The evaluation of reference points and stock productivity in the context of alternative indices of stock reproductive potential

M.J. Morgan, H. Murua, G. Kraus, Y. Lambert, G. Marteinsdóttir, C.T. Marshall, L. O'Brien, and J. Tomkiewicz

Abstract: In this study, we explore the impact of four alternative indices of reproductive potential (RP) on perceptions of population productivity for eight fish populations across the North Atlantic. The four indices of RP included increasing biological complexity, adding variation in maturation, sex ratio, and fecundity. Perceptions of stock productivity were greatly affected by the choice of index of RP. Population status relative to reference points, RP per recruit, and projections of population size all varied when alternative indices of RP were used. There was no consistency in which index of RP gave the highest or lowest estimate of population productivity, but rather, this varied depending on how much variation there was in the reproductive biology of the population and the age composition. Estimates of sustainable harvest levels and recovery time for depleted populations can vary greatly depending on the index of RP.

Résumé : Nous explorons dans notre étude les effets de quatre indices de rechange du potentiel reproductif (RP) sur la perception de la productivité de la population chez huit populations de poissons provenant de l'Atlantique Nord. Les quatre indices de RP comprennent l'accroissement de la complexité biologique, l'addition de variation dans la maturation, la proportion des sexes et la fécondité. Le choix d'indice de RP affecte considérablement la perception de la productivité des stocks. Le statut de la population en fonction des points de référence, le RP par recrue et les projections de la taille de la population varient tous en fonction de l'indice RP retenu. Il n'y a pas de cohérence en ce qui a trait à quel indice donne l'estimation la plus élevée ou la plus basse de la productivité de la population, mais il y a plutôt des résultats différents selon l'importance de la variation dans la biologie de la reproduction et la composition en âge de la population. Les estimations des niveaux admissibles de récolte et du temps nécessaire au rétablissement des populations épuisées peuvent varier considérablement selon l'indice de RP utilisé.

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Introduction

Estimating a population's productivity is key to sustainable management of fisheries. A population's level of productivity will determine the level of fishing mortality (*F*) that it can sustain as well as its ability to recover from a depleted state. The underlying determinant of a population's productivity is its stock–recruit (S–R) relationship. There is generally large variation around such S–R curves, making the estimation of productivity an extremely difficult, yet central, challenge in the study of the population dynamics and management of marine fish stocks (Hilborn and Walters 1992). This relationship is usually represented by the number of recruits produced by a specific biomass of spawners (spawning stock biomass (SSB)). This assumes that a population's reproductive potential (RP) is proportional to its SSB (Trippel et al. 1997), implying that the survival rates of offspring are independent of parental age, body size, or condition (Cardinale and Arrhenius 2000), and that total relative egg production per unit weight of adult stock is invari-

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ant over time (Marshall et al. 2003). However, SSB does not generally incorporate sex ratio and often does not include a time series of estimated proportion mature at age, both factors that are known to exhibit temporal variability (Jorgensen 1990; Marshall et al. 1998; Morgan and Brattey 2005). In addition, fecundity is rarely incorporated into measures of RP (Tomkiewicz et al. 2003) and is known to be variable (Kraus et al. 2002; Murua et al. 2006; Rideout and Morgan 2007). The use of SSB as an adequate measure of RP has therefore been questioned and it has been suggested that other measures of RP, which incorporate some of these variable reproductive characteristics, may better reflect a population's recruitment potential (Marshall et al. 1998, 2003; Marteinsdottir and Thorarinsson 1998).

Depending on the measure of RP, the relationship with recruitment may vary and result in a change in the perception of a population's productivity (Morgan and Brattey 2005). Many exploited fish populations are managed based on spawner–recruitment models, i.e., biological reference points are basically determined using S–R relationships. An altered relationship between indices of RP and recruitment (RP–R) can lead to a different perception of population status relative to limit reference points, both biomass and *F* based (Murawski et al. 2001). It can also produce different estimates of the level of *F* that is sustainable. Marshall et al. (2006) found that alternative estimates of RP for Northeast Arctic cod (*Gadus morhua*) led to variation in the RP–R relationship and that this affected the biological limit reference point, estimated as the change point in a segmented regression.

The impact of alternative indices of RP on perceptions of population productivity has not been explored extensively. In this study, we examine four indices of RP for eight populations across the North Atlantic. This study does not attempt to replicate the stock assessments conducted on each population but instead adopts a standard approach for the analyses of all stocks. This facilitated comparison between stocks and among the different measures of RP. We estimate productivity measures of the populations using different indices of RP and evaluate the impacts on limit reference points and estimates of population growth. Finally, we examine our results for consistency across populations in the impact of alternative indices of RP on perceived productivity.

Materials and methods

Populations

Data from eight populations from across the North Atlantic were examined (Fig. 1). These were Georges Bank cod (*Gadus morhua*) (Northwest Atlantic Fisheries Organization (NAFO) Div. 5Z), northern Gulf of St. Lawrence cod (NAFO Div. 3Pn4RS), southern Grand Bank cod (NAFO Div. 3NO), Grand Bank American plaice (*Hippoglossoides platessoides*) (NAFO Div. 3LNO), Icelandic cod (International Council for the Exploration of the Sea (ICES) Div. Va), Northeast Arctic cod (ICES Subareas I and II), Baltic cod (ICES IIId SD 25–32), and northern hake (*Merluccius merluccius*) (ICES Div. IIIa, SA II, IV, VI, and VII and Div. VIIIa, VIIIb, and VIIId). Population numbers at age and weights at age came from recent assessments of the populations (Georges Bank cod: O'Brien and Munroe 2001; northern Gulf of St. Lawrence cod: Fréchet et al. 2005; southern Grand Bank cod: Power et al. 2005; Grand Bank American plaice: Dwyer et al. 2005; Icelandic cod: ICES 2006*c*; Northeast Arctic cod: ICES 2006*a*; Baltic cod: ICES 2006*b*; northern hake: ICES 2007).

Reproductive biology

Data for proportion mature at age, sex ratio at age and fecundity at age were derived from research vessel surveys. For each population the weighted mean proportion mature, proportion female, and fecundity were calculated for each year. The weighting in each case was the population number at age. This provided an estimate of the degree of variation over time in these reproductive characteristics at the population level. The measure incorporated variation in both the reproductive characteristic and in population numbers at age. Because of the difference in scale, the weighted averages were standardized by dividing each series by its mean.

