How Much Spawning per Recruit is Enough?

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Mace, P. M. and M. P. Sissenwine. 1993. How much spawning per recruit is enough? p. 101–118. *In* S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

In order for fish stocks to persist, successive generations must replace each other on average. This means that fishing should not reduce the egg production or amount of spawning per recruit (SPR) below a threshold level that is necessary for replacement. For each fishery under Federal management, the United States requires definitions of overfishing that at the least guard against recruitment overfishing; 60% of these definitions are based on threshold levels of SPR, which have typically been chosen arbitrarily from the range 20–35% of the level that would occur if there were no fishing (referred to as the %SPR). Threshold replacement levels can be estimated from spawning-recruitment (*S-R*) data, using a conservative hypothesis that the median of the observed survival ratios is an estimate of the maximum average survival ratio. A survey of 91 sets of *S-R* data for fisheries resources of Europe and North America indicated that the replacement %SPR averaged slightly less than 20% overall. Some species (e.g., Atlantic cod and most flatfish) exhibit consistently low levels of replacement %SPR (high resilience to fishing), while the smaller gadoids and many of the small pelagic species have values as high as 40–60% (low resilience). Replacement %SPR was positively correlated with natural mortality and negatively correlated with both the maximum average body weight and the body weight at 50% maturity. Replacement %SPR is recommended as a reference point for defining overfishing since it is based on the premise of stock replacement, it can be estimated from standard stock assessment information and, where such information is lacking, taxonomic affiliation and life history parameters can be used to select preliminary estimates.

Pour que les stocks de poissons persistent, les générations successives doivent se remplacer les unes les autres en moyenne. Cette observation signifie que la pêche ne doit pas faire descendre la production d'oeufs ou la ponte par recrue (SPR) au-dessous du seuil nécessaire pour assurer le remplacement. Pour chaque pêche gérée par le gouvernement fédéral, les États-Unis exigent des définitions de la surpêche qui au moins assurent une protection contre la surpêche du recrutement; 60 % de ces définitions reposent sur des seuils de ponte par recrue qui ont été en général choisis arbitrairement dans la plage de 20 à 35 % du niveau qui existerait en l'absence de pêche (désigné comme % SPR). On peut estimer les seuils de remplacement à partir des données de ponte-recrutement, en appliquant une hypothèse prudente selon laquelle la médiane des taux de survie observés est une estimation du taux maximum moyen de survie. Une étude de 91 ensembles de données de ponte-recrutement pour les ressources halieutiques d'Europe et d'Amérique du Nord a montré que le %SPR de remplacement s'établissait en moyenne à un peu moins de 20 % dans l'ensemble. Chez certaines espèces (par exemple, la morue atlantique et la plupart des poissons plats), on observe constamment de faibles taux de %SPR de remplacement (forte résilience à la pêche), tandis que les gadidés de taille plus petite et de nombreuses espèces pélagiques de petite taille ont des valeurs qui peuvent atteindre 40 à 60 % (faible résilience). Le %SPR de remplacement présentait une corrélation positive avec la mortalité naturelle et une corrélation négative avec le poids corporel maximal moyen et le poids corporel à maturité de 50 %. Le %SPR de remplacement est recommandé comme point de référence pour définir la surpêche puisqu'il repose sur l'hypothèse du remplacement du stock; il peut être estimé à partir de données sur l'évaluation du stock normalisée et, en l'absence de ces données, des paramètres d'affiliation taxonomique et de cycle biologique peuvent être utilisées pour choisir les estimations provisoires.

Population persistence requires that successive generations replace or surpass each other on average. This means that year-classes must produce sufficient spawning units (usually expressed in terms of biomass or eggs) per recruit (SPR) over their lifespan to correspond to the average number of recruits (R) produced by a unit of spawning (S). The observed ratio of R/S is referred to as the "survival ratio", s. Thus, persistence requires that SPR $\geq 1/s^*$, where s^* is the average value of s. It is only recently that spawning per recruit analysis has begun to be calculated routinely and SPR criteria have begun to be given explicit consideration in fisheries management objectives. Yet in the last few years, SPR has become the most common basis of overfishing definitions for U.S. marine fisheries.

In spite of the actual and potential importance of SPR criteria as a basis of fisheries management, relatively little attention has been given to the question of "how much spawning per recruit is enough?". There are considerable data from a wide variety of fisheries that can be used to answer this question. This paper reports the most comprehensive compilation and analysis of such data to date. As background, it also reviews recent publications and events that have focused attention on the use of SPR criteria for defining overfishing.

Background

Development of SPR Reference Points

Spawning per recruit (SPR) analysis is a simple extension of the "dynamic pool" model used to calculate yield per recruit (YPR). Beverton and Holt (1957) give the classic derivation of the model, and Gabriel et al. (1989) specify the computational details. While maximum YPR usually occurs at an intermediate fishing intensity, SPR declines monotonically as fishing intensity increases (Fig. 1a). Biological reference points derived from YPR analysis ($F_{0.1}$ and F_{max}) have been widely applied, but until recently there were no reference points associated with SPR analysis.

Goodyear (1977, 1980) first developed a "compensation ratio" based on SPR criteria (defined as the ratio of SPR for an unfished population to the SPR for the fished population), and used it as an index of the resilience of a population to fishing and other stresses. However, Shepherd (1982) is generally credited with sparking interest in the development and application of SPR reference points by showing how a standard SPR analysis could be combined with spawning-recruitment (*S*-*R*) observations to generate reference fishing mortality rates. The relationship between the two types of information (Fig. 1) is straightforward: for any constant F, there is a corresponding SPR level from SPR analysis (Fig. 1a) that can be inverted and used as the slope of a straight line through the origin of the *S*-*R* scatterplot (Fig. 1b). Points along the line represent the average survival ratio (R/S) required to support that particular constant F. Observed survival ratios can therefore be used to define threshold and target levels of F, which can then be translated back to the SPR scale.

One potential candidate for a threshold F is the extinction threshold fishing mortality rate, which will be referred to here by the symbol, F_τ. For most of the commonly-used (non-depensatory) *S*-*R* relationships, F_τ is determined by the slope (survival ratio) at the origin of the relationship. Shepherd (1982) proposed that the observed 90th percentile survival ratio could be used as an estimate of the slope at the origin, and suggested that the corresponding F could be treated as a threshold that should not be exceeded. Subsequently, Sissenwine and Shepherd (1987) pointed out that the 90th percentile may overestimate the slope at the origin for two reasons. First, *S*-*R* observations with higher survival ratios may just reflect anomalously favourable environmental conditions, not the ability of the population to sustain fishing under average environmental conditions. Second, if the underlying *S*-*R* relationship exhibits little compensation (density-dependence) and/or the *S*-*R* observations are restricted to low stock sizes where the *S*-*R* relationship can be approximated by a straight line through the origin, fishing at a rate corresponding to the 90th percentile survival ratio will generally result in insufficient recruits to replace the spawning stock that produced them, and the stock will decline.

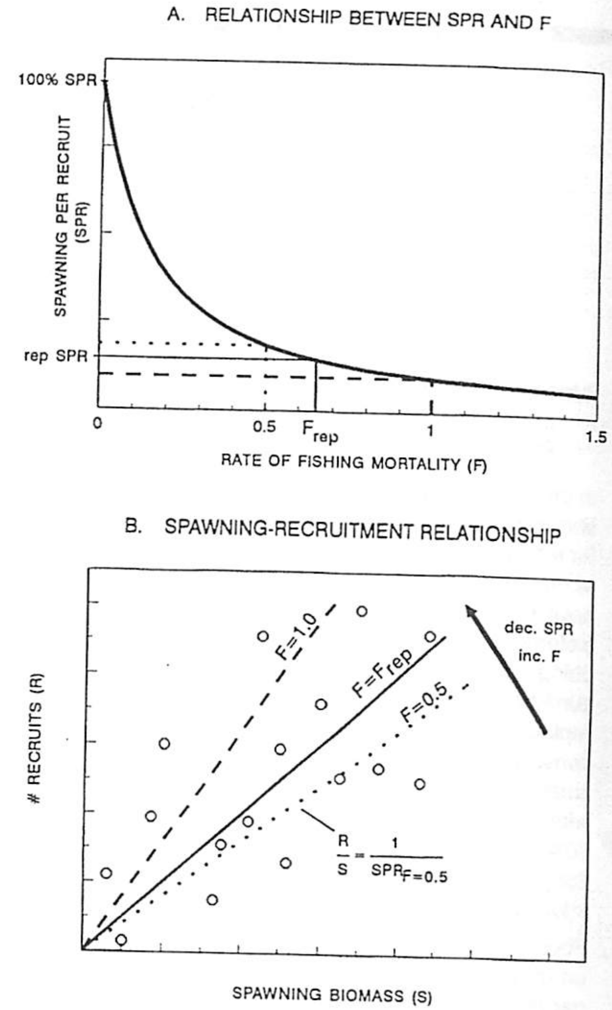

Fig. 1. Relationship between (A) spawning per recruit (SPR) levels derived from SPR analysis and (B) survival ratios (R/S) estimated from spawning-recruitment (*S*-*R*) scatterplots. A particular constant rate of fishing mortality (e.g., $F = 0.5$, Fig. 1a) corresponds 1:1 with an associated SPR level ($SPR_{F=0.5}$) which can be inverted and used as the slope of a straight line through the origin of the *S*-*R* scatterplot (dotted line, Fig. 1b). This line represents the average survival ratio required to support the corresponding (constant) F. Higher levels of F require higher survival ratios (higher slopes). The fishing mortality rate corresponding to the replacement line is referred to as F_{rep} (solid line, Fig. 1b); the corresponding level of SPR is called the replacement SPR (Fig. 1a). See text for further explanation.

