, M. 2007. Evaluation of the robustness of MSY-based management strategies to variations in carrying capacity or migration pattern of Atlantic bluefin tuna. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 837–847.
- 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.
- Krebs, C. J. 1994. *Ecology: the Experimental Analysis of Distribution and Abundance*, 4th edn. Harper Collins, New York. 801 pp.
- Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.-M., *et al.* 2006. Climate variability, fish, and fisheries. *Journal of Climate*, 19: 5009–5030.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15: 237–240.
- MacKenzie, K. 1985. The use of parasites as biological tags in population studies of herring (*Clupea harengus* L) in the North Sea and to the north and west of Scotland. *Journal du Conseil International pour l'Exploration de la Mer*, 42: 33–64.
- McPherson, A. A., Stephenson, R. L., O'Reilly, P. T., Jones, M. W., and Taggart, C. T. 2001. Genetic diversity of coastal north-west Atlantic herring populations: implications for management. *Journal of Fish Biology*, 59A: 356–370.
- Mitchell, J. M. 1864. *The Herring: its Natural History and National Importance*. Edmonston and Douglas, Edinburgh, UK. 372 pp.
- Molloy, J. 2006. *The Herring Fisheries of Ireland (1900–2005). Biology, Research, Development and Assessment*. Marine Institute, Galway, Ireland. 235 pp.
- Parrish, B. B., and Saville, A. 1965. The biology of the north-east Atlantic herring populations. *Oceanography and Marine Biology: an Annual Review*, 3: 323–373.
- Porch, C. E. 1997. *A User's Manual for VPA 2-Box*, version 2.0. National Marine Fisheries Service, Miami, FLA.
- Powers, J. E., and Porch, C. E. 2004. Approaches to developing management procedures which incorporate mixing. *Collective Volume of Scientific Papers ICCAT*, 56: 1144–1152.
- Punt, A. E., and Donovan, G. P. 2007. Developing management procedures that are robust to uncertainty: lessons from the International Whaling Commission. *ICES Journal of Marine Science*, 64: 603–612.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York. 542 pp.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. G. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, doi:10.1111/j.1467-2979.2008.00324.x.
- Ruzzante, D. E., Mariani, S., Bekkevold, D., Andre, C., Mosegaard, H., Clausen, L. A. W., Dahlgren, T. G., *et al.* 2006. Biocomplexity in a highly migratory pelagic marine fish, Atlantic herring. *Proceedings of the Royal Society of London, Series B*, 273: 1459–1464.
- Samuel, A. M. 1918. *The Herring: its Effect on the History of Britain*. John Murray, London. 199 pp.
- Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., *et al.* 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, 21: 289–347.
- Secor, D. H., Kerr, L. A., and Cadrin, S. X. 2009. Connectivity effects on productivity, stability, and persistence in a herring metapopulation model. *ICES Journal of Marine Science*, 66: 1726–1732.
- Shepherd, J. G. 1999. Extended survivors analysis: an improved method for the analysis of catch-at-age data and abundance indices. *ICES Journal of Marine Science*, 56: 584–591.
- Simmonds, E. J., and Keltz, S. 2007. Management implications and options for a stock with unstable or uncertain dynamics: west of Scotland herring. *ICES Journal of Marine Science*, 64: 686–692.
- Stephenson, R. L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fisheries Research*, 43: 247–249.
- Waldman, J. R. 1999. The importance of comparative studies in stock analysis. *Fisheries Research*, 43: 237–246.
- Waples, R. S., and Gaggiotti, O. 2006. What is a population? *Molecular Ecology*, 15: 1419–1439.

doi:10.1093/icesjms/fsp181