Indices of RP

For each population, four indices of RP were calculated. Although a common definition of the four indices of RP was attempted, the RP indices were estimated with slight differences depending on the data available for the stock (see Table 1). The four groups of RP (constant or knife edge maturity SSB, variable maturity SSB, female SB, or total egg production) were defined as follows:

The first estimate of RP (constant ogive or knife-edge maturity) assumed no change in the maturity schedule of the fish and applied a constant proportion mature at age:

$$(1)\qquad \mathrm{RP}_{\mathrm{constant}} = \sum_{a=i}^{j} N_{ay} W_{ay} \mathrm{PM}_{a}$$

where N_{ay} is the population number at age a in year y, W_{ay} is the weight at age a in year y, PM_a is the proportion mature at age a, and the age range is that in the sequential population analyses for the population.

The second estimate, $\mathrm{RP}_{\mathrm{SSB}}$, is calculated in the same way as $\mathrm{RP}_{\mathrm{constant}}$ but incorporates the estimated proportion mature at age for each cohort or year (sexes combined or female only), i.e., variable rather than constant maturity at age. This estimate will show the impact of changes in maturation over time:

$$(2)\qquad \mathrm{RP}_{\mathrm{SSB}} = \sum_{a=i}^{j} N_{ay} W_{ay} \mathrm{PM}_{ay}$$

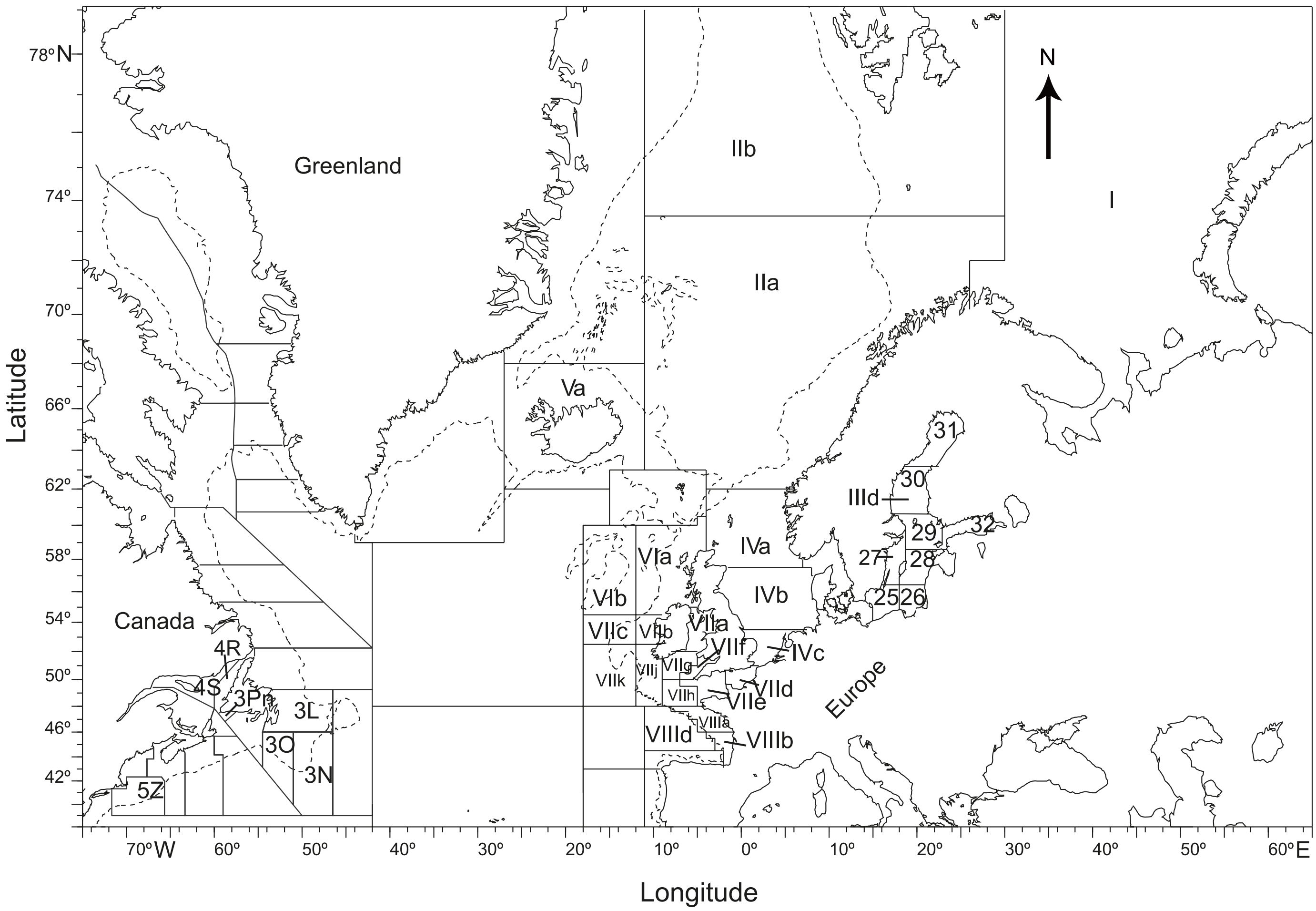
In the third estimate of RP (sex ratio at age constant or variable), we applied the sex ratios estimated along with the variable estimates of proportion mature at age:

$$(3)\qquad \mathrm{RP}_{\mathrm{FSB}} = \sum_{a=i}^{j} N_{ay} W_{ay} \mathrm{PM}_{ay} \mathrm{SR}_{ay}$$

where SR_{ay} is the proportion female at age a in year y and the other terms are as defined above.

The fourth estimate of RP incorporated estimates of fecundity at age and is an estimate of total egg production (TEP):

Fig. 1. Map of the North Atlantic showing Northwest Atlantic Fisheries Organization and International Council for the Exploration of the Sea divisions used to identify populations in this study.



$$\text{(4)} \qquad \mathrm{RP}_{\mathrm{TEP}} = \sum_{a=i}^{j} N_{ay}\mathrm{PM}_{ay}\mathrm{SR}_{ay}E_{ay}$$

where E_{ay} is the number of eggs produced per female at age a in year y and the other terms are as defined above. Weight at age is not included unless it forms part of the estimation of E_{ay} (see Table 1).

The four indices of RP are increasingly complex, adding more biological information in each case. The first index, $\mathrm{RP}_{\mathrm{constant}}$, assumes that all reproductive characteristics are constant with only weight and number at age varying. The other indices incorporate temporal variation in reproductive biology, adding additional biological complexity in each case.