Following on from an earlier discussion in Beverton et al. (1984), Sissenwine and Shepherd (1987) proposed an alternative approach based on the concept of replacement. If fishing occurs at a low rate such that the observed survival ratios tend to be mostly above the line with slope corresponding to the SPR for that F (lower broken line, Fig. 1b), then the average size of the population will increase; if fishing occurs at a high rate such that the observed survival ratios are mostly below the line (upper broken line, Fig. 1b), the population will tend to decrease. The replacement line is defined as the line with a slope equal to the observed average survival ratio. Sissenwine and Shepherd referred to the fishing mortality rate that corresponds to the average survival ratio as F_{rep} (F-replacement). They proposed estimating F_{rep} from the median survival ratio (solid line, Fig. 1b), in which case it may often be referred to, by the symbol, F_{med} (F-median).

They also defined recruitment overfishing as occurring when fishing mortality exceeds the level associated with the slope at the origin of the S-R relationship, and proposed that F_{rep} could be used as a biological reference point for defining recruitment overfishing (i.e., in the terminology used here, they proposed that F_{rep} could be used as an estimate of F_τ). The validity of this proposal depends on the degree of compensation in the underlying S-R relationship, the range of stock sizes covered by the observations, and environmental conditions and other factors that affect survival rates. It is most applicable in the cases where there is either little compensation over the entire range of the S-R relationship, or the S-R observations are restricted to low stock size where the relationship is approximately linear. This situation is referred to as the null model (no density-dependence over the observed range). If the null model of no density-dependence applies, fishing at F_{rep} should result in S varying without trend about recent levels. If the data exhibit compensation (density-dependence), then fishing at F_{rep} should result in S varying with a tendency toward the mid-range of the observed values of S. In either case, F_{rep} is an estimate of the fishing mortality that, on average, allows for replacement of successive generations over the observed range of S-R data.

It should be noted that use of the null model of no density-dependence does not necessarily mean that compensation does not exist; rather that it may not occur at all levels of S (particularly the levels of S observed in many heavily-exploited fisheries), or it may be obscured by recruitment variability. Rejection of the null model does not affect the validity of the replacement concept; however, for data that exhibit compensation, F_{rep} is likely to be a conservatively-biased estimate of F_τ. There are some circumstances where F_{rep} may even be more appropriate as a fishing target, rather than an overfishing threshold; e.g., stocks with moderate or strong compensation where the S-R observations are restricted to a range of stock sizes that are near or above optimal levels (e.g., near or above B_{msy}). The preceding statements are also contingent on the stability of environmental conditions: F_{rep} may over- or under-estimate F_τ if environmental conditions during the period of observation have produced unusually high or low survival rates, respectively.

Application of SPR Reference Points

Application of these and other SPR reference points has been sporadic. Following Shepherd's (1982) paper, the International Council for the Exploration of the Sea (ICES) Stock Assessment Methods Working Group advocated routine calculation of F_{high}, F_{med} and F_{low}, the reference fishing mortalities corresponding respectively to the 90th, 50th (or median) and 10th percentile survival ratios calculated from S-R data (ICES 1983, 1984). However, even though SPR reference points are now part of the standard output from ICES stock assessments, they are not used explicitly as a basis for management advice. The first fisheries management organization to explicitly use the concept of replacement SPR to define overfishing was the New England Fishery Management Council (NEFMC 1985, Sissenwine and Marchesseault 1985), one of eight regional U.S. Fishery Management Councils charged with assisting the National Marine Fisheries Service to develop Fisheries Management Plans (FMP's) to manage U.S. marine fisheries. It was several more years before the concept was applied elsewhere.

The impetus for wider application of SPR criteria as a basis for fisheries management in the U.S. came with the development of regulations requiring Fishery Management Councils to establish measurable definitions of overfishing for all managed stocks. The new regulations, published in July 1989 and referred to as the "50 CFR Section 602 Guidelines", now require FMP's to

> ...specify, to the maximum extent possible, an objective and measurable definition of overfishing for each stock or stock complex covered by that FMP, and to provide an analysis of how the definition was determined and how it relates to reproductive potential.

The guidelines also state that although some types of overfishing (growth, localised and pulse) may be permissible, the definitions must, at the least, guard against recruitment overfishing.

Here there is an implicit assumption that recruitment overfishing occurs at higher fishing intensity than growth overfishing, which is usually defined as occurring when F exceeds F_{max}, the fishing mortality rate associated with maximum YPR. However, the relationship between F_{max} (or $F_{0.1}$) and reference levels of SPR has not yet been examined. There are currently 33 FMP's in the U.S. covering over 100 stocks and stock-complexes; of these more than 80% use overfishing definitions based on threshold fishing mortality rates. About 20% have used $F_{0.1}$, F_{max} or F_{msy}, while 60% have adopted threshold levels of SPR, which correspond 1:1 with threshold levels of F (but not necessarily S).

In some ways it is surprising that SPR thresholds have been so widely adopted by the U.S. Fishery Management Councils since there are few U.S. fisheries where critical levels of SPR have been calculated explicitly from actual S-R data. Moreover, there are few studies, particularly empirical studies, that can be used to provide guidelines on the values to select. Goodyear (1989) suggested that a critical minimum of at least 20% of the maximum SPR (i.e., 20% $SPR_{F=0}$) should be maintained for stocks where the spawning-recruitment relationship cannot be determined. Clark (1991) suggested that a management target of 35% SPR should be capable of achieving high yields for a wide range of plausible spawning-recruitment relationships. Goodyear's proposal (for a management threshold) was based on limited empirical results, while Clark's proposal (for a management target) was based on a theoretical analysis. The levels chosen to represent overfishing thresholds by the Fisheries Management Councils have often been somewhat arbitrary, ranging anywhere from 5–70%, although usually falling within the range 20–35%.

Terminology

The amount of SPR that corresponds to F_{rep} is referred to in the present paper as the "replacement SPR". The term F_{rep} is used to refer to the replacement concept, whereas F_{med} is the statistic used to estimate F_{rep}. (More work is needed to determine whether the median is the best estimator of the replacement level; however, it is the estimator that has been the most widely adopted — e.g., ICES 1990a–o). Levels of SPR are often expressed as a percent of the maximum, which occurs at $F = 0$ (Fig. 1a).

It should be noted that the term percent spawning per recruit (%SPR) is analogous to the percent maximum spawning potential (%MSP) first used by NEFMC (1985) and the spawning potential ratio defined by Goodyear (1989) as the inverse of his compensation ratio. Thus, using similar logic to Goodyear (1977, 1980, 1989), the threshold replacement %SPR can be considered a measure of the total "compensatory reserve" of an unfished stock, and therefore as an index of the overall resilience of a stock to fishing pressure (with the degree of resilience being inversely related to the magnitude of the replacement %SPR). For the remainder of this paper, the replacement survival ratio, replacement SPR (i.e., the inverse of the replacement survival ratio), the replacement %SPR, and F_{rep} will be referred to collectively as the replacement reference points. In most contexts, it is preferable to talk about %SPR (or absolute SPR) rather than F_{rep} because the latter is actually a vector of numbers related to partial recruitment (PR), whereas the former is independent of PR.

Purposes of Present Study

The main purposes of the present study were to compile and summarise data on replacement %SPR and related reference points for a variety of well-studied fisheries, and to determine whether there are any consistent effects of taxonomic affiliation or life history parameters on these reference points. One of the primary reasons for investigating such relationships is that if they exist they may be extremely useful for inferring the location of overfishing thresholds for comparatively little-studied fisheries (e.g., most of the U.S. fisheries covered by FMP's), or to define default reference points that can be used until more information becomes available.

Methods

Two basic types of input were required to estimate the replacement SPR and F_{rep} using Sissenwine and Shepherd's (1987) approach: an SPR curve and a spawning-recruitment (S-R) scatterplot (Fig. 1). The replacement SPR was estimated as the inverse of the median survival ratio from the S-R scatterplots or, equivalently, the inverse of the slope of the straight line through the origin that bisects the S-R observations (solid line, Fig. 1b). The corresponding estimate of replacement fishing mortality, F_{rep}, was then obtained directly from the SPR curve (Fig. 1a). The replacement SPR was normalised by dividing by the maximum SPR ($SPR_{F=0}$), the result being referred to here as the replacement %SPR. SPR and %SPR levels corresponding to $F_{0.1}$ and F_{max} were also obtained from the SPR curve.

The main criterion used to select fish stocks for this survey was the availability of adequate stock assessment results. In cases where SPR curves and S-R scatterplots had already been provided in the stock assessment literature or by personal communication, they were used directly to calculate the replacement reference points. Otherwise, it was necessary to assemble the following data: estimates of natural mortality, a maturity ogive, and VPA-type output such as population numbers by age and year, annual mean weights at age, and age- and year-specific fishing mortality rates. The following conventions were adopted to construct S-R scatterplots and YPR and SPR analyses from these data. Spawning was always expressed in units of absolute stock biomass, except in two cases (Atlantic sea scallops) where biomass was only available as a relative index. Spawning stock biomass (SSB) was calculated by projecting forward from the standard January 1 reference time of VPA to the mid-point of the spawning season (provided this was known) both for the S-R plot and the SPR analysis; the last several years of VPA data (usually one more than the age of recruitment to the fishery) were generally omitted from S-R plots; the most recent five years of VPA results were used to calculate average partial recruitments, weights at age and maturity ogives for input to YPR and SPR; if sufficient data were available, the information used to calculate mean weights at age for the stock (e.g., survey data) differed from that used to calculate mean weights at age for the catch (e.g., commercial sampling data); and at least $3/M$ age groups (Anthony 1982) or, more commonly, a plus group (essentially an infinite number of age groups) was used to calculate YPR and SPR. (These conventions were based on the most common approaches adopted by the stock assessment groups that routinely produce S-R scatterplots and SPR analysis.) The sequence of calculations for YPR and SPR was identical to that outlined in Gabriel et al. (1989).

