Towards a new recruitment paradigm for fish stocks

D.J. Gilbert

Abstract: The stock recruitment paradigm involves the hypothesis that recruitment (R) to a fish stock is positively related to the spawning stock biomass (SSB) of the stock, at low SSB. I propose a "recruitment states" hypothesis wherein R is independent of SSB but has different mean values during successive periods. Meta-analysis was used to test the null hypothesis that recruitment is a series of random, independent events, against these two alternative hypotheses, for 153 marine spawning bony fish stocks and 31 salmonid stocks. A test statistic for the stock recruitment paradigm, based on estimating derivatives from the first differences of the time series, was not significant for the marine stocks. The null hypothesis was rejected for the salmonid stocks. Recruitment states models significantly fitted time series for the marine stocks. Ricker models also significantly fitted these data, conflicting with the derivatives test result. However, because SSB is dependent on R, lagged by the age at maturity, a period in a low recruitment state would tend to lead to a period of low SSB. Therefore, the significance of the fit to the Ricker model may have been spurious. The recruitment states model best explained the meta-dataset for the marine stocks.

Résumé : Le paradigme de recrutement d'un stock fait intervenir l'hypothèse que le recrutement (R) dans un stock de poisson est en corrélation positive avec la biomasse du stock de géniteurs (BSG) de ce stock, lorsque la BSG est faible. Je propose une hypothèse d'états de recrutement dans laquelle R est indépendant de la BSG, mais possède différentes valeurs moyennes au cours de périodes successives. La méta-analyse a été utilisée pour vérifier l'hypothèse nulle voulant que le recrutement soit une série d'événements indépendants et aléatoires, par rapport aux deux autres hypothèses dans le cas de 153 stocks de géniteurs de poissons téléostéens marins et de 31 stocks de salmonidés. Une variable à tester pour le paradigme de recrutement d'un stock, fondée sur l'estimation des dérivées des premières différences dans les séries chronologiques, n'était pas statistiquement significative pour les stocks de poissons marins. L'hypothèse nulle a été rejetée dans le cas des stocks de salmonidés. Les modèles d'états de recrutement s'ajustaient de manière significative aux séries chronologiques pour les stocks marins. Les modèles de Ricker s'ajustaient également de manière significative à ces séries chronologiques, situation en contradiction avec les résultats des dérivées du test. Cependant, comme la BSG est indépendante de R, décalé en fonction de l'âge à la maturité, une période au cours d'un état de recrutement faible aurait tendance à mener à une période de BSG faible. Par conséquent, la signification de l'ajustement au modèle de Ricker peut avoir été factice. Ce modèle d'états de recrutement est celui qui explique le mieux l'ensemble des méta-données pour les stocks marins.
[Traduit par la Rédaction]

Introduction

Several influential publications during the 1950s described (Ricker 1954; Beverton and Holt 1957) or implied (Schaefer 1954) hypothetical relationships between the size of a spawning stock of fish and the consequent number of recruits into that stock. What may be called the stock recruitment paradigm is now widely assumed in the fisheries science literature and in fisheries management policies worldwide. The paradigm involves the idea that the annual number of recruits (R) to a fish stock is positively related to the spawning stock biomass (SSB), at least at low SSB. This has lead to the widespread acceptance of spawning stock biomass (or egg) per recruit analysis (e.g. Gabriel et al. 1989; Mace and Sissenwine 1993; Thompson 1993; Myers et al. 1994). The lower the value of the spawning stock biomass per recruit ratio the greater must be the survival in the egg to recruitment stage to maintain a

constant level of R. It is not arguable that below some level of SSB, R must decline (zero or one spawner can only produce zero recruits). However, the fecundity of most fish species is such that it is feasible that R is generally not related to SSB down to a level of SSB that is practically not distinguishable from zero. Over a very wide range, more eggs may not lead to more recruits.