Each index of RP for each stock was divided by $\mathrm{RP}_{\mathrm{constant}}$ for the stock to determine if the relationship between them was consistent. This will provide an indication of the amount of variation in the reproductive characteristics and the impact of this variation on the time series of RP.

Limit reference points

RP and F giving maximum sustainable yield (MSY) were calculated to compare the stock trajectory in relation to limit reference points. Biomass (B) and fishing mortality (F) reference points (B_{lim} and F_{lim}) were taken as 30% $\mathrm{RP}_{\mathrm{MSY}}$ and F_{MSY}, respectively (NAFO 2004). This was calculated separately for each index of RP by applying various F levels to each population in simulations running for 500 years. The population model applied was

$$\text{(5)} \qquad N_{a+1,y+1} = N_{a,y}\mathrm{e}^{-(M+F_{a,y})}$$

where natural mortality $M = 0.2$ and $F_{a,y} = K_aF_y$, where K_a is the partial recruitment at age (the distribution of fishing mortality across age) and F_y is the fully recruited fishing mortality. For those populations where a plus group is used in the assessment:

$$\text{(6)} \qquad N_{p,y+1} = N_{p-1,y}\mathrm{e}^{-(M+F_{p-1,y})} + N_{p,y}\mathrm{e}^{-(M+F_{p,y})}$$

where N_p is the plus group age. From these deterministic simulations at different levels of F, MSY was determined along with F and RP giving this MSY.

In these simulations, recruitment was assumed to come from a Loess smoother of the relationship between the relevant RP and recruitment, where the smoothing window was chosen to minimize the Akaike information criteria. In a few cases (6 of 32), this approach led to undersmoothing and the smoothing window was adjusted to remove some of the higher frequency variation (SAS Institute Inc. 2004). This

Table 1. Specification of each index of reproductive potential (RP) for each population and the method used in the assessment for calculating the RP.

Stock	Index of RP				
	Assessment	$RP_{constant}$	RP_{SSB}	RP_{FSB}	RP_{TEP}
Georges Bank cod	Annual female ogive applied to total biomass at age	3+ biomass	5 year moving average of female ogive	5 year moving average of sex ratio	Constant fecundity at length, variable length at age
Northern Gulf of St. Lawrence cod	Annual female ogive applied to total biomass at age	4+ biomass	Variable female ogive by year	Variable sex ratio by year	Fecundity estimated as a function of condition and length
Grand Bank plaice	Female ogive by cohort applied to total biomass at age	9+ biomass	Variable female ogive by cohort	Variable sex ratio by cohort	Constant fecundity at length, variable length at age
Grand Bank cod	Female ogive by cohort applied to total biomass at age	6+ biomass	Variable female ogive by cohort	Variable sex ratio by cohort	Constant fecundity at length, variable length at age
Icelandic cod	Annual sexes combined ogive applied to total biomass at age	9+ biomass	Variable sexes combined ogive by year	Constant sex ratio at age	Constant fecundity at weight, variable weight at age
Northeast Arctic cod	Annual sexes combined ogive applied to total biomass at age	Constant ogive	Variable sexes combined ogive by year	Variable female ogive by year, sex ratio by year	Fecundity estimated as a function of condition and length
Baltic cod	Annual sexes combined ogive with some years averaged applied to total biomass at age	Constant ogive	Variable female ogive by year	6 blocks of sex ratio at age	Fecundity estimated as a function of prey availability
Northern hake	Constant sexes combined ogive applied to total biomass at age	Constant ogive	Variable female ogive by year	Variable sex ratio by year	Constant fecundity at weight, variable weight at age

allowed the same method to describe the relationship between RP and observed recruitment for all indices of RP and all populations and avoided any bias in results caused by assumptions about S–R models. Partial recruitment, weights, maturities, sex ratio, and fecundity at age were averaged over the entire time series for each population and used, as appropriate, to calculate RP. The starting population number at age in each simulation was the number at age in the final year of the assessment for the population. In each year of the 500 year simulations, the number at age was decreased by M and F (applied according to the partial recruitment) and RP calculated. Simulated recruitment was then calculated from the Loess smoother of the relationship between RP and observed recruitment. For simulated RP above the highest observed RP, the recruitment estimated for the highest observed RP was used, and for RP below the lowest observed, the lowest observed recruitment was used. These calculated reference points are not being suggested as the ones to use for these populations but rather are calculated as a way to explore the effect of different indices of RP on reference points.

Productivity over time

Changes in productivity over time were compared among the indices of RP by calculating RP per recruit (RPPR) for each index in each year. In each case, number at age was produced by starting with one recruit at age zero, applying M at each age until the last age used in the assessment, such that

$$(7) \qquad N_a = N_{a-1}\mathrm{e}^{-M}$$

for each age from zero to the maximum age in the sequential population analysis for each population (sometimes this was a plus group), where $M = 0.2$. The RP produced was calculated according to the equations given above and inserting the number at age from eq. 7. The result was then summed across all ages to give the RPPR for each index in each year. Each series of RPPR was standardized to its mean for comparison.

Projections of population size

As another indicator of differences in perceived productivity among the different indices of RP, 15 year deterministic projections were carried out for each population using each index of RP. Population numbers were projected assuming $F = 0$ and $M = 0.2$. Recruitment came from a linear regression of recruits per RP (R/RP) against RP, except for RP above the highest observed RP where R was RP times the R/RP for the highest observed RP. Weights, maturities, sex ratio, and fecundity at age were the average of the last 3 years before the projection period. The same population model was used as in the simulations to determine reference points (eqs. 5 and 6) and indices of RP were calculated as given above in eqs. 1–4. For each year of the projection period, each index of RP was divided by the B_{lim} estimated in the long-term simulations described above. This allowed a comparison of the trajectories in RP over the projection period.

Variation in F_{MSY} relative to variation in reproductive biology

The relationship between the variation in F_{MSY} and variation in maturation, sex ratio, and fecundity was examined. The coefficient of variation was calculated for the ratio of

RP to $RP_{constant}$ for each index of RP over the time series for each population. Correlation analyses were conducted between this measure of the impact of reproductive characteristics on RP and the absolute value of the difference between the F_{MSY} estimated for the particular index of RP and the F_{MSY} estimated for that population for $RP_{constant}$.