A factor that could have a substantial influence on the validity of the replacement reference points as indices of recruitment overfishing thresholds is the degree of compensation or concavity exhibited by the S-R data. An "index of concavity" was derived to test the null hypothesis that the S-R data could be adequately represented by a straight line through the origin (the median survival ratio) over the observed range of S. Since numeric values were not available for all sets of S-R observations, the index was based on a non-parametric rank sum method. It was calculated by ranking the observations

Table 1. Classification of species included in the survey. Numbers of stocks from each species are given in brackets. Superscripts indicate the number of stocks excluded from analyses involving the replacement reference points.

ORDER CLUPEIFORMES

Family Clupeidae - herrings

1. $(17)^{-1}$ Atlantic herring (*Clupea harengus*)
2. (1) Sardine or pilchard (*Sardina pilchardis*)
3. (2) Sprat (*Sprattus sprattus*)

ORDER GADIFORMES (ANACANTHINI)

Family Gadidae - codfishes

4. $(1)^{-1}$ Pacific cod (*Gadus macrocephalus*)
5. $(15)^{-1}$ Atlantic cod (*Gadus morhua*)
6. $(7)^{-1}$ Haddock (*Melanogrammus aeglefinus*)
7. (5) European whiting (*Merlangius merlangus*)
8. (2) Silver hake (*Merluccius bilinearis*)
9. (2) European hake (*Merluccius merluccius*)
10. $(1)^{-1}$ Pacific whiting or hake (*Merluccius productus*)
11. $(2)^{-1}$ Blue whiting (*Micromesistius poutassou*)
12. (6) Pollock or saithe (*Pollachius virens*)
13. (1) Walleye pollock (*Theragra chalcogramma*)

ORDER PERCIFORMES (PERCOMORPHI; ACANTHOPTERYGII)

Family Carangidae - jacks and pompanos

14. $(2)^{-1}$ Horse mackerel or scad (*Trachurus trachurus*)

Family Scombridae - mackerels and tunas

15. (2) Atlantic mackerel (*Scomber scombrus*)

Family Xiphiidae - swordfishes

16. (2) Swordfish (*Xiphias gladius*)

Family Scorpaenidae - scorpionfishes

17. $(1)^{-1}$ Redfish or ocean perch (*Sebastes marinus*)
18. (1) Deepwater redfish (*Sebastes mentella*)

ORDER PLEURONECTIFORMES (HETEROSOMATA)

Family Bothidae - lefteye flounders

19. (1) Megrim (*Lepidorhombus whiffiagonis*)
20. (1) Summer flounder (*Paralichthys dentatus*)

Family Pleuronectidae - righteye flounders

21. (1) Pacific halibut (*Hippoglossus stenolepis*)
22. (1) Yellowfin sole (*Limanda aspera*)
23. (2) Yellowtail flounder (*Limanda ferruginea*)
24. (5) European plaice (*Pleuronectes platessa*)
25. (2) Greenland halibut (*Reinhardtius hippoglossodes*)

Family Soleidae - soles

26. (6) Dover sole (*Solea vulgaris*)

INVERTEBRATES

27. (2) Atlantic sea scallops (*Placopecten magellanicus*)

based on the magnitude of S, summing the ranks on either side of the median survival ratio (R/S), subtracting the rank sum above the median R/S from the sum below, and dividing by the maximum possible difference ($\frac{1}{4}N^2$ for N even and $\frac{1}{4}(N^2 - 1)$ for N odd) to normalise it. The smallest rank sum was also used in a Wilcoxon two-sample rank test to test for the significance of deviation from the null hypothesis of no density-dependence (straight line through the origin). Values approaching the extremes of the possible range of the normalised index [-1,1] would occur if the data exhibited pronounced convexity or concavity, respectively. Statistically significant cases where the index is less than zero indicate depensation over the observed range of S and statistically significant cases where the index is greater than zero indicate compensation in the data. In the former case, the replacement survival ratio gives an overestimate of the slope at the origin of the full S-R relationship; in the latter case, it gives a conservative estimate.

Other variables that could potentially influence the replacement reference points include taxonomic affiliation and life history parameters. The life history parameters that were considered in the present analysis include natural mortality (M), the average body weight at 50% maturity, the maximum average body weight, and the maximum observed spawning stock biomass. Multiple linear regression and forward selection stepwise regression techniques were used to investigate the relative importance of these and other variables, including the index of concavity.

Table 2. Estimates of replacement %SPR and sources of information for stocks included in the survey, grouped by geographic location. Species numbers refer to Table 1.

Case No.	Stock	Species No.	Replacement %SPR	Sources of information
A. ICES stocks (Northeast Atlantic and associated areas)				
1	Irish Sea cod	5	3.9	1,15
2	Irish Sea whiting	7	11.4	1,15
3	Irish Sea plaice	24	10.1	1,15
4	Irish Sea sole	26	23.5	1,15
5	Celtic Sea cod	5	6.6	1,15
6	Celtic Sea whiting	7	6.9	1,15
7	Celtic Sea plaice	24	5.0	1,15
8	Celtic Sea sole	26	19.2	1,15
9	Blue whiting, northern stock	11	–	2,15
10	Blue whiting, southern stock	11	7.4	2,15
11	NE Arctic cod	5	5.8	3,15,*
12	NE Arctic haddock	6	24.3	3,15,*
13	NE Arctic saithe	12	9.8	3,15
14	Redfish in areas IIA & B	18	18.2	3,15
15	Greenland halibut in areas I & II	25	21.6	3,15
16	Icelandic summer herring	1	18.6	4,15,*
17	Norwegian spring herring	1	–	4,15,*
18	North Sea sole	26	12.3	5,15
19	North Sea plaice	24	11.2	5,15
20	Div. VIId sole	26	11.5	5,15
21	Div. VIIe sole	26	25.8	5,15
22	Bay of Biscay sole	26	5.6	5,15,*
23	Div. VIIe plaice	24	7.3	5,15
24	North Sea cod	5	3.4	6,15
25	Div. VIa cod	5	11.0	6,15
26	Div. VIId cod	5	5.3	6,15
27	North Sea haddock	6	15.5	6,15
28	Div. VIa haddock	6	18.2	6,15
29	North Sea whiting	7	50.1	6,15
30	Div. VIa whiting	7	37.2	6,15
31	Div. VIId whiting	7	42.7	6,15
32	North Sea saithe	12	16.7	6,15
33	Div. VI saithe	12	24.6	6,15
34	Cod in the Kattegat	5	8.2	7,15,*
35	Cod in the Skagerrak	5	6.1	7,15,*
36	Plaice in the Kattegat	24	8.7	7,15,*
37	North Sea herring	1	10.8	8,15,*
38	Celtic Sea herring	1	27.9	8,15
39	Div. VIa north herring	1	16.8	8,15
40	Clyde herring	1	23.0	8,15,*
41	Div. VIa south & VIIb,c herring	1	23.4	8,15
42	Div. VIIa herring	1	14.6	8,15
43	Baltic cod in area 22	5	2.5	9,15
44	Baltic cod in areas 22& 24	5	2.9	9,15
45	Baltic cod in areas 25–32	5	8.8	9,15
46	Herring in the Western Baltic & Kattegat	1	6.8	10,15,*
47	Herring in areas 25–29 and the Gulf of Riga	1	30.4	10,15,*
48	Herring in coastal areas 25–27	1	39.5	10,15,*
49	Herring in the Gulf of Riga	1	27.1	10,15,*
50	Herring in area 30E	1	63.5	10,15,*
51	Herring in area 31E	1	65.4	10,15,*
52	Herring in the Gulf of Finland	1	17.5	10,15,*
53	Sprat in areas 26& 28	3	45.8	10,15,*
54	Sprat in areas 22–32	3	35.7	10,15,*
55	Mackerel, western stock	15	42.8	11,15
56	Greenland halibut in areas V & XIV	25	8.5	12,15,*
57	Icelandic saithe	12	24.9	12,15
58	Faroe saithe	12	21.4	12,15,*
59	Cod in the Faroe Plateau	5	17.2	12,15,*
60	Faroe haddock	6	31.5	12,15,*
61	Hake, northern stock	9	51.5	13,15,*
62	Hake, southern stock	9	34.1	13,15,*
63	Megrim in areas VII & VIII	19	55.1	13,15,*

Table 2. Cont'd.

