

In search of thresholds for recruitment overfishing

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In this study we consider the problem of estimating, for management purposes, a minimum biomass reference level at which recruitment to a fish stock is seriously reduced. We take an empirical, comparative approach to the problem by examining observations on a wide range of fish stocks. Eight methods for estimating spawning stock biomass thresholds for recruitment overfishing are investigated. Their behaviour is tested using stock and recruitment data for 72 finfish populations, each with at least 20 years of data. We considered three classes of thresholds defined by: (1) the stock size corresponding to 50% of the maximum predicted average recruitment; (2) the minimum stock size that would produce a good year class when environmental conditions are favourable; and (3) the stock size corresponding to 20% of various estimates of virgin stock size. The estimators of the first type are generally preferable because they are easily understood, relatively robust if only data at low stock sizes are available, and almost always result in higher levels of recruitment above the threshold.

Key words: spawning stock biomass, Ricker curve, Beverton-Holt curve, Shepherd curve.

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Introduction

One of the major goals of most fishery management strategies is conservation of the resource base. In effect this means that the productivity of the population in terms of recruitment must be maintained, i.e. recruitment overfishing must be prevented. This goal is directly stated in the US guidelines for fishery management plans known as the 50 CFR Part 602 Guidelines (issued July 1989) for the Magnuson Fishery Conservation and Management Act of 1976. Prevention of recruitment overfishing is also the basis for development of management strategies that use reference fishing mortality or biomass levels such as the $F_{0.1}$ target adopted in Atlantic Canada (Rivard and Maguire, 1993), the "minimum biologically acceptable level" of biomass (MBAL) determined for stocks assessed by the International Council for the Exploration of the Sea (Serchuk and Granger, 1992), and the definition of "protected" stocks as those in which the abundance is 0.54 of the unexploited level used by the International Whaling Commission (Young,

1993). In many cases, a minimum biomass level is used in conjunction with other management measures that control exploitation above the threshold.

While thresholds based on fishing mortality rates are intended to prevent recruitment overfishing by controlling the rate of harvest, ultimately it is the spawning stock that must be maintained to ensure the future productivity of the resource. In order to frame the problem we need to define what is meant by poor recruitment. Though such a definition is essentially arbitrary, a good rule of thumb has been suggested by Mace (1994) as the point on a theoretical underlying stock and recruitment curve where recruitment is one half of the maximum of the curve. The corresponding spawning biomass threshold is the biomass which would produce one half of the maximum recruitment according to a theoretical relationship between stock and recruitment.

The relationship between spawning biomass and recruitment is notoriously variable and the underlying theoretical relationship is never known in practice. Thus,

the basic definition of poor recruitment and the implied spawning stock threshold can only serve as a guide. It is no simple task to estimate from empirical data a threshold below which recruitment is most likely to be poor. This is the problem addressed here: from the available data on a fish stock, can a spawning stock biomass threshold be estimated that will guide managers in protecting against recruitment overfishing? To evaluate whether a given method is appropriate and robust to the population dynamics of the stock and the range of observations available we compared results for many stocks with wide ranges of characteristics.

We have examined methods which can be applied to the types of observations commonly available on exploited fish stock and we sought to determine how well they performed given the real data available, since this is how any such method will need to be evaluated in practice. To do this we utilized the extensive database on stock and recruitment assembled by Myers *et al.* (in press). Three types of threshold estimation methods were considered: (1) methods that define the threshold as the spawning stock biomass (SSB) at which recruitment is reduced to one half of the maximum of that predicted by a parametric stock–recruitment model (Mace, 1994); (2) methods based on the non-parametric approach described by Serebryakov (1991); and (3) methods that define the threshold as a fraction of the virgin spawning biomass. The virgin biomass was estimated using the spawning biomass per recruit (SPR) estimates compiled by Mace and Sissenwine (1993) and Mace (unpublished updates).

To evaluate the appropriateness of an estimated threshold relative to the underlying concept of protecting against poor recruitment, we considered simple measures of performance. To justify the use of any particular threshold to fishery managers, a strong case must be made that there will be a negative impact on recruitment if the spawning stock falls below that level. To measure this we compare average recruitment above and below the threshold estimate. A reasonable threshold is at a stock size at which recruitment has been observed to decline. In many cases recruitment may never have obviously declined at the lowest levels of spawning stock observed. A reasonable threshold is then near or below the lower biomass levels observed. A threshold set at higher biomass is obviously more conservative than at a lower biomass. But, unless a full picture of the stock and recruitment relationship is available, we can only judge a threshold estimate as being conservative or risky by the slope of the observations of stock and recruitment in the vicinity of the estimate, i.e. whether recruitment is expected to increase, decrease, or remain the same at higher stock abundance. By comparing such measures across stocks we attempt to build a picture of the likely performance of each of our methods and suggest a procedure for evaluating a

threshold estimate on a particular stock. As we show below, no single method is best for every stock and for any given analysis in practice we recommend as many diagnostic measures be examined as possible.

Data sources

We selected stock–recruitment (S–R) data sets from the database compiled by Myers *et al.* (in press) containing at least 20 years of spawning stock and recruitment data where the maximum observed stock size was at least twice the minimum stock size to ensure some minimum amount of contrast in the data. Although we refer to spawning stock biomass (SSB) throughout this paper, for some of the data sets the spawning stock is not measured in units of biomass. For example, the Pacific salmon stocks are measured in numbers of spawners. For convenience, however, we simply refer to SSB. We used only data in which aging was not known to be problematic. In some species (e.g. tuna and swordfish), aging can only be undertaken via length-based methods; such stocks were not included in the analysis. In total, 72 stocks were extracted from the database, from a wide range of families (Table 1). A large number of herring (14) and cod (15) stocks were included.

Defining thresholds

We sought threshold definitions which are simple to calculate, have a basis in the literature, or in theory, and could be applied to the wide range of stocks included in our analysis. The threshold level should indicate a point at which recruitment is expected to be reduced if spawning biomass declines further. We investigated variations of three types of methods for a total of eight definitions (Table 2), discussed below.

Methods based on 50% of maximum predicted recruitment (50% R_{max})

Mace (1994) suggested that a threshold SSB level could be defined in terms of the biomass at which average recruitment is one half of the maximum of the underlying stock and recruitment (S–R) relationship. We considered three alternative S–R relationships: Beverton–Holt, Ricker, and Shepherd. The curves were fitted to the data using maximum-likelihood methods assuming lognormal errors (Myers *et al.*, in press). The threshold was defined to be the spawning biomass corresponding to the point on the curve where expected recruitment is one half of the maximum of the curve.

The Beverton and Holt relationship may be expressed as:

$$R_t = \frac{aS_{t-r}}{1+(S_{t-r}/K)}$$

where R_t is the recruitment in year t , S_{t-r} is the spawning biomass in year $t-r$, r is the age at recruitment, and α and K are parameters. For this relationship, the 50% R_{max} threshold is $BH50=K$. We have assumed that the replacement line intersects the S-R function to the right of K , otherwise the realized equilibrium SSB would be below K . This does not appear to occur for any of the data sets examined.