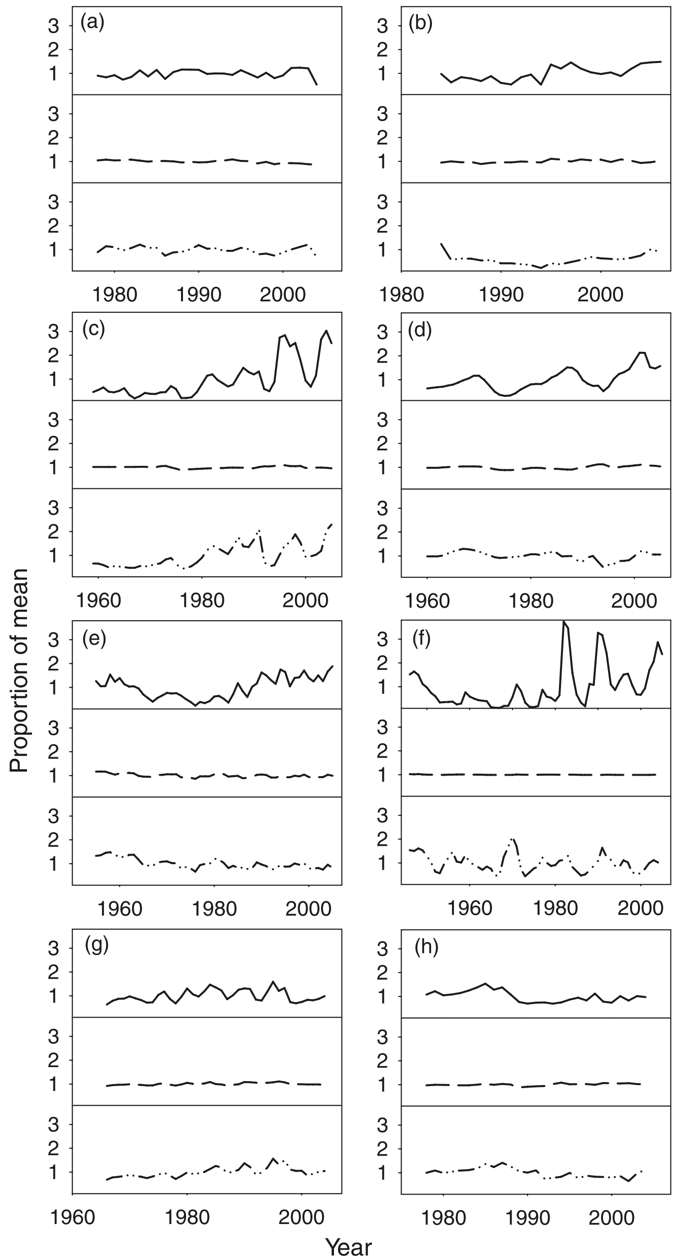
Results

The most variable reproductive characteristic was usually maturity at age (Fig. 2). Southern Grand Bank cod, Georges Bank cod, Icelandic cod, and Northeast Arctic cod in particular showed a large increase in the weighted proportion mature as fish matured younger. Sex ratio showed little variation for most stocks. The variation in fecundity was intermediate between maturity and sex ratio. The largest variation in weighted mean fecundity was for southern Grand Bank and Northeast Arctic cod.

For all stocks, the relationships between the alternative indices of RP and $RP_{constant}$ were not constant over time (Fig. 3). The ratio of RP_{SSB} to $RP_{constant}$ is higher than that of RP_{FSB} to $RP_{constant}$ because the population numbers for RP_{FSB} are lower for all ages that are not all female. The ratio of RP_{SSB} to $RP_{constant}$ provides an indication of how much variation is introduced by adding variable estimates of maturation to the estimate of RP. Comparing the trends over time in the ratios within a population will give an indication of the impact of maturity, sex ratio, and fecundity. Where the ratios of RP to $RP_{constant}$ diverge, it indicates a change in relationship among the different indices, usually the result of changes in biological parameters. In Icelandic cod, the rapid increase in the ratios of RP_{SSB}, RP_{FSB}, and RP_{TEP} to $RP_{constant}$ in the mid-1980s is the result of an increase in the proportion mature at age (Fig. 2) and a large decline in the number of fish older than age 9. For Northeast Arctic cod, the ratio of RP_{SSB} to $RP_{constant}$ diverges from the ratio of RP_{FSB} to $RP_{constant}$ starting in about 1980. In this case, this is the result of a deviation in the female proportion mature at age from the combined ogive used in the calculation of RP_{SSB}. As another example, the ratio of RP_{TEP} to $RP_{constant}$ for Georges Bank cod shows a large decline over the last few years of the time series, while that for RP_{SSB} to $RP_{constant}$ varies with little trend over the same time period. This is the result of some increase in weights of fish in the last years while numbers of fish continued to decline. Weight is used in the calculation of all of the indices except RP_{TEP}. For most populations, there is little divergence in the ratios of the indices to $RP_{constant}$, indicating that much of the difference between the indices and $RP_{constant}$ comes from the incorporation of variable maturity estimates.

The Loess smoothers of the relationships between R and RP used in simulations of different reference points are shown in Fig. 4. The RP for most populations covers a broad range but the maximum observed is less than would be expected at virgin biomass. For all populations, each index of RP has a different relationship with R, although this difference is greater for some populations than for others. For example, the shape of the relationships between R and RP varies greatly among indices of RP for southern Grand Bank cod and varies much less for northern hake. The simulations of different reference points showed that in no case

Fig. 2. Standardized weighted mean average proportion mature, proportion female, and fecundity for each population: (*a*) Georges Bank cod, (*b*) northern Gulf cod, (*c*) southern Grand Bank cod, (*d*) Grand Bank American plaice, (*e*) Icelandic cod, (*f*) Northeast Arctic cod, (*g*) Baltic cod, and (*h*) northern hake. Each series was standardized by dividing by its mean. Each is shown in a separate plot with the top panel being proportion mature (solid line), the middle panel proportion female (dashed line), and the bottom panel fecundity (dashed–dotted line).



were the estimates from all four of the indices of RP the same (Table 2). This is the result of the variation in the relationships between R and RP. Differences in MSY varied from less than 5% to 38%. The F limit reference point F_{MSY} varied by as much as 50%. The percentage of years in which stock status was below B_{lim} and for which F was above F_{lim} varied among indices of RP. In no population was the time series of stock status with respect to the refer-

Fig. 3. Ratio of each index of reproductive potential (RP) (RP_{SSB}, RP_{FSB}, and RP_{TEP}) to $RP_{constant}$ for each population: (*a*) Georges Bank cod, (*b*) northern Gulf cod, (*c*) southern Grand Bank cod, (*d*) Grand Bank American plaice, (*e*) Icelandic cod, (*f*) Northeast Arctic cod, (*g*) Baltic cod, and (*h*) northern hake. Each is shown in a separate plot with the top panel being $RP_{SSB}/RP_{constant}$ (solid line), the second panel $RP_{FSB}/RP_{constant}$ (dashed line), and the bottom panel $RP_{TEP}/RP_{constant}$ (dashed–dotted line).