Case No.	Stock	Species No.	Replacement %SPR	Sources of information
64	Sardine in areas VIIIc & IXa	2	55.4	14,15
65	Horse mackerel, western stock	14	–	14,15,*
66	Horse mackerel, southern stock	14	22.3	14,15,*
B. Northwest Atlantic stocks (Canada)				
67	Pollock in NAFO areas 4VWX & 5Zc	12	23.7	16,17,18,*
68	Haddock in NAFO area 4X	6	26.0	19,*
69	Haddock in NAFO areas 5Zjm	6	–	18,20,*
70	Cod in NAFO areas 5Zjm	5	–	21,*
71	Herring in NAFO area 4T	1	9.5	22,23,24,25,*
C. Northwest Atlantic stocks (USA)				
72	Georges Bank cod	5	11.9	26,27
73	Gulf of Maine cod	5	8.4	28,29,*
74	Georges Bank haddock	6	20.6	30,31,32,33
75	Silver hake, northern stock	8	30.8	26,34,*
76	Silver hake, southern stock	8	42.4	26,34,*
77	Georges Bank yellowtail flounder	23	14.2	18,28,35,*
78	Southern New England yellowtail flounder	23	10.3	18,28,35,*
79	Summer flounder	20	3.7	26,36,*
80	NW Atlantic Redfish	17	–	30,37
81	Gulf of Maine herring	1	14.9	26,38,39,*
82	NW Atlantic mackerel	15	40.7	18,28,40,*
83	Georges Bank scallops	27	2.0	28,41,42,43,44,*
84	Mid-Atlantic scallops	27	2.9	28,41,42,43,44,*
D. Atlantic stocks (Highly migratory)				
85	North Atlantic swordfish	16	8.6	42,45,*
86	NW Atlantic swordfish	16	10.1	42,45,*
E. Pacific coast stocks (USA)				
87	Pacific whiting	10	–	46,47,48,*
88	East Bering Sea Pacific cod	4	–	49,50,51,*
89	Bering Sea walleye pollock	13	43.8	52,53,54,*
90	Pacific halibut	21	24.6	52,55,56,*
91	Bering Sea yellowfin sole	22	20.4	52,54,57,*

* S-R plots and/or YPR and SPR analyses derived by present author from VPA-type output or reanalysis of published data.

1–15 ICES (1990a)–ICES (1990o)
16 Annand et al. (1990)
17 C. Annand, Bedford Institute of Oceanography, Halifax, NS, pers. comm.
18 O'Brien et al. MS
19 O'Boyle et al. (1989)
20 S. Gavaris, St. Andrews Biological Station, St. Andrews, NB, pers. comm.
21 J.J. Hunt, St. Andrews Biological Station, St. Andrews, NB, pers. comm.
22 M. Chadwick, Department of Fisheries and Oceans, Moncton, NB, pers. comm.
23 Claytor et al. (1991)
24 R. Claytor, Department of Fisheries and Oceans, Moncton, NB. pers. comm.
25 Messieh (1976)
26 NMFS (1990)
27 Serchuk (1990)
28 NMFS (1991)
29 Serchuk et al. (1991)
30 Gabriel (1985)
31 Gabriel et al. (1989)
32 NMFS (1986)
33 Overholtz et al. (1986)
34 NEFMC (1990)
35 Conser et al. (1991)
36 Gabriel (1990)
37 Mayo et al. (1983)
38 NMFS (1989)
39 Stevenson and Lazzari (1990)
40 Overholtz (1991)
41 Conser (1991)
42 R. Conser, Northeast Fisheries Science Center, Woods Hole, MA, pers. comm.
43 Serchuk and Wigley (1991)
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46 M. Dorn, Alaska Fisheries Science Center, Seattle, WA, pers. comm.
47 Dorn et al. (1990)
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49 T. Sample, Alaska Fisheries Science Center, Seattle, WA, pers. comm.
50 Thompson (1990)
51 G.G. Thompson, Alaska Fisheries Science Center, Seattle, WA, pers. comm.
52 Megrey and Wespestad (1990)
53 Wespestad et al. (1990)
54 V.G. Wespestad, Alaska Fisheries Science Center, Seattle, WA, pers. comm.
55 W. Clark, International Pacific Halibut Commission, Seattle, WA, pers. comm.
56 A.M. Parma, International Pacific Halibut Commission, Seattle, WA, pers. comm.
57 Bakkala and Wilderbuer (1990)

Finally, relationships between the reference points of recruitment overfishing and the more widely used reference points from YPR analysis ($F_{0.1}$ and F_{max}) were examined by comparing their relative magnitudes.

Results

To date, 91 stocks distributed amongst 27 species have been included in the survey (see Tables 1 and 2). Of the 91 stocks, there were 66 from the Northeast Atlantic and associated areas (ICES stocks); five from the Canadian coast and 13 from the U.S. coast of the Northwest Atlantic; two highly-migratory swordfish stocks from the North Atlantic; and 5 stocks from the U.S. coast of the Northeast Pacific (Table 2). It was difficult to develop objective criteria, *a priori*, to determine whether particular data sets were likely to produce estimates of F_{rep} that would be "unacceptably-biased" estimates of recruitment overfishing thresholds (the latter being equated with F_{τ}, the threshold fishing mortality rate associated with extinction of the stock). Cases were excluded only if it seemed likely that F_{rep} would be an extremely conservative estimate of F_{τ}. In particular, F_{rep} values less than zero imply that the population is unable to replace itself even in the complete absence of fishing (suggesting that it is either near or beyond "virgin" levels, or has otherwise attained a size greater than that which can be

Table 3. Estimates of replacement %SPR by (A) all cases, (B) whether or not the index of concavity was statistically significant, and (C) taxonomic group. Calculated statistics were derived from arcsine-transformed percentages and then back transformed.

Cases considered	N	Mean	Median	Mean ± 2(s.e.)	Range
A.					
All cases	83	18.7	17.2	15.5–22.0	2.0–65.4
B.					
concavity sign.	36	19.3	18.9	15.4–23.5	2.9–51.5
concavity non-sign.	46	17.5	13.2	13.1–22.4	2.0–65.4
C.					
Atlantic cod	14	6.8	6.3	4.9–9.0	2.5–17.2
other gadoids	23	25.7	24.6	20.2–31.5	6.9–51.5
Atlantic herring+	9	17.4	16.8	13.5–21.6	9.5–27.9
other clupeids	10	37.5	37.6	25.0–51.0	6.8–65.4
flatfish	19	14.5	11.5	10.0–19.6	3.7–55.1
Perciformes	6	22.4	20.2	11.6–35.5	8.6–42.8

+ excludes Baltic stocks of Atlantic herring, which are grouped in the other clupeids category.

Table 4. Bivariate correlations between variables considered in regressions. rep%SPR is the replacement %SPR; WT_{max} is the average body weight of the oldest age group considered in YPR and SPR calculations; $WT_{50\%mat}$ is the average body weight at 50% maturity; SSB_{max} is the maximum observed SSB over the range of observations used to construct the S-R plot; M is natural mortality; **concav** is the index of concavity in the S-R data. Probability levels: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

	log rep %SPR	log WT_{max}	log $WT_{50\%mat}$	log SSB_{max}	M	log (**concav**+1)
log (rep %SPR)	1					
log (WT_{max})	-0.47***	1				
log ($WT_{50\%mat}$)	-0.41***	0.96***	1			
log (SSB_{max})	0.46***	-0.19ns	-0.21ns	1		
M	0.27*	-0.03ns	-0.09ns	0.22ns	1	
log (**concav**+1)	0.25*	-0.02ns	0.04ns	0.09ns	0.07ns	1

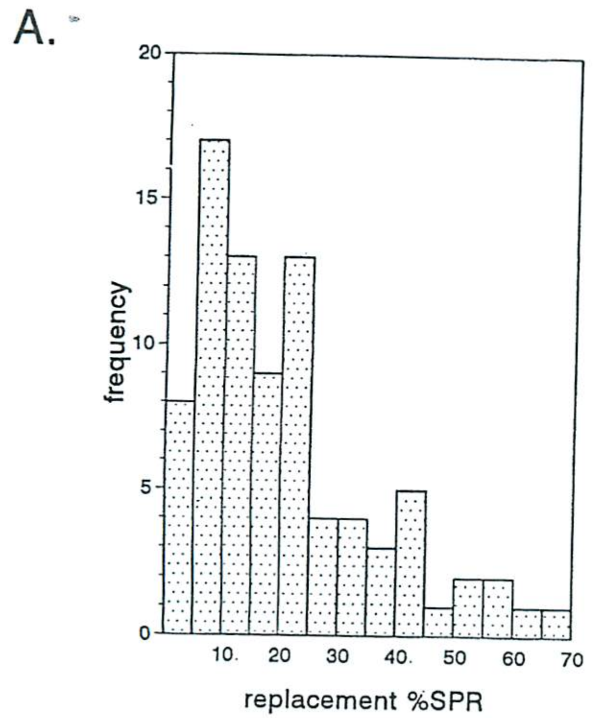
supported by current levels of recruitment), and are implausible as estimates of F_τ under "average" conditions. F_{rep} will also be an overly-conservative fishing threshold if most of the observations are made near virgin stock size for a strongly-compensatory S-R relationship, such that the slope of the line bisecting the observations considerably underestimates the slope at the origin; however such situations are difficult to identify since both virgin stock size and the underlying S-R relationship are generally unknown.

Eight of the 91 cases were excluded from analyses of recruitment overfishing thresholds because either: (i) $F_{rep} < 0$ (replacement %SPR > 100%) for either the first half, the last half, or all of the time series of S-R observations, (cases 9, 17, 65, 69, 80, 87 and 88 in Table 2), or (ii) the data were dominated by occasional years of exceptionally high recruitment that resulted in stock size moving systematically away from the origin for several successive years (cases 65, 70 and 87). The latter category, although somewhat more arbitrary, excluded only one additional stock (case 70).

For the remaining 83 cases, the replacement %SPR ranged from 2.0 to 65.4%, with a mean of 18.7% (Table 3). The untransformed distribution was highly skewed (Fig. 2). As expected, the mean replacement %SPR was higher for cases with a significant index of concavity (36 cases) compared to those with a non-significant index (46 cases, for a total of 82 cases where the index could be computed); but the differences were not significant (t-test, arcsine-transformed data, $p > 0.05$). Differences between the medians were more pronounced, but also not significant (median test and Kolmogorov-Smirnov two-sample test, $p > 0.05$).