Many fish stock datasets of SSB and R do not appear to be consistent with the paradigm. A substantial literature has developed to explain why the data frequently do not conform to the paradigm and to warn of the difficulties in estimating relationships between SSB and R (e.g., Walters and Ludwig 1981; Walters 1985; Caputi 1988; Armstrong and Shelton 1988; Koslow 1992; Hilborn and Walters 1992). Recruitment is typically highly variable; time series are often short; SSB and R data may have estimation error that is random, systematic, autocorrelated, or with correlated time trends. Relationships between SSB and R could therefore be obscured or distorted. Because a spawning causes recruitment that augments the SSB in a subsequent year, an (SSB, R) dataset is not a set of independent observations. This last fact leads to what have been called time series effects. One time series effect is that an estimate of the slope of a relationship between SSB and R may be negatively biased (Walters 1985). Another results

D.J. Gilbert. National Institute of Water and Atmospheric Research Ltd., P.O. Box 14-901, Kilbirnie, Wellington, New Zealand. e-mail: d.gilbert@niwa.cri.nz

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from the observation that if a period of systematically low R occurs, this will inevitably lead to a period of low SSB. This may generate the spurious appearance of a relationship between SSB and R.

Whereas there have been some papers showing that R is related to SSB for selected individual stocks (e.g., Fargo 1994; Jacobson and MacCall 1995) there have been very few published tests of the null hypothesis that, in general, recruitments are random and independent events. If a general test cannot reject the null hypothesis, then it is possible that the individual stock results are merely some of the small percentage of cases that would arise by chance. A test based on a set of stock recruitment datasets may be called a meta-analysis. By including many stocks, a test sufficiently powerful to overcome data error may be possible. Iles (1994) has carried out tests by fitting models to individual flatfish stocks. Myers and Barrowman (1996) have used nonparametric, meta-analytic methods. Both papers reject the null hypothesis in favour of the stock recruitment paradigm. Here I use an alternative approach to analysing the meta-dataset of Myers et al. (1995) and conclude that the null hypothesis can only be rejected for salmonids. My test avoids some potential time series effects. I also show evidence for a recruitment mechanism in which a stock switches between different levels of mean recruitment from time to time. This mechanism can lead to the spurious appearance of a relationship between SSB and R.

The meta-analyst must define a statistic on the set of datasets that has a critical region corresponding to an alternative hypothesis. Several test statistics were developed here on the basis of the following idea. An intermediate statistic is calculated on each of the fish stock datasets. It is compared with its known median for that stock, under the null hypothesis. The probability of each intermediate statistic exceeding (or falling below) each median is 0.5. The test statistic for the set of stocks is the number of stocks for which the intermediate statistic exceeds (or falls below) its corresponding median. The test statistic falls into the critical region if it exceeds (or falls below) a cutoff value that can be obtained from the binomial distribution (a one-tailed test).

Stock and recruitment data

The selection of data to be included in a meta-analysis has the potential to bias the result. Here I used those datasets supplied to me by Dr. R.A. Myers in 1994. The meta-dataset described by Myers et al. (1995) containing 274 fish stocks had been somewhat expanded from that supplied to me. I used only datasets that contain at least six successive (SSB, R) data (the minimum necessary for one of the analyses) and I excluded substocks. Two categories of species were analysed separately, 4 salmonids (31 stocks; 871 SSB, R data) and 50 marine-spawning bony fishes (153 stocks; 3164 SSB, R data) (see Appendix). For the salmonids, the SSB data are recorded in numbers of fish rather than biomass. This is immaterial to the analyses.

Alternative recruitment models

Time series of recruitment often contain successive periods of high and low values. I conjecture that typically the biological system in which recruitment to a stock occurs can occupy one of several distinct states (driven by environmental factors).

From time to time the system switches between these states. Each state has a different level of mean recruitment. I will refer to this hypothesis as the recruitment states hypothesis.

Here I fitted a two-state recruitment model to each stock: the recruitment to a stock may occupy either of two states; while it is in a particular state it varies around the mean for that state; the recruitment to a stock always occupies a particular state for at least 3 years and this period must occur wholly within the time series being fitted (i.e., 1- or 2-year periods are not allowed at the start or end); in all of the observed datasets either one or two state switches occur (irrespective of the length of the time series).

This model has four parameters: two mean recruitment levels and two state-switching dates (one possibly null). The model is therefore expressed as follows:

$$R = \begin{cases} R_1 & t_0 \le t < t_1 \\ R_2 & t_1 \le t < t_2 \\ R_1 & t_2 \le t \le t_n \end{cases}$$

where R is recruitment, t_0 and t_n are the first and last years (known), and R_1, R_2, t_1, and t_2 are unknown parameters such that $t_1 = t_0$ or $t_1 - t_0 \ge 3$, $t_2 - t_1 \ge 3$, and $t_n - t_2 \ge 2$.