The Ricker relationship may be expressed as:

$$R_t = \alpha S_{t-r} e^{-\beta S_{t-r}}$$

where α and β are parameters. The maximum recruitment occurs when $S=1/\beta$ and is given by $R_{max}=\alpha/(\beta e)$. Let $RK50$ be the SSB level corresponding to half maximum recruitment. Therefore:

$$\frac{\alpha}{2\beta e} = \alpha RK50 e^{-\beta RK50}$$

thus:

$$2e(\beta RK50)e^{-(\beta RK50)} - 1 = 0.$$

The solution to this equation is approximately given by $\beta RK50 \approx 0.231961$. Thus:

$$RK50 \approx \frac{0.231961}{\beta}$$

The Shepherd relationship:

$$R_t = \frac{\alpha S_{t-r}}{1 + (S_{t-r}/K)^\gamma}$$

was first proposed by Maynard Smith and Slatkin (1973) and is discussed in Bellows (1981). Shepherd (1982) discusses the interpretation of parameters α , β , and γ . The parameter γ may be called the "degree of compensation" of the model, since it controls the degree to which the (density-independent) numerator is compensated for by the (density-dependent) denominator. Note that when $\gamma=1$ the Shepherd model reduces to the Beverton-Holt model. For use in defining threshold stock levels, three constraints were placed on the parameters of the Shepherd model. For a given data set, the initial slope α was constrained to be no greater than the maximum observed survival rate (R_t/S_{t-r}) to prevent unreasonable behaviour near the origin. The K parameter was constrained to be no greater than the maximum observed SSB. Finally, the compensation parameter γ was constrained to be at least 1 (to ensure a maximum) and no greater than 10 (this constraint was only applied to one stock to prevent any unreasonably sharp drop). For this constrained Shepherd model, the SSB where recruitment is one half of the maximum is called $SH50$. Although there is no closed-form analytical solution, a numerical root-finding algorithm may be used to compute $SH50$.

Methods based on survival and recruitment percentiles

The second class of rules for estimating threshold SSB levels was based on the ideas of Serebryakov (1991) and Shepherd (1991). These authors suggested using the SSB corresponding to the intersection of the 90th percentile of the observed survival rate (R_t/S_{t-r}) and the 90th percentile of the recruitment observations as an estimate of threshold stock size (called S_b here). The idea is to determine a low level of stock size which is none the less capable of producing a good year class when environmental conditions are favourable for survival.

Methods based on 20% virgin biomass (20% B_0)

A reference biomass of 20% virgin or unexploited biomass (20% B_0) is the most commonly adopted "overfishing threshold" in the fisheries literature (Beddington and Cooke, 1983; Getz and Haight, 1989). This formed the basis for the third class of methods. Three of the estimates of B_0 were determined from the intersection of the three fitted S-R relationships with the $F=0$ replacement line. The replacement line is a straight line through the origin. When SSB and recruitment are measured in the same units and the species is semelparous, the slope of the line is 1. Otherwise, the slope of the line is given by the inverse of the spawning biomass per recruit when the fishing mortality rate is zero, denoted here by $SPR_{F=0}$. In the literature there is some variance in notation: spawning stock biomass per recruit is denoted as SPR by Mace and Sissenwine (1993), as $SSBR$ by Goodyear (1993), and as SSB/R by Gabriel *et al.* (1989). Note that Goodyear (1993) uses the term SPR to refer to "spawning potential ratio", an entirely different quantity. Estimates of $SPR_{F=0}$ (Beverton and Holt, 1957; Goodyear 1977; Gabriel *et al.*, 1989) were extracted from the database compiled by Mace and Sissenwine (1993) and were based on the same age at recruitment, growth, and maturation schedules used in the Myers *et al.* (in press) database of S and R estimates.

The first three thresholds were defined to be 20% B_0 obtained from the intersection of the replacement line for a fishing mortality rate of zero with the fitted Beverton-Holt (BH_v), Ricker (RK_v), and Shepherd (SH_v) S-R relationships. A fourth estimate of B_0 was the SSB given by the intersection of the $F=0$ replacement line with the mean recruitment. The threshold definition corresponding to 20% of this level was called $Rmnv$.

We considered other versions of the three types of methods discussed above. In particular, we considered using methods that used the best-fitting stock-recruitment model (either Ricker or Beverton-Holt) to define the threshold based upon a goodness-of-fit test. However, we found that these methods did not outperform the models based upon the Ricker function. These methods are not presented here. We also considered

Table 1. Thresholds tabulated by stock. Threshold values are given as proportion of virgin biomass, computed as the intersection of mean recruitment with the replacement line. n is the number of pairs of stock–recruitment observations available. BH50=SSB at 50% of maximum predicted recruitment (50% R_{max}) from fitted Beverton–Holt curve. RK50=SSB at 50% R_{max} from fitted Ricker curve. SH50=SSB at 50% R_{max} from fitted Shepherd curve. Sb=SSB at intersection of 90th percentile of observed survival rate and 90th percentile of recruitment observations. BHv=20% virgin biomass (20% B_0) from fitted Beverton–Holt curve and F=0 replacement line. RKv=20% B_0 from fitted Ricker curve and F=0 replacement line. SHv=20% B_0 from fitted Shepherd curve and F=0 replacement line. Rmnv=20% B_0 from mean recruitment and F=0 replacement line.

Stock	n	BH50	RK50	SH50	Sb	BHv	RKv	SHv	Rmnv
Clupeiformes									
Clupeidae									
Atlantic menhaden (<i>Brevoortia tyrannus</i>)									
US Atlantic	35	1	4	1	4	24	11	21	20
Herring (<i>Clupea harengus</i>)									
Central coast BC	38	2	4	4	14	23	10	10	20
Eastern Bering Sea	26	0	14	5	28	15	21	14	20
Gulf of Maine	23	0	2	3	8	22	7	7	20
Iceland (spring spawners)	23	315	59	21	21	201	74	21	20
Iceland (summer spawners)	43	19	15	19	18	43	27	43	20
North Sea	41	5	4	3	6	33	11	23	20
North Strait of Georgia	38	11	9	8	22	29	17	18	20
North-west coast Vancouver Island	38	0	9	5	21	20	17	18	20
Norway (spring spawners)	39	13	16	13	19	31	30	31	20
Prince Rupert District	38	3	5	3	18	24	12	20	20
Queen Charlotte Islands	38	3	6	3	10	24	14	15	20
South-east Alaska	30	0	29	6	126	19	21	19	20
South-west coast Vancouver Island	38	0	5	1	7	22	14	20	20
Southern Strait of Georgia	38	10	6	6	19	29	13	14	20
Pacific sardine (<i>Sardinops caerulea</i>)									
California	31	295	77	42	57	103	67	37	20
Southern African pilchard (<i>Sardinops ocellatus</i>)									
South Africa	31	6	6	5	12	28	14	25	20
Engraulidae									
Northern anchovy (<i>Engraulis mordax</i>)									
California	25	0	17	15	59	21	22	21	20
Gadiformes									
Gadidae									
Blue whiting (<i>Micromesistius pouassou</i>)									
Northern ICES	20	0	6	5	29	20	14	14	20
Cod (<i>Gadus morhua</i>)									
Baltic Areas 22 and 24	20	65 137	97 960 060	4	3	414 115	294 775 932	43	20
Celtic Sea	20	52 660	12 254 042	11	5	204 941	31 890 596	61	20
Faroe Plateau	28	0	2	2	11	21	7	11	20
ICES VIa	23	0	2	2	12	20	7	9	20
Iceland	34	1	2	2	7	22	6	14	20
Irish Sea	22	0	0	1	4	20	2	2	20
NAFO 1	31	8	10	8	5	48	26	48	20
NAFO 2J3KL	27	8	7	8	8	36	16	36	20
NAFO 3NO	28	5	4	5	9	35	10	35	20
NAFO 3Ps	26	4	3	3	9	28	7	9	20
NAFO 4TVn	37	0	6	4	15	20	13	18	20
NAFO 4VsW	31	0	1	1	7	20	5	8	20
NAFO 4X	41	0	1	2	7	20	4	5	20
North-east Arctic	38	6	3	6	4	48	8	48	20
North Sea	27	3	1	2	5	33	5	3	20
Haddock (<i>Melanogrammus aeglefinus</i>)									
Faroe Plateau	27	0	2	8	22	22	8	8	20
Iceland	28	0	3	2	10	19	9	16	20
NAFO 4TVW	38	10	6	10	7	41	15	41	20
NAFO 4X	24	1	1	4	7	23	5	7	20
NAFO 5Z	58	181 589	191 892 069	41	21	244 857	338 611 788	85	20
North-east Arctic	39	61 183	19 661 192	29	6	142 610	43 023 134	92	20
North Sea	30	4	4	5	5	32	10	10	20
Vla	24	0	4	1	9	19	10	16	20