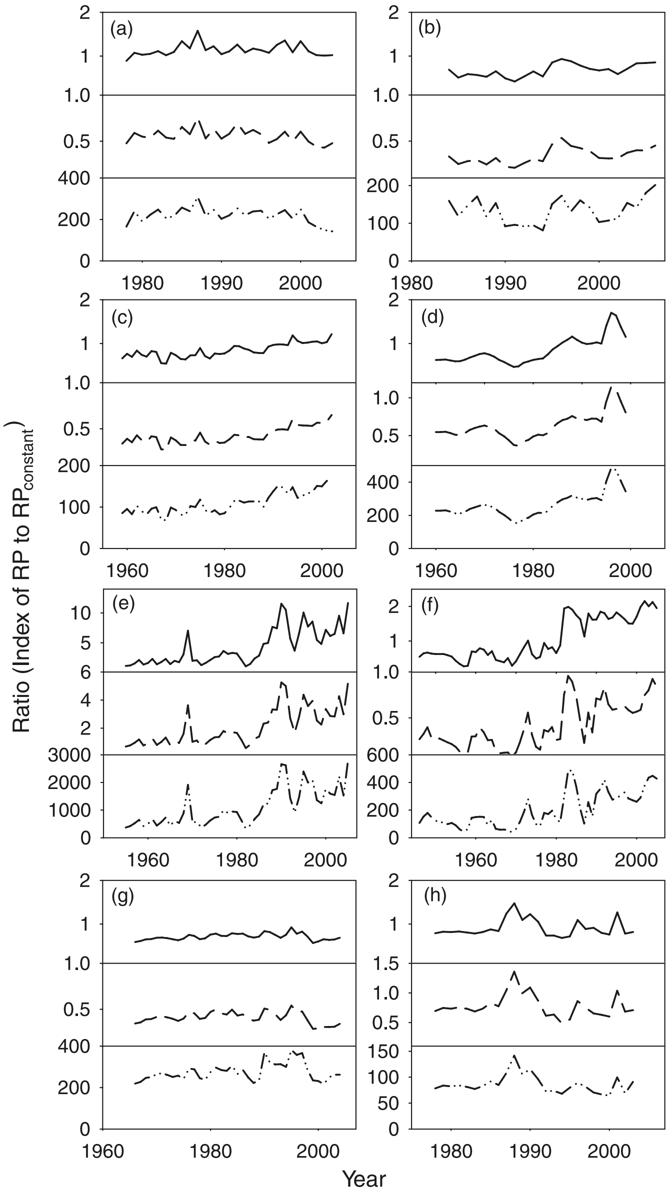
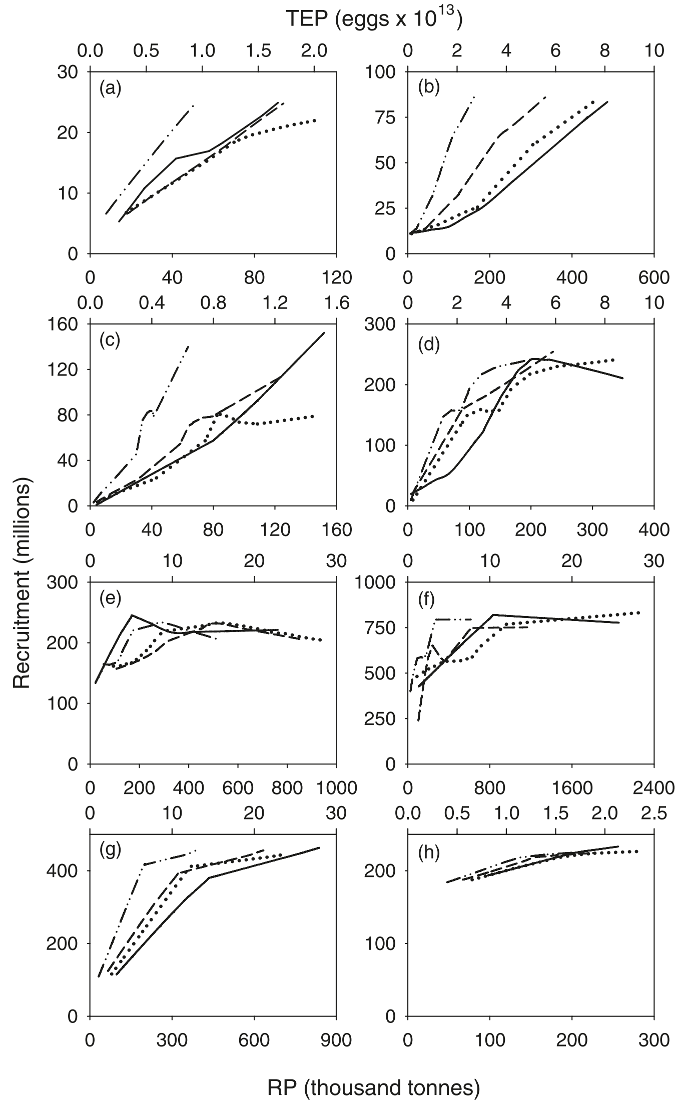


Fig. 4. Loess smooth of recruitment against each index of reproductive potential (RP) for each population: (*a*) Georges Bank cod, (*b*) northern Gulf cod, (*c*) southern Grand Bank cod, (*d*) Grand Bank American plaice, (*e*) Icelandic cod, (*f*) Northeast Arctic cod, (*g*) Baltic cod, and (*h*) northern hake. Solid line, $RP_{constant}$; dashed line, RP_{SSB}; dashed–dotted line, RP_{FSB}; dotted line, RP_{TEP}. RP_{TEP} is plotted on a secondary *x*-axis on the top of each panel. TEP, total egg production.



ence points the same for all indices of RP, i.e., the years in which the population was below B_{lim} or F above F_{lim} were not the same for the different indices of RP. The B_{MSY} varied among indices of RP for a population by as little as less than 5% to more than 60%. The proportion that B_{MSY} was of the biomass at zero fishing (B_{virgin}) also varied among indices of RP for most populations. There was no indication that any particular index of RP had a tendency to result in higher or lower reference point estimates.