A two-parameter Ricker model (Ricker 1954) was also fitted to each stock.

$$R = aSe^{-bS},$$

where R is recruitment, S is spawning stock biomass, and a and b are unknown parameters.

This is a commonly used model within the stock recruitment paradigm that is dome shaped when b is positive and S takes values above and below $1/b$. The two models are simple and correspond to the alternative hypotheses. They may not be the best models for particular stocks, but if either hypothesis were widely true, the corresponding model would significantly explain variance in the whole meta-dataset.

Sum of squares hypothesis tests

The sum of squares of differences between the logarithm of the observed R and the logarithm of the fitted R was minimized for each model, for each stock. This sum of squares was used as the intermediate statistic, lower values indicating better fits. Logarithms were taken because recruitment often appears to follow a lognormal distribution (e.g., Beddington and Cooke 1983; Caputi 1988, Hilborn and Walters 1992). An effect of taking logarithms is to reduce the influence of occasional very large Rs. Figures 1 and 2 show the two models fitted to the Atlantic cod (*Gadus morhua*) North Atlantic Fisheries Organization (NAFO) 1 stock and the Fraser River chum salmon (*Oncorhynchus keta*) stock. For the salmon stock, b is estimated to be negative in the Ricker model, which gives a curve that is slightly concave upwards. This is consistent with the stock recruitment paradigm.

A bootstrap was used to obtain the median sum of squares for each stock, for each model, under the null hypothesis. R values were shuffled at random (i.e., without replacement) in the time series, for each stock. Both models were then fitted and this process was repeated 200 times to give the medians. Under the null hypothesis, the probability of the observed sum of squares falling below the median for a stock is 0.5. Significance

Fig. 1. NAFO 1 Atlantic cod (*a*) recruitment (log scale) versus spawning stock biomass (Ricker model fitted by least squares) and (*b*) recruitment time series (recruitment states model fitted by least squares; the stock occupies one of two states for at least 3 years, each with a different level of mean recruitment and up to two state changes).
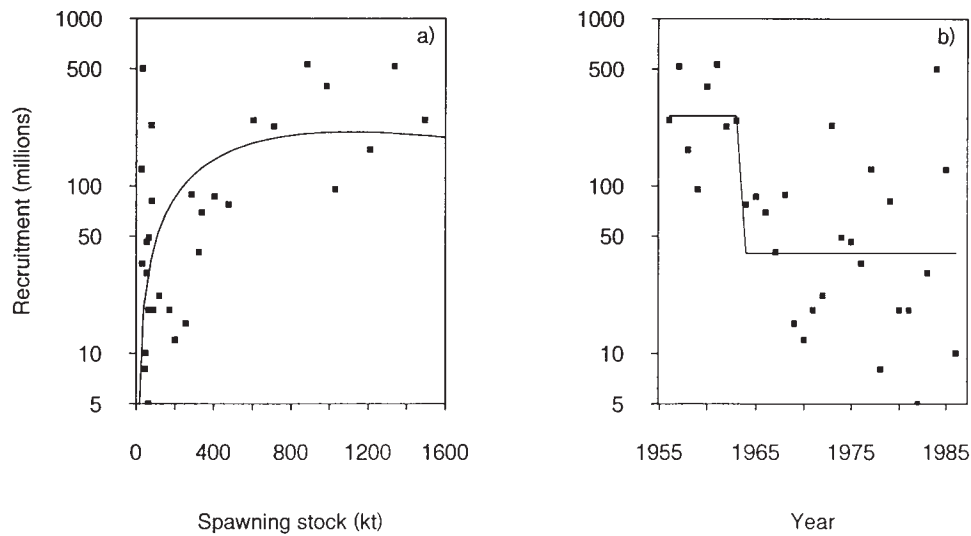