Table 1. Continued.

Stock	n	BH50	RK50	SH50	Sb	BHv	RKv	SHv	Rmnv
<i>Gadiformes Continued</i>									
<i>Gadidae Continued</i>									
Pollock or saithe (<i>Pollachius virens</i>)									
Faroe	28	0	3	8	20	20	8	7	20
ICES VI	20	0	4	7	21	19	10	10	20
Iceland	26	0	3	3	13	20	9	10	20
North-east Arctic	21	3	2	2	6	28	7	24	20
North Sea	21	3	5	4	11	25	11	19	20
Walleye pollock (<i>Theragra chalcogramma</i>)									
Eastern Bering Sea	24	0	12	11	42	20	19	19	20
Gulf of Alaska	21	0	14	10	58	24	22	20	20
Whiting (<i>Merlangius merlangus</i>)									
ICES VIa	25	0	6	15	36	20	13	11	20
North Sea	26	0	8	10	37	21	16	16	20
<i>Merlucciidae</i>									
Hake (<i>Merluccius capensis</i>)									
South Africa 1.6	20	0	6	5	14	20	13	15	20
Pacific hake (<i>Merluccius productus</i>)									
W. US+Canada	30	24	28	9	96	23	23	22	20
Silver hake (<i>Merluccius bilinearis</i>)									
Mid Atlantic Bight	33	95	37	95	37	59	43	59	20
NAFO 5Ze	33	680	203	143	73	154	130	50	20
<i>Perciformes</i>									
<i>Scombridae</i>									
Mackerel (<i>Scomber scombrus</i>)									
NAFO 2 to 6	28	2	2	2	3	45	6	45	20
Pacific mackerel (<i>Scomber japonicus</i>)									
Southern California	36	0	30	3	26	25	47	28	20
<i>Pleuronectiformes</i>									
<i>Pleuronectidae</i>									
Pacific halibut (<i>Hippoglossus stenolepis</i>)									
Pacific	47	1	5	5	17	21	11	12	20
Plaice (<i>Pleuronectes platessa</i>)									
Irish Sea	26	0	2	2	6	19	6	9	20
Kattegat	22	10	4	10	8	44	11	44	20
North Sea	33	0	1	4	10	20	5	4	20
<i>Soleidae</i>									
Sole (<i>Solea vulgaris</i>)									
ICES VIIe	22	101	30	34	23	96	44	46	20
Irish Sea	20	0	2	3	15	20	7	7	20
North Sea	34	0	3	1	6	20	7	13	20
<i>Salmoniformes</i>									
<i>Salmonidae</i>									
Sockeye salmon (<i>Oncorhynchus nerka</i>)									
Adams Complex, BC, Canada	38	104	32	46	21	183	62	33	20
Birkenhead River, BC, Canada	37	14	8	14	12	42	18	42	20
Chilko River, BC, Canada	38	40	15	14	16	62	27	24	20
Early Stuart Complex, BC, Canada	38	49	30	49	23	73	51	73	20
Horsefly River, BC, Canada	38	223 474	1.7×10^9	68	14	366 895	3.2×10^9	27	20
Rivers Inlet, BC, Canada	36	4	12	7	28	22	20	22	20
Skeena River, BC, Canada	45	69	25	23	42	43	29	24	20
Stellako River, BC, Canada	38	43	15	43	16	69	28	69	20

variations of the class of methods that are based on survival and recruitment percentiles, i.e. we examined methods that used the intersection of the 80th and 90th percentile survival with the 50th, 80th, and 90th percentile recruitment. These alternatives also did not perform better than Sb and will not be presented in detail.

Comparing the performance of thresholds

One may obtain a subjective impression of the appropriateness of the various threshold definitions by inspecting S-R plots and noting the relative positions of alternative

Table 2. Summary of biomass thresholds defining recruitment overfishing. Note that R_{\max} is the maximum predicted recruitment and B_0 is the virgin biomass.

Type	Estimator	Method
50% R_{\max} rules	BH50	SSB at 50% R_{\max} from fitted Beverton–Holt curve
	RK50	SSB at 50% R_{\max} from fitted Ricker curve
	SH50	SSB at 50% R_{\max} from fitted Shepherd curve
Survival–recruitment percentile rules	Sb	SSB at intersection of 90th percentile of observed survival rate and 90th percentile of recruitment observations
20% B_0 rules	BHv	20% B_0 from fitted Beverton–Holt curve and $F=0$ replacement line
	RKv	20% B_0 from fitted Ricker curve and $F=0$ replacement line
	SHv	20% B_0 from fitted Shepherd curve and $F=0$ replacement line
	Rmnv	20% B_0 from mean recruitment and $F=0$ replacement line

threshold stock-level estimates. A threshold set at a high stock level is clearly more conservative than one set at a lower stock level. In some cases the existence of a threshold stock size may be suggested by a clear break in the data below which recruitment is reduced. For example, the data for several of the sockeye salmon stocks (e.g. Adams Complex, Early Stuart Complex; Table 1) show this feature, as does South African pilchard (Fig. 1). However, for the majority of the stocks, there is no obvious threshold which can be identified by inspection. For illustrative purposes we selected eight stocks that demonstrate a variety of situations (Fig. 1).

Atlantic menhaden shows a relatively flat relationship between recruitment and stock biomass. The thresholds based on estimates of 20% B_0 are conservative relative to the 50% R_{\max} estimates. Though a wide range of stock sizes have been observed, expected recruitment may not decline until very low abundance is reached.

North Sea herring and Southern African pilchard show a variable recruitment with constant mean above a threshold, and a close to linear relationship below. The 20% of B_0 estimates again are conservative compared to the 50% R_{\max} methods. The Serebryakov estimate appears to fall close to the natural break in the data, intermediate to the other two groups of methods.