The range of results given above does not include those for northern Gulf of St. Lawrence cod, which varied widely. The results for this population deserve particular mention. For the simulations involving $RP_{constant}$ and RP_{TEP} for this stock, MSY is not well defined. In these two cases, recruitment decreases rapidly at low levels of F, while yield increases slightly and then reaches an asymptote at a low level. The results for these two indices of RP do not seem reasonable given the catch history of the population, which had catches in excess of 60 000 t from the mid-1960s to the mid-1980s (Fréchet et al. 2005). However, the results for this stock as well as for the others clearly illustrate the impact of the relationship between RP and R and how this can impact perceptions of productivity.

There was generally some coherence in the long-term patterns of productivity among indices of RP for a population as measured by RPPR at F = 0 (Fig. 5). This coherence re-

Table 2. Results of calculations of reference points.

	RP index	Georges Bank cod	Northern Gulf of St. Lawrence cod	Southern Grand Bank cod	Grand Bank American plaice	Icelandic cod	Northeast Arctic cod	Baltic cod	Northern hake
F_{MSY}	Constant	0.35	0.46	0.15	0.16	0.54	0.6	0.28	0.25
	SSB	0.35	0.14	0.18	0.23	0.6	0.3	0.28	0.25
	FSB	0.35	0.15	0.15	0.27	0.59	0.3	0.28	0.25
	TEP	0.33	0.56	0.25	0.28	0.6	0.3	0.28	0.25
B_{MSY}	Constant	154	44	797	469	1634	3984	1280	435
	SSB	154	452	543	465	1441	5524	1261	419
	FSB	152	464	732	396	1586	5837	1267	421
	TEP	142	45	304	388	1666	5900	1229	423
B_{MSY}/B_{virgin}	Constant	0.27	0.08	0.58	0.65	0.35	0.22	0.32	0.35
	SSB	0.27	0.75	0.54	0.54	0.32	0.32	0.32	0.35
	FSB	0.27	0.77	0.58	0.48	0.37	0.32	0.32	0.35
	TEP	0.29	0.08	0.42	0.47	0.36	0.32	0.32	0.35
MSY	Constant	36	7	90	40	436	1068	238	67
	SSB	35	29	73	50	412	956	236	64
	FSB	35	31	83	47	449	1010	236	65
	TEP	31	8	56	47	448	1020	229	65
% $>F_{lim} = F_{MSY}$	Constant	85	48	85	84	75	80	100	78
	SSB	85	70	76	69	71	97	100	78
	FSB	85	67	85	64	75	97	100	78
	TEP	85	48	70	64	71	97	100	78
% $<B_{lim}$ = 30% RP_{MSY}	Constant	48	0	100	35	51	48	62	19
	SSB	48	63	98	37	4	92	74	22
	FSB	44	63	100	33	10	93	77	26
	TEP	44	4	53	33	8	93	79	26
	Same years	No	No	No	No	No	No	No	No

Note: The F at maximum sustainable yield, the biomass giving maximum sustainable yield, the ratio of B_{MSY} to virgin biomass, the maximum sustainable yield (thousand tonnes), and the percentage of years that the stock was estimated to be above F_{lim} or below B_{lim} are given. Whether or not the years above F_{lim} or below B_{lim} are the same for each index of RP for a stock is also indicated.

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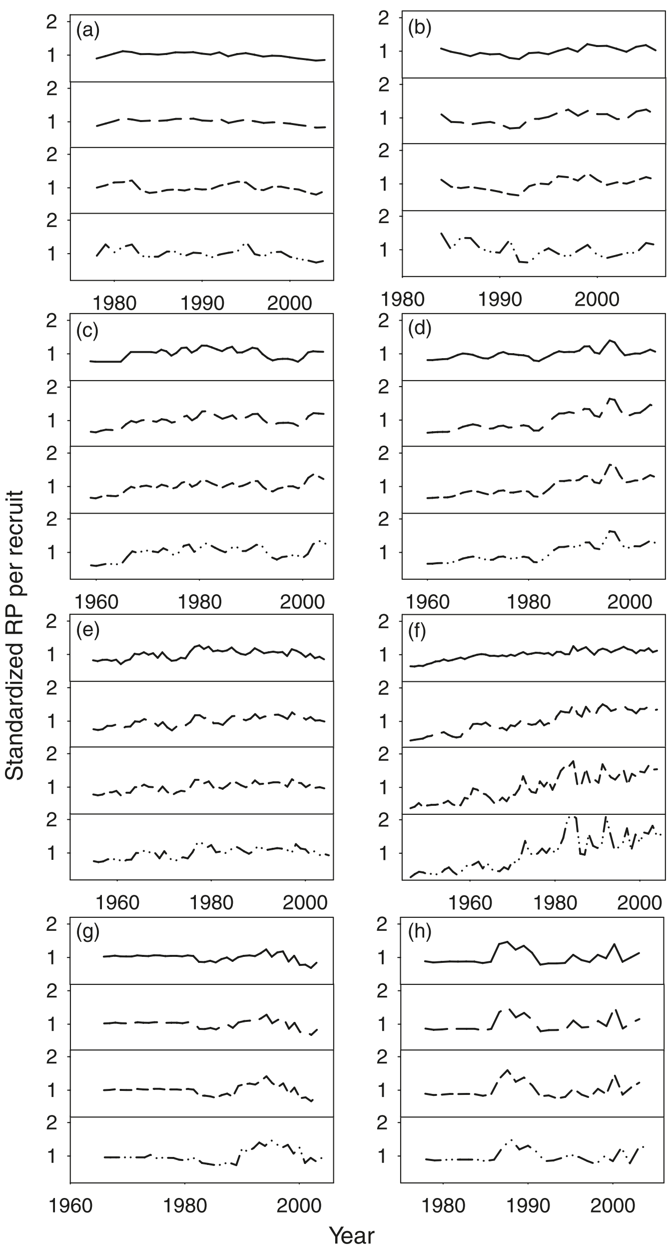
Fig. 5. Standardized reproductive potential (RP) per recruit for each index of RP for each population: (*a*) Georges Bank cod, (*b*) northern Gulf cod, (*c*) southern Grand Bank cod, (*d*) Grand Bank American plaice, (*e*) Icelandic cod, (*f*) Northeast Arctic cod, (*g*) Baltic cod, and (*h*) northern hake. RP per recruit for each index is standardized by dividing by the mean for the time series. Each is shown in a separate plot with the top panel being RPPR for $RP_{constant}$ (solid line), the second panel RP_{SSB} (long-dashed line), the third panel RP_{FSB} (short-dashed line), and the bottom panel RP_{TEP} (dashed–dotted line).