Fig. 2. Fraser River chum salmon (*a*) recruitment (log scale) versus spawning stock biomass (Ricker model fitted by least squares) and (*b*) recruitment time series (recruitment states model fitted by least squares; the stock occupies one of two states for at least 3 years, each with a different level of mean recruitment and up to two state changes).
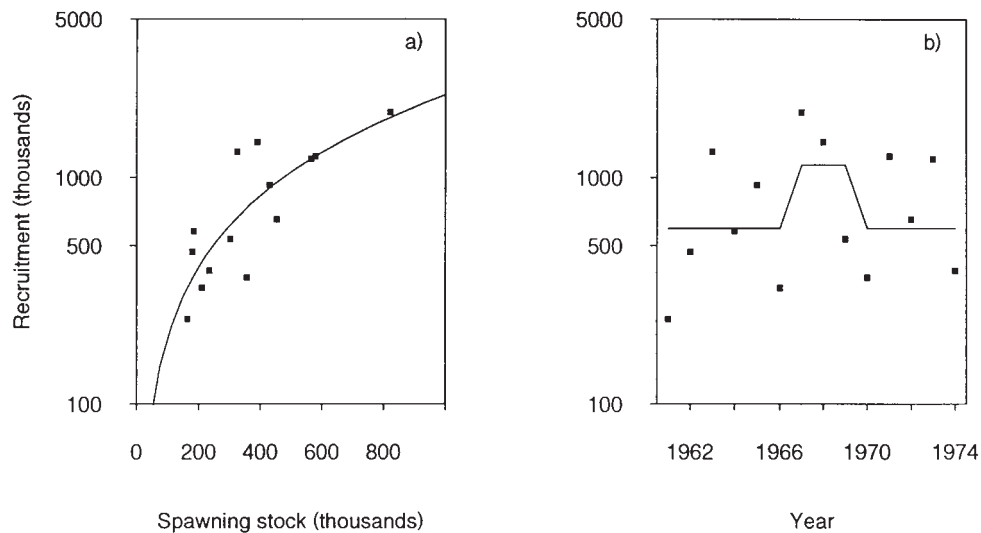

levels were obtained from the binomial distribution to test the null hypothesis against each of the two models (Table 1). For the salmonids, the null hypothesis could be rejected ($p = 0.0004$) against the Ricker model but not against the recruitment states model.

For the marine spawning bony fishes, the null hypothesis could be rejected ($p = 10^{-7}$) against the Ricker model. This is apparently consistent with the nonparametric result of Myers and Barrowman (1996). The null hypothesis could also be rejected against the recruitment states model and with a smaller type I error ($p = 10^{-14}$). Hence, either alternative hypothesis could be generally true or each could be true for a subset of stocks.

Walters (1985) described a time series effect. He showed that if a stock recruitment relationship existed, a model fitted to (SSB, *R*) data as though the observations were independent would tend to underestimate its slope for short time series. The term time series effect applies more generally to describe any situation where the fact that SSB is augmented by recruitment from previous spawnings distorts results obtained under the assumption that SSB and *R* are independent. Under the recruitment states hypothesis there is a time series effect that could produce an apparently positive relationship between SSB and *R*. A period in a low recruitment state would inevitably lead to low SSB, as the weak year-classes entered the spawning stock. A period in a high recruitment state would tend to lead to high SSB. The *R* versus SSB scatterplot could show a positive relationship, especially at low SSB, even though no causative relationship existed. It follows that the rejection of the null hypothesis in favour of the Ricker model by the sum of squares test may be spurious.

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Table 1. The number of stocks for which the sum of squares for the fitted model fell below the bootstrap median sum of squares under the null hypothesis.

Model	Stocks	Number	Number of sums of squares below median	Probability[a]
Ricker	Salmonids	31	25	0.0004
Recruitment states	Salmonids	31	18	0.24
Ricker	Marine spawning bony fishes	153	109	10^{-7}
Recruitment states	Marine spawning bony fishes	153	123	10^{-14}
Ricker	Marine spawning bony fishes (recruitment states sum of squares above its median)	30	14	0.71

[a]Probability of at least the observed number falling below the median under the null hypothesis.

Table 2. The number of stocks for which the median slope, $\Delta R/\Delta SSB$, exceeded zero.