In contrast, there were clear and statistically significant differences among species groups (Table 3). In earlier analysis species were grouped solely on the basis of the taxonomic category of Order, but preliminary cluster analysis suggested pronounced differences between Atlantic cod and the rest of the gadoids, and Atlantic herring outside of the Baltic compared to other clupeids. Atlantic cod had the smallest mean replacement %SPR, suggesting that it has relatively the greatest resilience to fishing. Flatfish and Atlantic herring outside of the Baltic appear to have higher than average resilience, and many of the other gadoids and small pelagics apparently have relatively low resilience to fishing. The following paired comparisons between means were significantly different (t-tests, arcsine-transformed data, $p < 0.05$): Atlantic cod and each of the other species-groups, flatfish with other gadoids and other clupeids, and Atlantic herring and other clupeids.

Stepwise multiple linear regression (MLR) was conducted using both untransformed and log-transformed variables. Log transformations generally seemed to improve the correlations



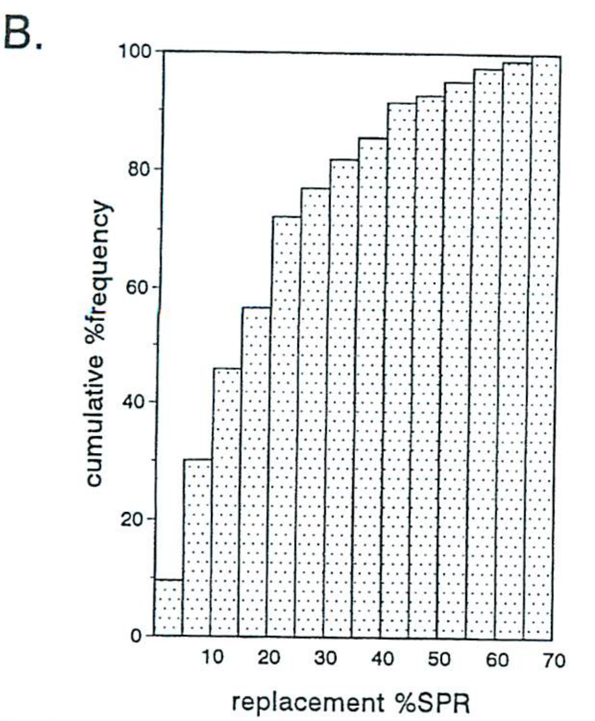


Fig. 2. Frequency histogram (A) and cumulative frequency histogram (B) of replacement %SPR ($N = 83$).

between variables. Bivariate correlations between the logarithm of replacement %SPR and life history parameters exhibiting significant correlations ranged from −0.47 to 0.46 (Table 4). Replacement %SPR was also significantly correlated with the index of concavity. The only significant correlation among the independent variables themselves was the two body weight variables. Three cases had missing values for either maximum SSB or the index of concavity.

The first regression considered all of the variables in Table 4, along with the categorical variable, species name. The second omitted maximum SSB and the index of concavity, since these are the two variables that are the least likely to be known for most stocks. Results were verified by considering all possible subsets in standard MLR analysis. Both regressions were highly significant ($p < 0.001$) and in each case the proportion of variation explained exceeded 60% (Table 5). In both examples, maximum average body weight was the most important covariate (first to be entered by the forward selection process). Maximum SSB, species name and the index of concavity also contributed significantly to the first regression. The second regression included only species and maximum body weight. Omission of maximum SSB and the index of concavity from the list of variables considered did not substantially alter the significance of the regression or the proportion of variation explained, primarily because the increased sample size happened to result in the addition of two species. One of these (NW Atlantic sea scallops, the only invertebrate species in the survey, see Table 1) was such a clear outlier in bivariate regressions of replacement %SPR on body weight (Fig. 3) that it was probably largely responsible for species name becoming the first variable to be entered by the forward selection procedure. Subsequent regressions only considered the 80 cases with complete information for all life history parameters. (Note that this reduction in sample size, together with the cases excluded due to a probable bias in the estimate of replacement %SPR (Table 1), reduces the number of species included in the regression analyses from 27 to 22.)

The problem with regressions that include species as a categorical variable is that they cannot be used for predictive purposes unless the species of interest is one of those already incorporated in the regression. However, omission of species from the list of potential independent variables resulted in a substantial reduction in the proportion of variation explained, particularly when maximum SSB was also excluded (Table 6). An alternative was to conduct analyses separately by taxonomic group. Four Orders were considered: Gadiformes (gadoids only), Clupeiformes (clupeids only), Pleuronectiformes (flatfish) and Perciformes. For each group, maximum body weight was the first variable entered into the regression and, for all groups excepting the gadoids, it was the only variable (Table 6). Relationships between replacement %SPR and maximum body weight are shown separately by taxonomic group in Fig. 4. For flatfish, the regression was nonsignificant when the three stocks of halibut were included. The regression for Perciformes should also be treated with caution since it was based on only six observations.

Values of %SPR corresponding to the $F_{0.1}$ and F_{max} reference points from YPR analysis were remarkably consistent (Fig. 5 and Table 7). Interquartile ranges (25th to 75th percentiles) were respectively 35.0–40.2% and 17.3–24.5% (compared to 8.6–27.1% for the replacement %SPR); ranges encompassing 90% of the estimates were respectively 31–46% and 12–29%. Some of the differences between species and species-groups (Table 7) were statistically significant, but the magnitude of the differences was never large. The mean

Table 5. Stepwise regression results for log replacement %SPR. (A) Independent variables considered for selection were species, $\log(WT_{max})$, $\log(WT_{50\%mat})$, $\log(SSB_{max})$, M and $\log(\mathbf{concav}+1)$. (B) As for A, but excluding $\log(SSB_{max})$ and $\log(\mathbf{concav}+1)$. See Table 4 for descriptions of the variables.

		A	B
N		80	83
Variables selected	1.	$\log(WT_{max})$	species
	2.	$\log(SSB_{max})$	$\log(WT_{max})$
	3.	species	M^+
	4.	$\log(\mathbf{concav}+1)$	$\log(WT_{50\%mat})^+$
	5.	M^+	
	6.	$\log(WT_{50\%mat})^+$	
Adjusted R^2		61.4%	64.3%
probability level		< 0.001	< 0.001

$^+$ subsequently removed (i.e., excluded from final regression results).

replacement %SPR of 18.7% is only slightly lower than the mean %SPR at F_{max} but considerably lower than the mean %SPR at $F_{0.1}$ (Table 7). On average, the corresponding values of F_{rep} exceeded F_{max} by a factor of 1.4, and $F_{0.1}$ by a factor of 2.4 (Table 8). Overall, F_{rep} was more than four times $F_{0.1}$ 25.0% of the time; and more than four times F_{max} 7.1% of the time (Fig. 6). Atlantic cod stood out from the other species groups in terms of the relative magnitude of F_{rep} in relation to both $F_{0.1}$ and F_{max} (Table 8).

However, there are also numerous instances where F_{rep} fell below one or both of the reference points from YPR analysis (Fig. 6 and Table 8). F_{rep} was less than $F_{0.1}$ in 12.5% of the cases where they were both known; and less than F_{max} in 37.1% of the cases where both were defined. Cases where $F_{0.1}$ exceeded F_{rep} included zero Atlantic cod stocks, 3 of a total of 22 other gadoid stocks (13.6%), 4 of 17 clupeid stocks (23.5%), 1 of 19 flatfish stocks (5.3%), and 2 of 6 Perciformes stocks (33.3%). Cases where F_{max} exceeded F_{rep} included zero Atlantic cod stocks, 13 of 20 other gadoid stocks (65%), 5 of 5 clupeid stocks (100%), 5 of 18 flatfish stocks (27.8%), and 3 of 5 Perciformes stocks (60%). Thus, if F_{rep} is an appropriate measure of the recruitment overfishing threshold, adoption of either $F_{0.1}$ or F_{max} as management targets will not necessarily guard against recruitment overfishing.

The stocks considered in this study have been fished at a wide range of fishing mortality rates relative to F_{rep}. Fishing mortality rates averaged over the most recent 10 years of observations ranged from 0.19 to 2.50 F_{rep}, with 77.1% of the stocks falling between 0.5 and 1.5 F_{rep}, and 38.6% in the range 0.8–1.2 F_{rep}. The median result was 1.17 F_{rep}, which should have resulted in an overall trend of declining spawning stock biomass.

Discussion and Conclusions

Replacement biological reference points show great promise as a basis for overfishing definitions for fishery management. They are already widely used in the U.S. They can be easily and objectively calculated from common stock assessment information, such as VPA-type outputs and results from dynamic pool models. Four additional attributes, that are new results from this study, are:

1. Replacement %SPR levels are strongly influenced by taxonomic affiliation and life history parameters.

2. While the replacement biological reference points may sometimes be conservative estimates of recruitment overfishing thresholds (because they do not take account of compensation), for the cases analysed here the degree of apparent compensation in the data had relatively little effect of the magnitude of estimates of replacement %SPR.

3. The combined effect of (1) and (2) is that the replacement %SPR relationships derived in this paper can be used to provide guidance for selecting preliminary or default estimates for recruitment overfishing thresholds when the required stock assessment results are not available.

4. For the cases considered here, F_{rep} was usually higher than the common management targets of $F_{0.1}$ and F_{max}; but this was not always so. Thus, if F_{rep} is a valid recruitment overfishing threshold, $F_{0.1}$ and F_{max} management strategies may not always guard against recruitment overfishing.