flects changes in size at age (weight or length) over time, which is included in all indices. However, it is also evident that each index of RP shows different detail in that trend. For example, for Georges Bank cod, RP_{TEP} ranged from 0.7 to 1.4 times its mean, while $RP_{constant}$ showed only a range of 0.8–1.1 times its mean. For Northeast Arctic cod, all indices of RP showed an increase in RPPR up until the late 1960s, after which RPPR for $RP_{constant}$ remained relatively stable, while the other three indices continued to increase. For northern hake, all indices started out in the late 1970s at a similar level relative to their mean. In the most recent year for which data were available, there was a 20% difference between the indices of RP in standardized estimates of RPPR. For Baltic cod, $RP_{constant}$ started the time series as the highest of the standardized indices of RPPR. In 1990, there was an abrupt change and the standardized $RP_{constant}$ index became the lowest of the standardized indices. Although the details are specific to each population, differences between estimated productivity using the different indices of RP are evident for all populations.

The different indices of RP sometimes gave very different perceptions of stock status relative to B_{lim} over the 15 year projection period (Fig. 6). The index of RP giving the greatest increase in population size relative to B_{lim} was not always the same. For Baltic cod, northern hake, southern Grand Bank cod, and northern Gulf cod, RP_{TEP} clearly gave the largest population size relative to B_{lim}. However, for Icelandic cod, $RP_{constant}$ gave the largest population size relative to B_{lim}, while for American plaice, $RP_{constant}$ gave the smallest increase in population size relative to B_{lim}.

The different indices of RP vary by the sequential addition of more biological data, first adding maturity at age, then sex ratio, and then fecundity. The ratio of the index of RP to $RP_{constant}$ shows the impact of this incorporation of biological data on the time series of estimates of RP. There was a significant positive correlation (Pearson product moment correlation: $r = 0.47$, $p = 0.02$) between the coefficient of variation of the ratio of the index of RP to $RP_{constant}$ and the difference between estimates of F_{MSY} (Fig. 7).

Discussion

Alternative indices of RP resulted in different estimates of population productivity for all populations. This was the result of variation in underlying reproductive biology (maturity, sex ratio, and fecundity at age) and changes in age composition of the populations (Morgan and Brattey 2005). The use of an index of RP that does not incorporate variation in reproductive characteristics ($RP_{constant}$) as the measure determining recruitment assumes that this is an adequate index of RP of the population. Variability in reproductive biology or stock age composition/condition may mean that indices of RP that do not incorporate these factors may not be representative of RP.

For all populations, the relationship between $RP_{constant}$ and alternative indices of RP was not constant owing to changes in reproductive parameters and (or) adult population condition. This lack of constancy has been used to argue that $RP_{constant}$ is not a good index of RP because it is not directly proportional to egg production (Marshall et al. 2006). In other words, $RP_{constant}$ can be improved by adding more biological information to represent the "production" processes that yield the number of potential eggs, which becomes modified by mortality processes during the dynamics of early life stages to result in the number of recruits (Ulltang 1996; Marshall et al. 1998). The lack of constancy between indices means that the relationship between RP and R will not be the same for each index and perceptions of productivity will vary.

Fig. 6. Proportion of B_{lim} for each index of reproductive potential (RP) to $RP_{constant}$ for each population for every year of 15 year projections of population size: (*a*) Georges Bank cod, (*b*) northern Gulf cod, (*c*) southern Grand Bank cod, (*d*) Grand Bank American plaice, (*e*) Icelandic cod, (*f*) Northeast Arctic cod, (*g*) Baltic cod, and (*h*) northern hake. Solid line, $RP_{constant}$; dashed line, RP_{SSB}; dashed–dotted line, RP_{FSB}; dotted line, RP_{TEP}.

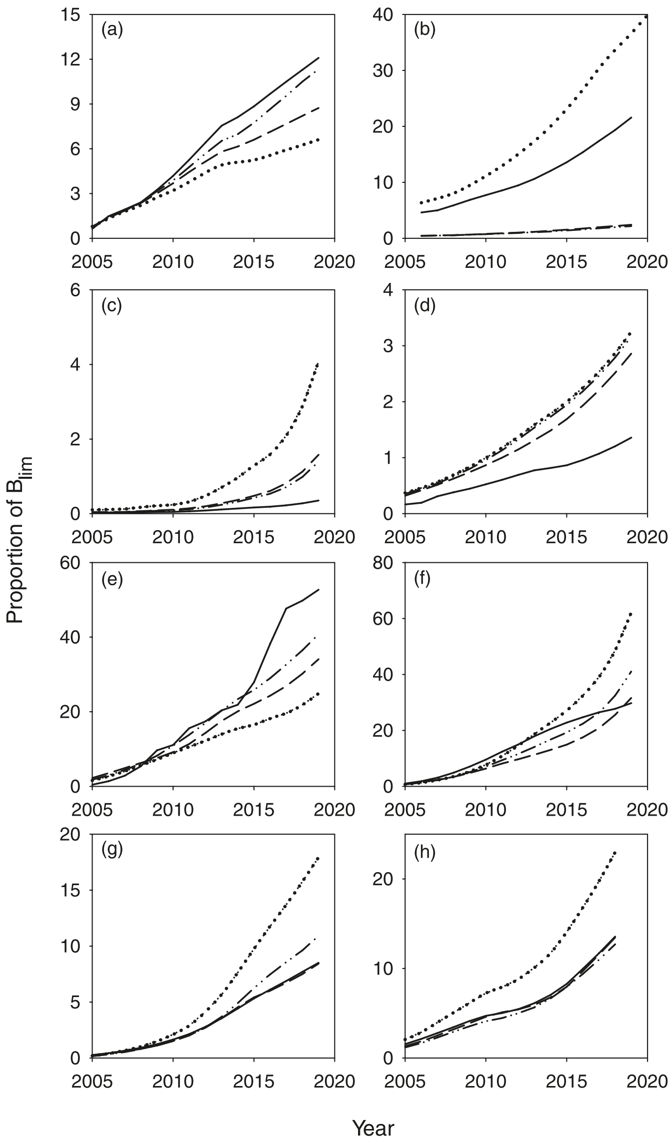
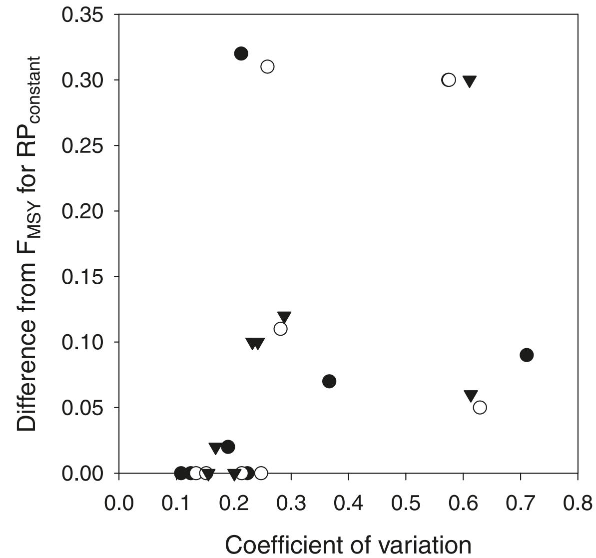