Haddock from NAFO Division 4TVW and cod from NAFO Division 2J3KL show a positive but variable relationship between stock and recruitment. As in the previous examples the methods based on one half of the maximum predicted recruitment and the Serebryakov (1991) method are less conservative than those based on 20% B_0 . The former fall slightly below the visual break in the observations, while the more conservative methods are above this breakpoint.

Silver hake in NAFO region 5Ze shows a nearly linear relationship between stock and recruitment. In this case

no method can be expected to perform well because there is no basis for selecting a threshold. For this stock, the methods based on 50% R_{\max} estimate the threshold level to be above the maximum observed stock size. If a decision were based solely on the S–R data, this might not be an unwise threshold for such a case. The 20% B_0 methods are lower, while the Serebryakov threshold is close to the median stock size. Saithe from the Faroe plateau and Iceland show a descending limb of the stock–recruitment relationship. In this case we would judge threshold estimates near the lower end of the range of observations reasonable. The 50% R_{\max} rules based upon the Beverton–Holt function are clearly unreasonable because they fall at zero stock size. Again, the 20% B_0 methods are more conservative than the other methods and may overly restrict the fishery.

Table 1 summarizes the threshold estimates obtained for each stock. The thresholds have been expressed as a percentage of the virgin biomass estimated by the intersection of the mean observed recruitment and the $F=0$ replacement line. Thus, entries for Rmnv always equal 20, which can be used as a point of reference. Thresholds based on rules using 50% R_{\max} are usually below Rmnv. This is also true for the Serebryakov method where only 24 of the estimates are larger than the corresponding Rmnv threshold. For the other methods based on 20% B_0 , BHv thresholds are usually larger than Rmnv, while RKv and SHv are more evenly divided above and below Rmnv. The overall average ranking of the estimates (in order of ascending threshold SSB) was SH50, BH50, RK50, Sb, RKv, Rmnv, SHv, BHv. Very large thresholds occur in Table 1 when there is a nearly linear relationship between stock and recruitment. In these cases, the Sb method often gives lower threshold levels than the other methods. Low thresholds were estimated for 50% R_{\max} methods when the estimated slope at the origin was high, often due to a lack of data or no

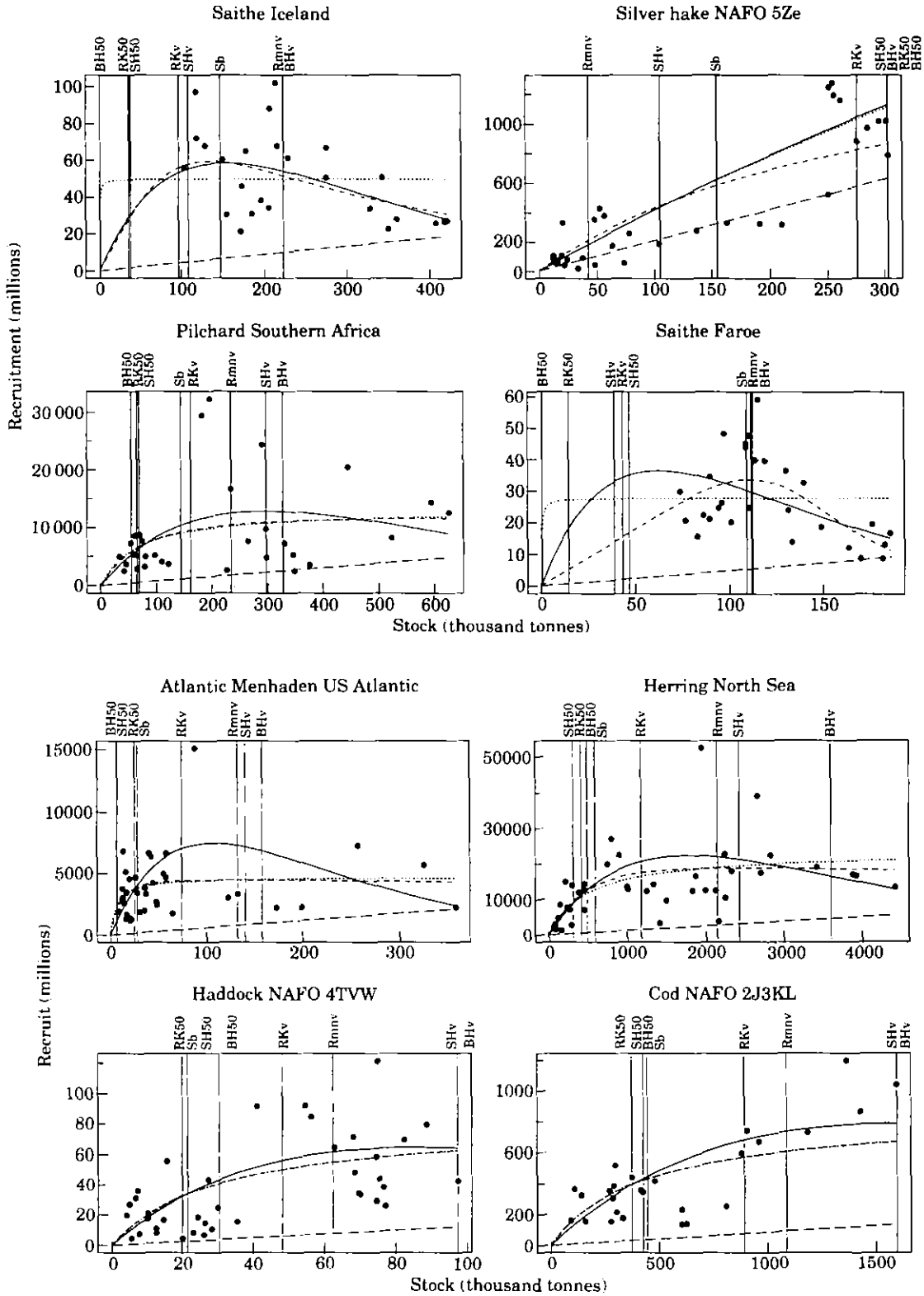


Figure 1. Stock and recruitment data for eight example stocks. Threshold estimates using all observations for each method are indicated by vertical lines. The fitted Ricker model is shown with a solid line, Shepherd with a dashed line, and Beverton-Holt with a dotted line. The straight line through the origin (dashed) is the $F=0$ replacement line.

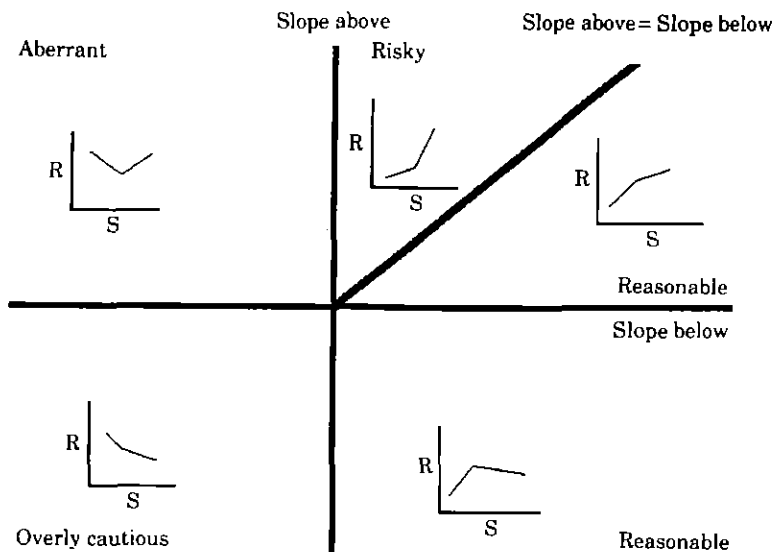


Figure 2. Decision diagram for categorizing threshold estimates based on the slopes of log-transformed data above and below the estimated threshold biomass levels.

discernible decline in recruitment at low stock sizes. The S_b method usually falls between the other types in these cases.