Influence of Taxonomic Affiliation and Llife History Parameters on Replacement %SPR

Although this study represents only a preliminary analysis of replacement reference points (primarily replacement %SPR and F_{rep}) and associated data, the results are promising and some general conclusions have emerged. First, there appear to be consistent differences in levels of replacement %SPR between some taxonomic groups (Table 3). Flatfish and large gadoids such as Atlantic cod have relatively low values of replacement %SPR (suggesting relatively high resilience to fishing), while the smaller gadoids and many of the small pelagics have relatively high values of replacement %SPR (low resilience). These between-species and species

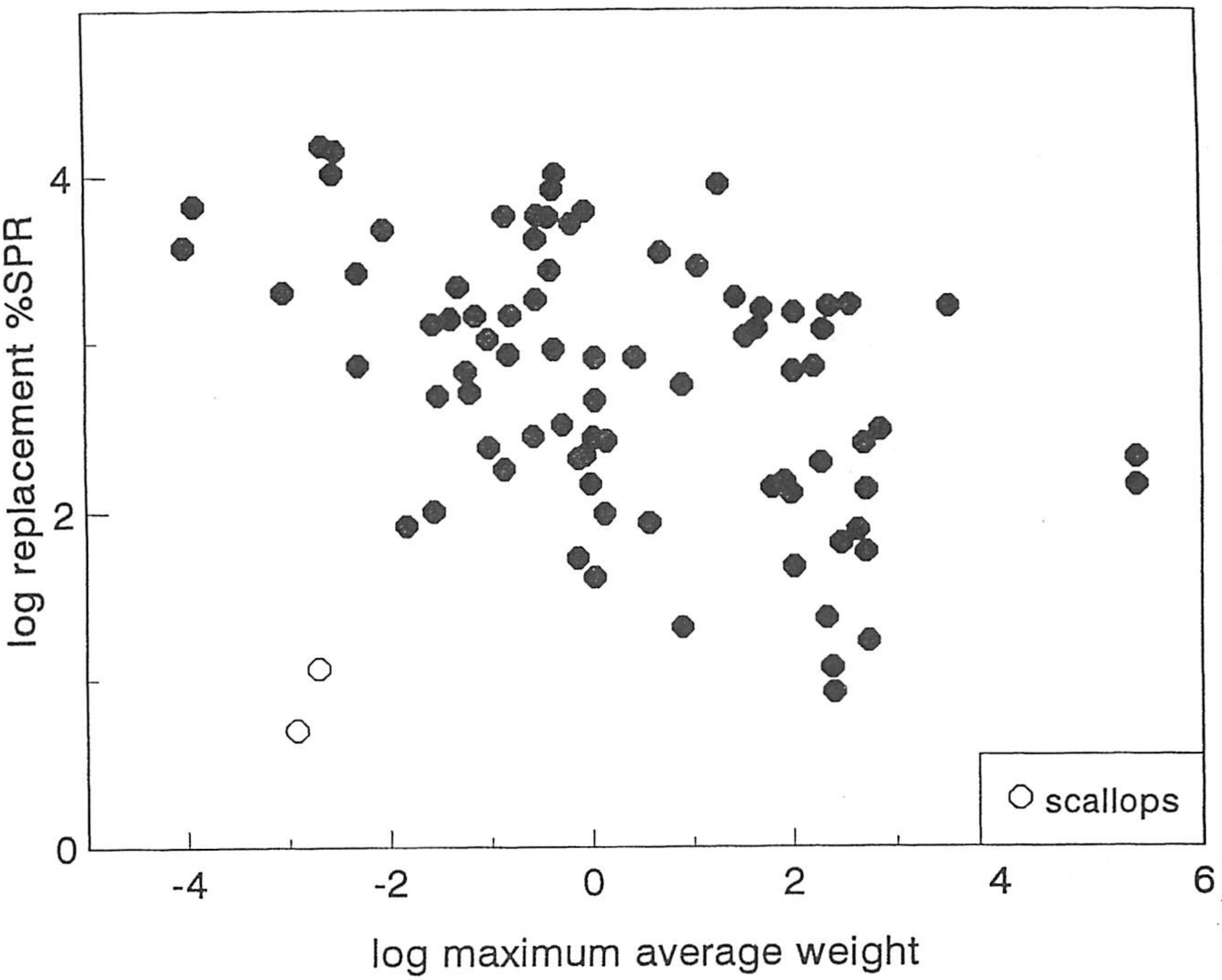


Fig. 3. Relationship between replacement %SPR and observed maximum average body weight ($N = 83$).

group differences appear to be more important than any potential biasing effect of concavity in the S-R observations (Table 5, case A).

Second, a substantial proportion of the variation in replacement %SPR can be explained by certain life history parameters. The most important parameters identified to date are the maximum body weight or the body weight at 50% maturity (Figs. 2 and 3 and Tables 4–6). In particular, gadoids and pelagics that reach relatively small maximum size and/or mature at a small size seem to have high replacement %SPR. Pope (1990; ICES 1990p) has also found a relationship between %SPR and average body weight at 50% maturity. It is worth examining the possible causes of these and other correlations in Table 4.

First, it is unlikely that the correlation with body weight can be extended across all taxa involved in commercial fisheries. For example, elasmobranchs have large body size but generally do not exhibit high resilience to fishing and would probably have moderate or high threshold values of replacement %SPR. Body size is probably a proxy for fecundity, which may be more strongly tied to resilience and therefore to replacement %SPR. Other authors have already suggested that high fecundity may be associated with high resilience (e.g., Cushing and Harris 1973). Certainly the life history parameters considered here do not capture all between-species differences. Omission of species from the overall regression resulted in a decrease in the proportion of variation explained from 61.4% to 42.6% (Tables 5 and 6).

There is also an indication that stocks with high biomass may have relatively low resilience to fishing, particularly for the gadoids (Tables 4–6). However, this result seems somewhat counter-intuitive and may be spurious. The maximum observed SSB depends both on the maximum possible stock size (virgin biomass) and the level of exploitation applied during the period of the observations. For a given stock under stable conditions, replacement %SPR will be positively correlated with stock size. Stocks that are closer to virgin levels might also be expected to exhibit greater concavity in the S-R observations. However, there was no significant correlation between the maximum observed SSB and the index of concavity (Table 4), perhaps partially due to the fact that SSB was expressed in absolute terms and here are probably wide disparities in the maximum observed levels relative to virgin levels.

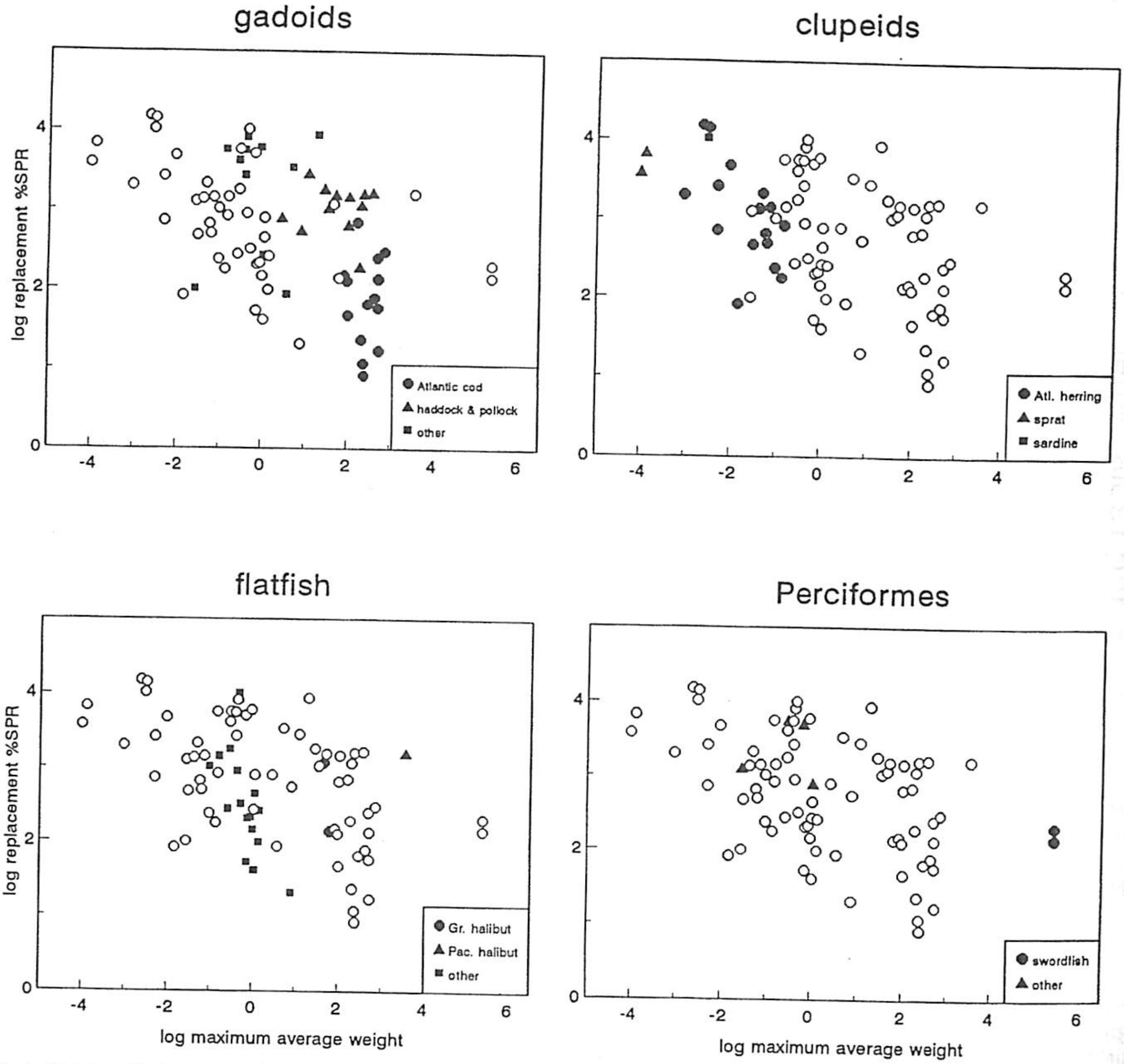


Fig. 4. Relationship between replacement %SPR and observed maximum average body weight by taxonomic group: gadoids ($N = 37$), clupeids ($N = 19$), flatfish ($N = 19$), and Perciformes ($N = 6$).