Fig. 7. Absolute value of F_{MSY} estimated for the particular index of reproductive potential (RP) minus the F_{MSY} estimated for that population for $RP_{constant}$ plotted against the coefficient of variation of the ratio of each index of RP to $RP_{constant.}$ Solid circles, RP_{SSB}; open circles, RP_{FSB}; triangles, RP_{TEP}.



The amount of RP produced per recruit is known to vary and has been used in evaluating the level of F that a population can sustain (Mace and Sissenwine 1993; O'Farrell and Botsford 2006; Shelton et al. 2006). For all populations examined here, RPPR varied over time, but also, perceptions of the level of RPPR depended on which index of RP was being used. These calculations were carried out for $F = 0$ and calculations at actual levels of F experienced by the population could diminish the differences in RPPR (Scott et al. 1999; Morgan and Brattey 2005). Nevertheless, the results show clear differences in the potential productivity of populations under no exploitation, depending on the index of RP.

For all populations examined, estimated F_{lim} and (or) B_{lim} varied using the different indices of RP. This is the result of variation in the RP–R relationship. Murawski et al. (2001) and Marshall et al. (2006) also found that the relationship between R and alternative indices of RP varied and that this could lead to a change in the estimates of reference points. The perception of stock status relative to limit reference points (i.e., whether stock size is healthy or F is too high) varies depending on which index of RP is used. However, there was no consistency in which indices of RP were more conservative, and in half of the cases, the lowest F_{lim} was associated with $RP_{constant}$.

The amount of variation in estimated reference points among the indices of RP varied across populations, some showing large differences and others small. The populations varied in the degree of change in maturity, sex ratio, and fecundity and also different levels of change in age composition. This results in various degrees of difference between indices of RP in the RP–R relationship, leading to different amounts of variation between indices of RP in estimated reference points. As changes occur in the reproductive biology of a population, the amount of variation among alternative indices of RP could change. A population with little variation in estimated reference points using alternative indices of RP could have a large difference if reference points are reestimated in the future provided that change in reproductive biology has occurred.

Projections of growth in population size also varied for all populations when different indices of RP were used in the projection. As with other measures of productivity, there was no consistency in which index of RP gave the highest estimates of productivity. In some cases, the differences in projected 15 year population growth relative to B_{lim} were very large. Such variation will have particular implications for the evaluation of recovery potential for populations that are below B_{im}. Given the possible impact on recovery planning, careful consideration should be given in developing the best indices of RP for depleted stocks.

The alternative indices of RP that were examined in this study were constructed by sequentially adding information on reproductive biology. Maturation showed the most variation over time and some of the largest differences in perceived productivity tended to be between RP_{SSB} and $RP_{constant}$. Sex ratio showed the least variation and generally the relationship between RP_{SSB} and RP_{FSB} was similar. The addition of sex ratio did, however, result in some deviation between the two indices. Fecundity at age showed intermediate levels of variation and its addition resulted in further deviation from $RP_{constant}$. Despite these generalities, there was no consistency in which index of RP gave the highest or lowest estimate of population productivity. This is because the degree of variation in reproductive characteristics varied from population to population, as did the pattern of variation across time.

How well an index of RP reflects the population's true RP will depend on how well the underlying parameters are estimated. A good example of this is RP_{TEP} where the method of estimating fecundity differed greatly between populations. For most populations, estimates of fecundity simply reflected changes in weight or length at age, as only constant fecundity weight or length relationships were available. Fecundity at length and weight can vary substantially (Kraus et al. 2002; Murua et al. 2006; Rideout and Morgan 2007) and the use of constant relationships will only capture some of the dynamics of this factor. In northern Gulf of St. Lawrence cod and Northeast Arctic cod, an attempt has been made to capture some of this added variability by including condition in the fecundity length relationships. For Baltic cod, fecundity has been related to prey availability. Estimates of RP will be improved if times series of maturity, sex ratio, and fecundity better reflect the true variation in the population. If parameters are poorly estimated, then simpler indices of RP may perform better than more complex indices (DeOliveira et al. 2006). More studies of this type need to be conducted.

One important aspect that is not dealt with in this study is the possible effects of environmental variation on RP. Perhaps the best example of this is for Baltic cod where a strong impact of environment on R has been demonstrated through the volume of water suitable for egg survival (Köster et al. 2001). An improvement in the relationship between RP and R has been shown for that population when variable maturity, sex ratio, and fecundity are incorporated, but the relationship is improved further with the addition of environmental information (Köster et al. 2001; Kraus et al. 2002). For that population, the effect of the environment is known to be large and should probably be incorporated into estimates of reference points if possible. Study of environmental effects on RP should be continued for other populations as well.

Population status relative to reference points, RPPR, and projections of population size were all affected by using alternative indices of RP. It has not been determined which gives the best estimate of R. However, it is clear that estimates of sustainable harvest levels and recovery time for depleted populations can be greatly affected by alternative indices of RP. Research should continue on producing and validating alternative indices of RP and on their incorporation into advice for fisheries management. Simulations evaluating the performance of different indices of RP in maintaining populations within safe biological limits should be explored. Such simulations should be stochastic in nature, incorporating uncertainty, including on the estimates of reproductive characteristics used in the calculation of the indices of RP. The evaluation should use the best S–R relationship for each index of RP being examined and should use reference points derived from each index being evaluated. These studies would need to be stock specific and the best index of RP will likely vary among populations, depending on the degree of temporal variation in reproductive characteristics and the quality of the estimates of these characteristics. The potential for impact of different indices of RP revealed in this study highlights the need for these evaluations.

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