The effect of the shape of the stock–recruitment relationship

The most important criterion for the application of any of the methods described here is whether the threshold estimate is sufficiently conservative without needlessly restricting the harvest. If there is little benefit in terms of recruitment in maintaining SSB above the estimated threshold it may be judged too conservative. If the threshold level is too low, the risk of poor recruitment may be unacceptably high. Obviously, it is difficult to make an objective determination of the conservatism of any particular method (except for those estimates at or near zero which can be *a priori* classified as too risky). In this section we provide some guidance to evaluate the threshold estimates in light of the shape of the S–R relationship.

For each stock, regressions were performed on log-transformed S–R data above and below the threshold level. Differences between the two slopes were used to indicate whether or not a particular threshold was conservative in protecting against poor recruitment without unduly restricting the fishery. In cases where there were fewer than five points on one side of the threshold, only one slope was calculated. In this situation, it is difficult to generalize about the appropriateness of the location of the threshold, except in a few extreme instances. Thresholds that occur at the low end of the observed SSB range are likely to be risky if the

slope above is positive, indicating recruitment may increase substantially at higher stock levels. On the other hand, thresholds that occur near the highest observed levels of SSB are likely to be overly conservative if the slope below is negative, indicating overcompensation and increased expected recruitment at lower stock levels.

Where the threshold is sufficiently far from either extreme of the observed range of SSB, the slope above can be compared to the slope below to determine whether there is any justification for the location of the threshold (Fig. 2). Cases where both slopes are negative (lower left quadrant, Fig. 2) are likely to be overly conservative. In these cases it appears that the observations all come from a region where overcompensation dominates and a more appropriate threshold is likely to be near or below the lowest observed SSB. The same conclusion may also apply when the slope is near zero on both sides of the threshold. When the S–R observations are dome-shaped, thresholds that result in a positive slope below and a negative slope above (lower right quadrant, Fig. 2) would be judged sensible in most cases. However, they could be bordering on being risky if located low on the ascending limb of the dome, or conservative if located near or above the peak of the dome. In any case, recruitment would be expected to decline if SSB was reduced too far below the threshold level. If the slopes on both sides of the threshold are positive, but the slope above is less than the slope below (upper-right quadrant below the diagonal line, Fig. 2) expected recruitment is, appropriately, increasing more slowly with increasing stock biomass above the threshold. However, any point on a Beverton–Holt S–R curve would satisfy this condition and, once again,

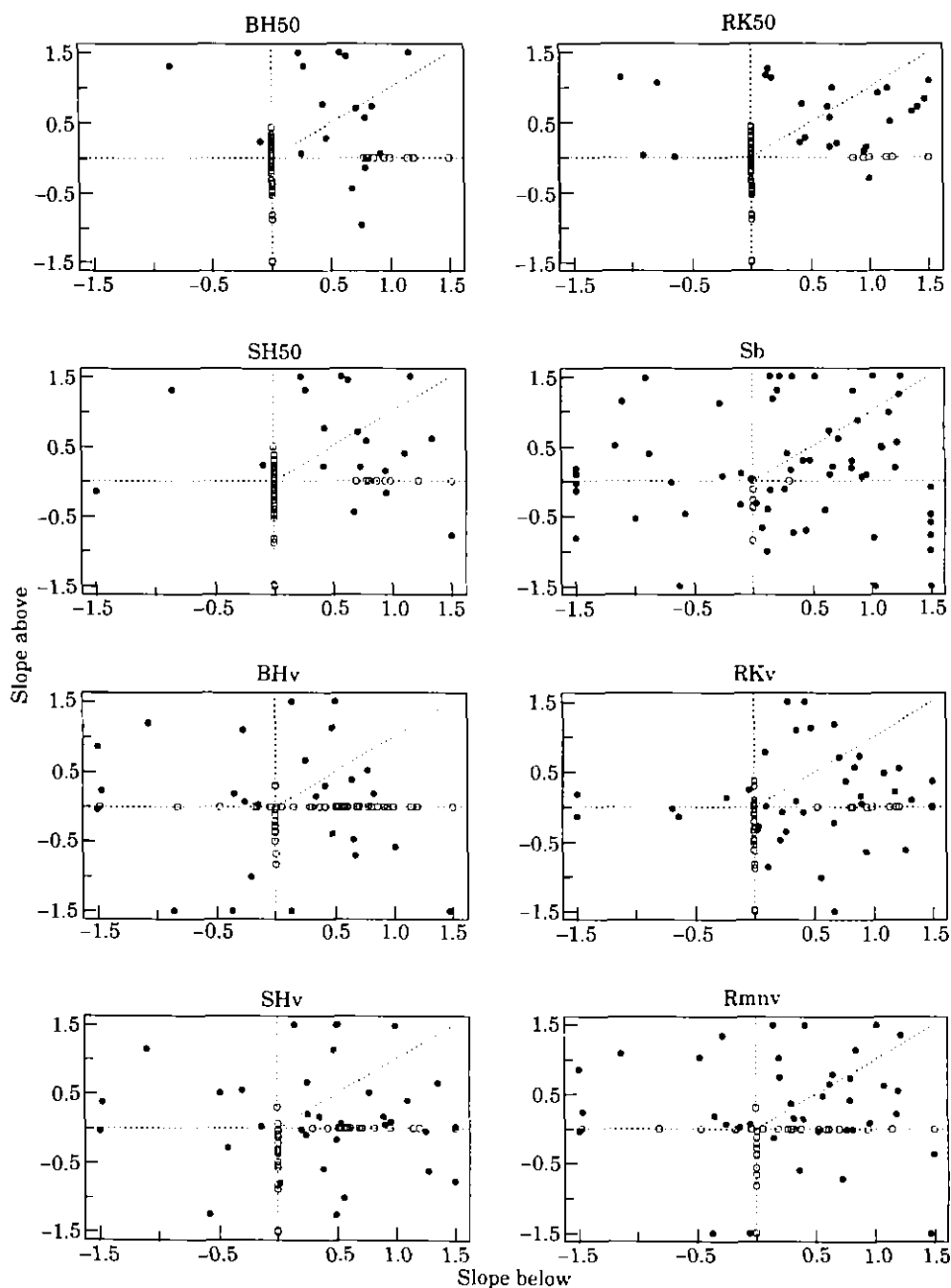


Figure 3. Decision diagrams for the eight definitions of thresholds applied to the 72 stocks. The open circles on the abscissa indicate slopes below the threshold for stocks with less than five observations above the threshold. Open circles on the ordinate indicate slopes above the threshold for stocks with less than five observations below the threshold. Solid dots are stocks where both slopes could be estimated.

thresholds at low SSB could verge on risky, while those at high SSB could verge on being overly conservative. Cases where the two slopes are positive and increasing indicate risky estimates of the threshold (upper-right quadrant above the diagonal line, Fig. 2). Large gains in recruitment are to be expected if SSB is higher than the

threshold level. Finally a V-shaped pattern of S-R data (upper-left quadrant, Fig. 2) has been labelled as aberrant since it has no obvious interpretation.