Replacement Biological Reference Points as Estimates of Recruitment Overfishing Thresholds

The validity of using the replacement reference points as reference points for recruitment overfishing thresholds depends on the validity of the assumption that F_{rep} is an estimate of F_τ, the threshold fishing mortality rate associated with extinction (or, equivalently, that the replacement survival ratio is an estimate of the slope at the origin of the full S-R relationship). There are two major types of situations where F_{rep} might overestimate F_τ: the case of a depensatory S-R relationship, and the situation where environmental conditions or other factors have led to unusually high survival rates through much of the period used to estimate the replacement reference points. Similarly, the main factors causing F_{rep} to underestimate F_τ are a compensatory S-R relationship where most of the S-R observations come from stock sizes above the point where the S-R relationship can be approximated by a straight line through the origin, and an unusually high proportion of years with poor survival rates. Biases may also result from estimation errors and the use of life history information from a fished-down stock to calculate the maximum (unfished) SPR ($SPR_{F=0}$). For example, if the SPR analysis is based on a plus group weight at age derived from a fished-down stock, $SPR_{F=0}$ will be underestimated and replacement %SPR will therefore be overestimated. Similarly, density-dependent effects that result in earlier maturity and faster growth at lower density will lead to overestimates of $SPR_{F=0}$ and underestimates of replacement %SPR. However, F_{rep} (as estimated by F_{med}) may be relatively robust to a number of other sources of error in inputs and assumptions (e.g. M) because their effects on S-R data and SPR analysis tend to cancel (Jakobsen 1993).

Table 6. Stepwise regression results for log replacement %SPR when the categorical variable, species, is omitted. All cases (2) is identical to all cases (1) except that SSB_{max} was removed from the model. Other numbers in brackets refer to the order of selection of the regression variables. Probability levels: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. See Table 4 for descriptions of the variables.

	N	intercept	log WT^{1}_{max}	log SSB^{2}_{max}	log $WT^{1}_{50\%mat}$	log concav+1	M	adj. R^2	p
All cases (1)	80	2.18	-0.52(1)	0.15(2)	0.41(3)		2.71(4)	42.6%	***
All cases (2)	80	2.69	-0.51(1)		0.38(2)		3.52(3)	31.5%	***
gadoids	37	2.42	-0.63(1)	0.21(2)	0.38(4)	0.87(3)		55.5%	***
clupeids	19	2.35	-0.42(1)					35.3%	**
flatfish[3]	15	2.21	-1.00(1)					60.7%	***
Perciformes	6	3.25	-0.18(1)					63.7%	*

[1] units=kg
[2] units=thousands of metric tons
[3] excludes halibut

Table 7. Estimates of %SPR at (A) $F_{0.1}$ and (B) F_{max}, by taxonomic group. Calculated statistics were derived from arcsine-transformed percentages and then back transformed.

Taxonomic group	N	Mean	Median	Mean ± 2(s.e.)	Range
A. %SPR at $F_{0.1}$					
All cases	88	37.8	37.8	36.6–39.0	23.3–65.1
Atlantic cod	15	39.4	40.0	37.7–41.0	31.7–43.8
other gadoids	26	40.1	38.5	37.3–42.9	29.4–65.1
Atlantic herring⁺	10	34.6	34.4	30.8–38.5	23.3–45.9
other clupeids	8	34.1	35.8	30.9–37.4	26.5–40.0
flatfish	19	37.1	36.9	35.5–38.7	29.8–44.9
Perciformes	8	36.0	37.2	32.3–39.7	28.6–44.2
B. %SPR at F_{max}					
All cases	68	21.1	20.8	19.6–22.8	10.6–55.3
Atlantic cod	15	24.1	23.7	22.1–26.1	17.8–31.9
other gadoids	22	23.1	21.9	19.5–26.9	10.6–55.3
Atlantic herring⁺	3	18.5	20.5	11.2–27.2	11.1–24.0
other clupeids	2	17.0	17.0	–	13.5–20.8
flatfish	18	18.7	18.2	16.8–20.7	12.5–29.5
Perciformes	6	16.6	15.8	11.8–22.1	10.8–27.9

⁺ excludes Baltic stocks of Atlantic herring, which are grouped in the other clupeids category.

In general, one would expect there to be more cases where F_{rep} is a conservatively-biased estimate of F_{τ} (i.e., it underestimates F_{τ}), due primarily to the fact that there is often evidence of concavity in the S-R observations. In fact, although the null hypothesis of linearity through the origin could not be rejected in most cases (56%), there was an even greater number of cases (82%) where the alternative null model of a (median) straight line with zero slope could not be rejected using a similar non-parametric test. This alternative null model has not been given serious consideration here because it is an inappropriate (risk-prone) null hypothesis for fisheries management. Rather than assuming that the maximum survival ratio is infinite, we have assumed that the replacement (median) survival ratio is a valid estimate of the maximum survival ratio under average (environmental) conditions. Since evidence of apparent compensation in the data did not lead to significantly higher estimates of replacement %SPR on average (Table 3), both sets of data can be considered to be more or less equally valid estimates of recruitment overfishing thresholds. It should be noted, however, that this conclusion cannot be generalised beyond the present analysis (and obviously does not hold for the data sets explicitly excluded from the analysis). Most of the fisheries considered here have had a long history of exploitation and are probably well beyond the fishing-down phase. But the null hypothesis of a straight line through the origin would generally be expected to be overly-conservative for developing fisheries where accumulated biomass is still being fished down.

Guidance for Selecting Estimates of Recruitment Overfishing Thresholds

The regressions derived in this paper (Tables 5 and 6) are all highly significant and generally explain a moderate to high proportion of the variation in the dependent variable (replacement %SPR). These results, together with the basic statistics for the species subgroups (Table 3) can be used to set preliminary recruitment overfishing thresholds, particu-

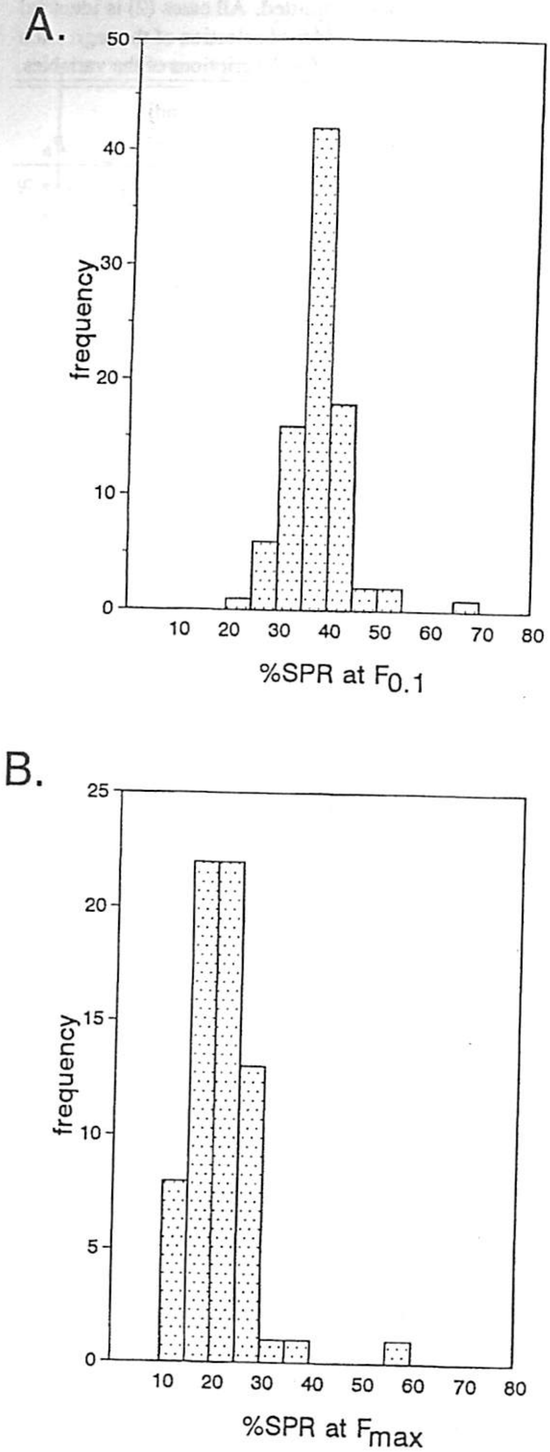


Fig. 5. Frequency histograms of %SPR at (A) $F_{0.1}$ ($N = 88$) and (B) F_{max} ($N = 68$).