Slopes on either side of the eight threshold definitions for each of the 72 selected stocks are plotted in Fig. 3. Results are summarized in Table 3 using the

Table 3. Summary of the performance of each of the eight methods with respect to the decision diagram, Figure 2. When there are at least five points above and below the threshold estimate, both slopes are estimated and the results are tentatively classified as sensible (OK), overly conservative (Cons.), risky, or aberrant (Abb.). When only one of the slopes is estimable, it is not possible to determine whether the threshold estimate is conservative, risky, or sensible, except in the special cases where the threshold occurs at low SSB (Low) and has a positive slope above (Risky) or the threshold occurs at high SSB (High) and has a negative (or zero) slope below (overly conservative). Other situations are classified as unknown (UK).

Method	Threshold with at least five observations each side of estimate				Threshold with less than five observations				Totals	
	OK	Cons.	Risky	Abb.	Low		High		Cons.	Risky
					UK	Risky	UK	Cons.		
BH50	9	0	6	2	29	14	12	0	0	20
RK50	15	0	6	4	28	12	7	0	0	18
SH50	10	1	6	2	29	15	9	0	1	21
Sb	34	9	12	11	4	1	1	0	9	13
BHv	11	4	4	7	9	1	29	7	11	5
RKv	26	3	6	3	18	7	9	0	3	13
SHv	20	3	6	5	19	2	17	0	3	8
Rmnv	17	3	10	9	10	1	15	7	10	11

classification outlined in Fig. 2 and explained above. Open circles on the horizontal (vertical) axis of Fig. 3 indicate that no slope above (below) the threshold was estimated because there were fewer than five observations in this region. Thresholds near or beyond the extremes of the observed range of SSB were often obtained for the methods based on 50% R_{max} from a fitted S-R relationship (BH50, RK50, and SH50; Fig. 3). In these cases, it is often difficult to draw conclusions about the appropriateness of the location of the threshold (Table 3). However, when the estimates for these methods were within the range of the data, they generally appeared to be sensible without being overly cautious.

Serebryakov's (1991) method (Sb) always estimates the threshold level to be within the range of the data, although there may not always be enough points on either side of the threshold to estimate slopes. Nearly half of the cases for this method fell in the sensible or cautious regions (Table 3). However, 23 cases were within the risky or aberrant regions and another nine were overly conservative. This may suggest that this method is not robust across data sets.

Is recruitment reduced below the threshold?

As noted in the introduction, the evaluation of any particular method for determining a threshold SSB should take into account the productivity of the stock above and below the estimated level. In other words, is there evidence that recruitment is generally lower when the stock is below the threshold than when the stock is above the threshold? Here, we calculate the log (base 10) of the ratio between average recruitment above and below the threshold level of SSB for each stock and threshold definition (Fig. 4). The requirement of at least

five points either side of the threshold was relaxed, with sample sizes in Figure 4 representing all cases where the threshold was within the range of the data.

One problem with the use of this simple ratio for assessing the validity of a threshold definition is that positive differences between recruitment levels immediately above and below the threshold may be masked by overcompensation at higher levels of SSB. Nevertheless, on average across all stocks, each of the estimators except BHv appears to have found a point below which recruitment is reduced. Methods based on 50% R_{max} generally had higher ratios than the other methods because they tend to estimate lower SSB thresholds. However, there was a wide range in the log ratio of recruitment above and below the estimated thresholds due to the variability in the stock and recruitment patterns. Grouping the stocks taxonomically (Fig. 4) indicates that the salmon stocks often have the clearest positive slope in their stock and recruitment data and therefore the threshold estimators usually find a point below which recruitment is reduced. This is not the case for stocks such as pollock which exhibited a negative or only slightly positive relationship between stock and recruitment. For such data the reference levels probably should be below the minimum observed stock size, a result that is usually obtained for the methods based on 50% R_{max} (e.g. see Fig. 1). For haddock stocks, the methods that use 20% B_0 performed poorly on this test (Fig. 4). Haddock appear to be quite plastic in terms of growth and maturation, so the replacement line used to define virgin biomass may not accurately reflect the unexploited condition. This caveat may also apply to cod and herring stocks to some extent.

In some cases, particularly for the BH50, RK50, and SH50 methods, there were no observations below the threshold (54, 46, and 53% of cases, respectively). In