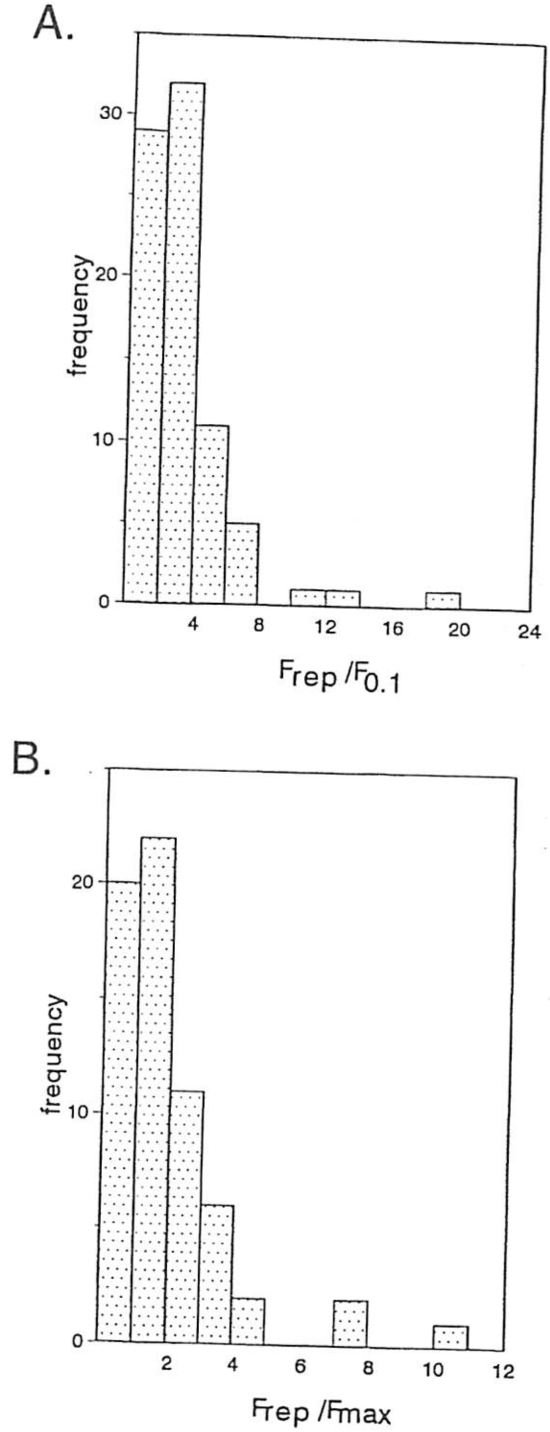


Fig. 6. Frequency histograms of the ratio of F_{rep} to (A) $F_{0.1}$ ($N = 80$) and (B) F_{max} ($N = 64$).

larly in situations where there are insufficient data to calculate the reference points explicitly. Due to the preliminary nature of the analysis, and other uncertainties, estimates based on this study need to be treated with caution.

If there is little or no basic life history information, then it will obviously be difficult to provide definitive guidelines for management. At best, it may be possible to use the results of this study to make some tentative, qualitative statements about whether the stock is likely to have low or high resilience to fishing depending on, for example, the maximum body size of individuals in the population and the taxonomic relationship, if any, to species included in this survey. Stocks of fish that do not attain a very large body size are apparently likely to have relatively low resilience. In particular, a cautious approach to management may be required for some of the smaller gadoids and pelagics. Also, stocks with large virgin biomass or high

Table 8. Estimates of the ratio of F_{rep} to (A) $F_{0.1}$ and (B) F_{max}, by taxonomic group. Calculated statistics were derived from log-transformed ratios and then back transformed. The reported mean is the geometric mean (i.e., uncorrected for bias).

Taxonomic group	N	Mean	Median	Mean ± 2s.e.	Range
A. $F_{rep}/F_{0.1}$					
All cases	80	2.4	2.3	2.0–2.8	0.3–19.1
Atlantic cod	14	4.6	4.9	3.7–5.8	2.4–11.4
other gadoids	22	1.8	1.9	1.4–2.3	0.7–7.3
Atlantic herring+	9	2.3	2.2	2.0–2.7	1.5–3.0
other clupeids	8	1.0	1.1	0.5–2.0	0.3–4.6
flatfish	19	2.9	2.9	2.2–3.8	0.7–7.6
Perciformes	6	1.6	2.0	1.1–2.3	0.8–2.4
B. F_{rep}/F_{max}					
All cases	64	1.4	1.3	1.2–1.7	0.2–10.5
cod	14	2.7	2.8	2.1–3.5	1.0–7.3
other gadoids	20	0.9	0.8	0.7–1.2	0.2–4.0
Atlantic herring+	3	1.2	1.3	1.0–1.4	1.0–1.3
other clupeids	2	1.4	1.4	–	0.8–2.5
flatfish	18	1.4	1.4	1.0–1.9	0.4–4.6
Perciformes	5	0.8	1.1	0.5–1.4	0.3–1.1

+ excludes Baltic stocks of Atlantic herring, which are grouped in the other clupeids category.

natural mortality may be relatively less resilient to fishing (may not be able to withstand large reductions in biomass).

In situations where there is sufficient information to construct YPR and SPR curves, but fewer than 10 or so S-R observations, the results of this study can be used more directly. For species that are dissimilar to any of those well-represented in this survey, it might be appropriate to use, say, the 80th percentile of the observations as a preliminary estimate of the threshold replacement %SPR, and to then find the corresponding estimate for F_{rep} on the SPR curve. Use of the 80th percentile of the cases in this study results in a default estimate for the threshold replacement %SPR of 30.8% (Fig. 2), which we will round down to 30%. It is interesting to note that Clark (1991) suggested a %SPR value of 35% to achieve at least 75% of the MSY yield when the S-R relationship is unknown; i.e., this study suggests 30% as a default 'threshold', whereas Clark recommended 35% as a management 'target'. The two levels are too similar to be used concurrently as indicators of danger zones and safe zones, respectively, within the same management plan. It is likely that Clark's suggested target will be too low (optimistic) for some stocks because it was based on theoretical models that did not take account of recruitment variability and other sources of uncertainty, and may not have covered the full range of possible degrees of compensation. On the other hand, the 80th percentile of the observations included in this survey will be an overly-conservative threshold for most stocks.

An alternative to the 80th percentile result is to use the overall average replacement %SPR of about 20% (Table 4) as the default (which is, coincidentally, the default that has been used by the New England Fishery Management Council to define overfishing thresholds for groundfish stocks, and the default suggested by Goodyear 1989, 1993 based on limited empirical information). However, we suggest that 20% should generally be considered too low for use as a default threshold since it is risky to assume that a stock is "average" when nothing is known about the spawning-recruitment relationship. Another alternative is to obtain a preliminary estimate of the threshold replacement %SPR from one of the overall regressions on life history parameters (Table 6).

Obviously, the results from this survey are most applicable to the situation where the species is closely related to one or more of those well-represented in the survey. In this case, the mean and confidence interval for that species or species-group (Table 3) or one of the regressions based on the taxonomic group of Order (Table 6) could be used directly. Alternatively, if there is sufficient information (SPR analysis and preferably 10 or more S-R observations) to calculate the replacement biological reference points explicitly, the results from this study can be used as a check on the empirical estimates.

Relative magnitudes of F_{rep}, $F_{0.1}$ and F_{max}

The U.S. 50 CFR Section 602 Guidelines (see Background) imply that growth overfishing occurs at a lower fishing mortality rate than recruitment overfishing. If F_{max} and F_{rep} are used as the biological reference points of growth and recruitment overfishing, respectively, then the present study indicates that this generalisation is true only 63% of the time. On average, F_{rep} was 1.4 times F_{max} (Table 8); however, the average %SPR associated with F_{max} was only slightly higher than the average %SPR associated with F_{rep} (Table 7).

Another widely-held belief is that $F_{0.1}$ is a conservative reference point for defining recruitment overfishing. Assuming that F_{rep} is the true recruitment overfishing threshold, the present study indicates that while this belief is generally valid ($F_{0.1}$ was only about 40% F_{rep} on average, Table 8), there was an appreciable number of cases included in the survey (12.5%) where F_{rep} was less than $F_{0.1}$. This suggests that a management target of $F_{0.1}$ may not always prevent recruitment overfishing. The average %SPR associated with $F_{0.1}$

was 37.8% (Table 7), about 8% higher than the default threshold (30%) suggested above.

Concluding Remarks

There is no single, simple answer to the question of how much spawning per recruit is enough. The results of this study do however provide some guidance, particularly for species similar to those included in the survey and when certain life history parameters are known. Based on the overall cumulative distribution of replacement %SPR (Fig. 2), a conservative strategy would be to maintain at least 30% SPR as a default value when there is no other basis for estimating the replacement level. A 30% level of SPR was enough for 80% of the fish stocks considered; however, it may be overly-conservative for an "average" stock.

It is important to remember that the replacement biological reference points calculated in this study are intended to serve as management thresholds, not targets. In general, it should be expected that threshold fishing mortality rates such as F_{rep} will be higher than targets such as $F_{0.1}$ and F_{max}. The fact that this was not always so in the present study indicates that it is essential to consider recruitment overfishing reference points explicitly. In cases where F_{rep} exceeds F_{max}, it does not make sense to apply a fishing mortality rate of F_{rep} since it will produce less yield. On the other hand, if F_{rep} is near or below F_{max} (or $F_{0.1}$), it may be prudent to sacrifice some yield and fish conservatively. For populations that are depleted, the fishing mortality rate should be less than F_{rep} to promote rebuilding.

Acknowledgements

Numerous groups and individuals provided the stock assessment information and related analyses required to estimate the replacement reference points. In particular, we wish to mention the ICES Stock Assessment Working Groups (ICES 1990a–o) and to give special thanks to the scientists acknowledged as personal communications in Table 2. Mike Fogarty and Jake Rice reviewed an earlier draft and provided helpful suggestions for revision. The first author is also grateful to the New Zealand Ministry of Agriculture and Fisheries for providing funding for the initial phases of the study, and to the National Research Council-NMFS Research Associateship program which enabled the work to be completed.

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