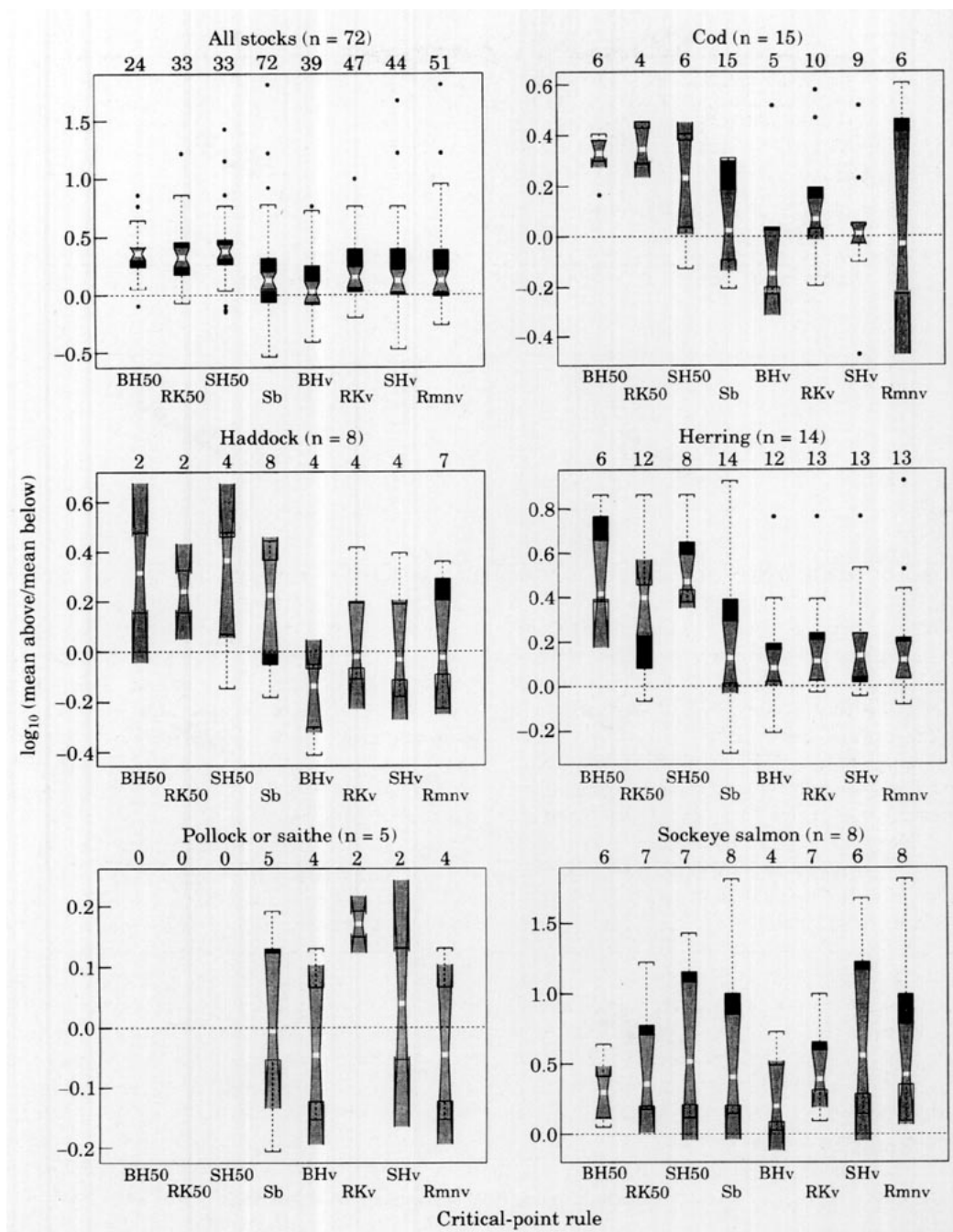


Figure 4. Box and whisker plots (Hoaglin *et al.*, 1983) of the log of the ratio of mean recruitment above and below the threshold spawning biomass estimated by eight methods. The width of each box is proportional to the square root of the number of data points. The white line in the middle of the box shows the median. The notch indicates the 95% confidence interval for the median. The outline of the box gives the upper and lower quartile. The whiskers are drawn to the nearest value not beyond 1.5* (inter-quartile range) from the quartiles. Points indicate outliers.

other cases, particularly for the BHv, SHv, and Rmnv methods, there were no observations above the estimated threshold (36, 19, and 21% of cases, respectively). This means that the appropriateness of the estimated

level cannot be quantified using the ratio method. However, it cannot be concluded that a particular estimated threshold value is unreasonable or inappropriate, unless the estimate is zero. Note that although the methods

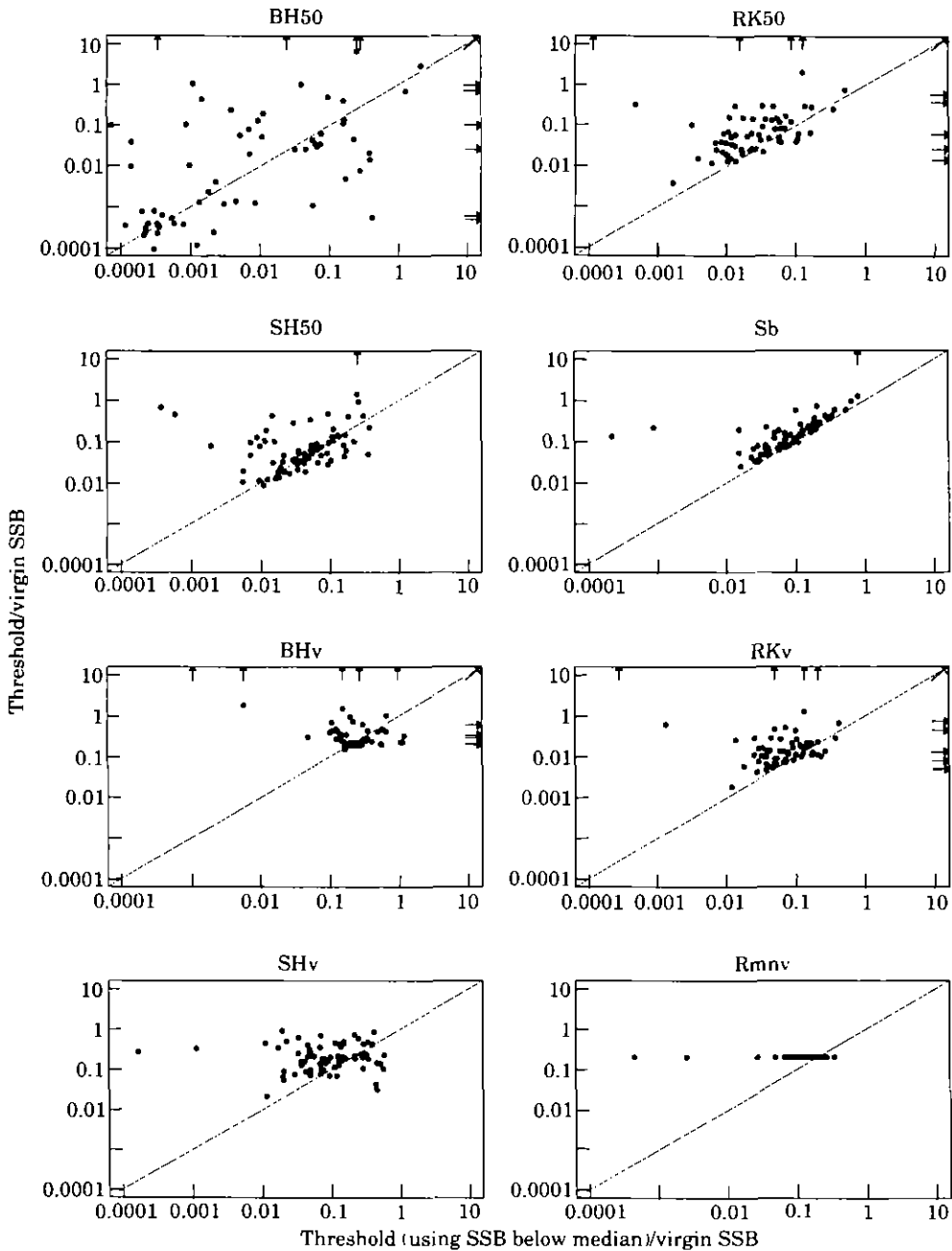


Figure 5. Comparison of estimated threshold made using all stock and recruitment observations (vertical axis) with estimates based on SSB observations below the median for each stock (horizontal axis). The thresholds are normalized by dividing by the estimated virgin SSB calculated as the SSB that results from the mean recruitment with no fishing. Each frame is for a different estimation method. The lines are the one-to-one line (i.e. equal estimates) for each method. The data are presented on a \log_{10} scale. Outliers are identified by arrows.

based on 50% R_{max} (BH50, RK50 and SH50) only give estimates within the range of the data in less than half the cases. when they do, they appear to define a point below which recruitment is markedly poorer (Fig. 4). Provided the data do not exhibit pronounced overcom-

penation, the mean above the 50% R_{max} point should be about twice the mean below (i.e. a base 10 log ratio of about 0.3). As it happens, this is approximately the result obtained across all stocks as well as for individual taxonomic groups (Fig. 4).

Sensitivity to the range of the data

Use of the observed data to determine whether recruitment is on average reduced below the threshold cannot be the sole criterion for judging the appropriateness of a particular method. Indeed, this could be very misleading. Suppose, for example, that all the observations were taken close to the origin of the S–R relationship so that the slope of the points was clearly positive (as is the case for many of the stocks used in this study). In this situation, the log of the ratio of average recruitment above and below may be greater than zero, but there will be further gains to be made in average recruitment if the stock is well above the threshold level. In other words, problems may arise because of lack of contrast in the range of stock sizes observed.

A simple way to examine this problem is to compare the thresholds estimated using all the data with the thresholds estimated using only the SSB observations below the median biomass. Figure 5 shows the estimates using the full data sets (ordinate) versus the estimates using only the lower half of each data set (abscissa). Note that the two estimates for the Serebryakov method (Sb) are strongly correlated. This is to be expected because, unlike the other methods, the Sb method constrains the threshold to be within the range of the data. For 90% of the stocks, the Sb method gave lower thresholds when the upper half of the data was excluded (i.e. 90% of the estimates were above the 1:1 line in Fig. 5). Similarly, when the data set was restricted in this way for Rmnv, RK50, and RKv, about 70% of the estimates were reduced. This is clearly an undesirable property; it means that estimates of overfishing thresholds will be progressively reduced as a stock becomes depleted. The BH50 and SH50 methods are somewhat more robust according to this criterion, with a more even distribution on each side of the one-to-one reference line. Methods based on 50% R_{\max} appear to be more robust than the corresponding methods based on 20% B_0 . This is probably because removal of the observations at high SSB has a greater influence on the shape parameter (which primarily affects the estimate of B_0) than it does on the slope parameter (which primarily affects the estimate of 50% R_{\max}). Note also that although a lack of robustness to the data may be an undesirable property it may also be unavoidable for most S–R data sets. The result for Rmnv indicates that mean recruitment was lower for data below the median SSB for about 70% of the cases.

In general, the slope of the relationship between stock and recruitment should be related to the range of % B_0 covered by the observations. It would be expected that observations with a small range restricted to low stock levels would have a positive slope, while those with a small range restricted to high SSB would have a near-zero or negative slope. Cases covering a large range of

SSB should have moderate or near-zero slopes, unless there is pronounced overcompensation in the underlying S–R relationship. However, such patterns were not obvious when we plotted the slope of the log–log transformed data against the range covered by the observations (computed using Rmnv). This is probably due to difficulties in calculating realistic estimates of virgin biomass, and differences in the degree of compensation (and therefore the relationship between the slope and the range) exhibited by different stocks.

Discussion

This empirical analysis of S–R data has produced several important results. First, it should help dispel the widely-held notion that observed recruitment is “usually” independent of spawning biomass and therefore S–R data cannot be used to define biomass thresholds. One of the factors that made a comprehensive analysis such as this difficult in the past was the shortness of the time series of S–R data. However, we believe the major reason that S–R relationships have not been used is that often there is only a short range of SSBs observed, and under these conditions the variability in recruitment (Goodyear, 1993) will make it difficult to detect the underlying functional relationship between SSB and recruitment. For most of the 72 stocks examined in this study, there are biomass thresholds that could be used to protect recruitment. That is, the mean recruitment was generally greater above the threshold than below, except for species such as saithe which had a negative relationship between stock and recruitment (Fig. 4).

Second, we believe that the methods based on 50% R_{\max} provide the most reliable estimated threshold levels overall. Their theoretical basis is clear, they are reasonably robust (Fig. 5), and they nearly always result in threshold levels in which the mean recruitment is higher above the threshold (Fig. 4). However, there are two cases where these methods may be overly risky or conservative. If the mean recruitment is a nearly constant or monotonically decreasing function of stock size, the estimated slope at the origin is often exceedingly high and the corresponding threshold based on 50% R_{\max} may be dangerously low. Conversely, if there is a positive linear relationship between stock and recruitment these methods may estimate a threshold level that is extremely high. In both instances the definition of a threshold level is inherently difficult since there are insufficient data to define either the initial slope or the peak of the S–R relationship, and no method would be expected to work well. The best approach for such data is to examine stock and recruitment data for similar stocks, in the hope of discerning a general pattern.

For several of our evaluation criteria it would appear that the Serebryakov estimates generally perform well (Fig. 3; Table 3). However, this method is sensitive to the range of the data observed (Fig. 5) and should be used cautiously when only low stock abundance occurs in the data set. The Sb method may be a good option when there is no detectable decline in recruitment over a wide range of stock sizes since it is often intermediate between the other methods.

Methods based on 20% B_0 were included in this study because they have been widely applied (Beddington and Cooke, 1983; Francis, 1992); however, based on both empirical and theoretical considerations we do not recommend them for general use. These methods often placed the critical point well beyond the range of the observations (e.g. in 36% of cases for BHv). In addition, they suffer from two other related problems: inaccuracies in the estimates of virgin biomass, and the inappropriateness of applying the 20% level universally. Estimates of virgin biomass calculated by the method used here are inaccurate because they assume stationarity (e.g. no density-dependent processes) to calculate the $F=0$ replacement line and generally rely on extrapolating the S-R data beyond the range of the observations.

Similarly, a threshold of 20% B_0 will not be universally applicable since different stocks have different degrees of compensation (i.e. density-dependence) in recruitment and other life-history processes. In contrast, methods using 50% R_{max} take account of the degree of compensation in the S-R relationship (Mace, 1994). In effect they define levels of % B_0 that are inversely related to the slope at the origin.

Calculating the ratio of recruitment above and below the estimated threshold is important for developing an argument that reducing the stock below the estimated level has a demonstrable effect on productivity. This is a crucial argument for fishery managers. Otherwise, they must take on faith the scientific advice that the threshold should not be crossed. In cases where there is no clear evidence of an effect on recruitment at low stock biomass, this should be clearly stated, noting that the threshold is essentially a precautionary measure.

Despite the difficulty of estimating virgin biomass, it is important to know the approximate range of SSB covered by the observations in order to assess the validity of the threshold. The ability of any of the methods to estimate a reasonable threshold level is closely related to the range of observed SSB. If all of the observations are near the origin, with little information on the level of maximum recruitment, then the threshold level should probably be near or above the highest observed SSB. On the other hand, if the slope computed using all of the points is negative and the observations are restricted to high levels of biomass then a reasonable threshold level may be near or

below the lowest observed SSB. Threshold estimates should be updated as new information becomes available.

Another important consideration is the statistical significance of the threshold estimates, an issue that was not addressed specifically in this comparative study. For many of the stocks in this study, the variability of the data and the relatively small number of observations may mean that adjacent slopes are not significantly different from each other, and ratios of mean recruitment above and below the thresholds are not significantly different from unity. However, given that the slopes and ratios are used as a guidance tool, the significance level may be less stringent (say, 75% rather than 95%) than in other applications. On a case-by-case basis, significance of the slope and ratio estimates should be carefully considered.

We have by no means examined an exhaustive list of methods for estimating thresholds. However, for any additional methods, it would be prudent to perform some or all of the analyses presented here on a wide range of data sets. It is evident from our analyses that no single evaluation criterion we examined should be used as the sole basis for determining the appropriateness of a threshold biomass estimate. Judgements about the degree of risk or conservatism of a particular threshold depend on the action to be taken when the threshold is crossed. The extreme is to close the fishery. Alternatively, fishing mortality may be reduced according to some control law which relates fishing mortality to spawning biomass. The appropriateness of a given threshold will need to be determined on a stock-by-stock basis, but should be strengthened by the comparative study presented here.

We believe that estimating threshold SSB levels for exploited fish stocks is an important step in providing advice for resource management. Quinn *et al.* (1992) have shown some of the benefits of managing stocks using a minimum escapement level. In addition, estimates of threshold levels can be used as provisional stock rebuilding targets for resources already depleted and can serve to bound the harvest under a range of management strategies.

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