Stocks	Number[a]	Number of median slopes above zero	Probability[b]
Salmonids	31	28	10^{-6}
Marine spawning bony fishes	148	74	0.53
Marine spawning bony fishes (censored for dome-shaped relationships)[c]	142	72	0.47

Note: Stocks whose age at maturity is 1 year have been excluded.

[a]Stocks whose median slope was zero have been excluded

[b]Probability of at least the observed number of slopes exceeding zero under the null hypothesis.

[c]Where the maximum to the fitted Ricker model fell within the range of SSB, only observations of $\Delta R/\Delta SSB$ to the left of this maximum were included.

To address this problem, the sum of squares test was applied only to those stocks for which there was no evidence to support the recruitment states hypothesis. Stocks were excluded when the sum of squares of the fit to the recruitment states model fell below the bootstrap median. This left 30 stocks. When the Ricker model was fitted to these, only 14 sums of squares fell below the median. This was not significant (Table 1). This test on the restricted set of stocks suggests that if the recruitment states hypothesis were true then the rejection of the null hypothesis in favour of the Ricker model for the unrestricted meta-dataset may have been spurious.

Any test that treats the R versus SSB data in a way that ignores this time series effect, whether parametric, such as the above tests and those of Iles (1994), or nonparametric, such as those of Myers and Barrowman (1996), may give misleading results. The problem is therefore to find a test that avoids this effect.

Hypothesis test based on derivatives

I develop a test based on the derivative of R with respect to SSB. If R were a function of SSB of the kind assumed within the stock recruitment paradigm, then its derivative (the slope of the function) would be positive, except perhaps at high SSB. Estimates of the derivative are obtained by taking the ratios of the first differences of the time series, $\Delta R/\Delta SSB$. Under the null hypothesis $\Delta R/\Delta SSB$ would scatter randomly about zero. Under the recruitment states hypothesis $\Delta R/\Delta SSB$ would do likewise with occasional large positive or large negative values at state switches. For each stock, the median of $\Delta R/\Delta SSB$ is the intermediate statistic. Under the null hypothesis the median slope would vary around zero. I count the number of stocks with positive median slopes (Table 2). Two anchovy stocks were excluded because their age at maturity is 1 year (Peruvian

anchoveta, *Engraulis ringens*, and South African anchovy, *Engraulis capensis*). For these stocks the time series effect described by Walters (1985) may cause negatively biased estimates of slope under the paradigm. Three stocks whose median $\Delta R/\Delta SSB$ was zero were also excluded.

For Atlantic cod NAFO 1 the plot of $\Delta R/\Delta SSB$ versus SSB at the midpoint of the values over which ΔSSB was calculated shows slopes scattering around zero, consistent with the null hypothesis (Fig. 3*a*). The Fraser River chum salmon plot shows predominantly positive slopes, consistent with the stock recruitment paradigm (Fig. 3*b*). For the salmonids, the null hypothesis could be rejected ($p = 10^{-6}$). This confirms the result of the sum of squares test.

The null hypothesis could not be rejected for the marine spawning bony fishes (Table 2). This is consistent with the result from the restricted sum of squares test that the rejection of the null hypothesis in favour of the Ricker model for the whole meta-dataset may have been misleading. The time series dependence of SSB on R, and the occurrence of periods of high and low recruitment, could produce the appearance of a relationship between SSB and R where none existed.

The analysis of Myers and Barrowman (1996) may also suffer from this effect. Although their results appear to be robust, they may be making a type IV error: incorrectly interpreting the rejection of a null hypothesis. The fact that they show increasingly strong rejection of the null hypothesis as the range of SSB increases may be explained by the recruitment states hypothesis. For example, if a stock switches from a very high to a very low recruitment state, then the SSB in the later state will be very much lower than in the former. There will appear to be strong evidence for a stock recruitment relationship, whatever statistical method is used. A large range in SSB for a stock makes Myers and Barrowman's tests more powerful, against both the stock recruitment paradigm and the recruitment

Fig. 3. The derivative of recruitment with respect to spawning stock biomass, ΔR/ΔSSB, estimated by dividing the annual change in recruitment by the annual change in spawning stock biomass, versus spawning stock biomass, for (*a*) NAFO 1 Atlantic cod (millions of recruits per thousand tonnes of spawners) and (*b*) Fraser River chum salmon (number of recruits per spawner).
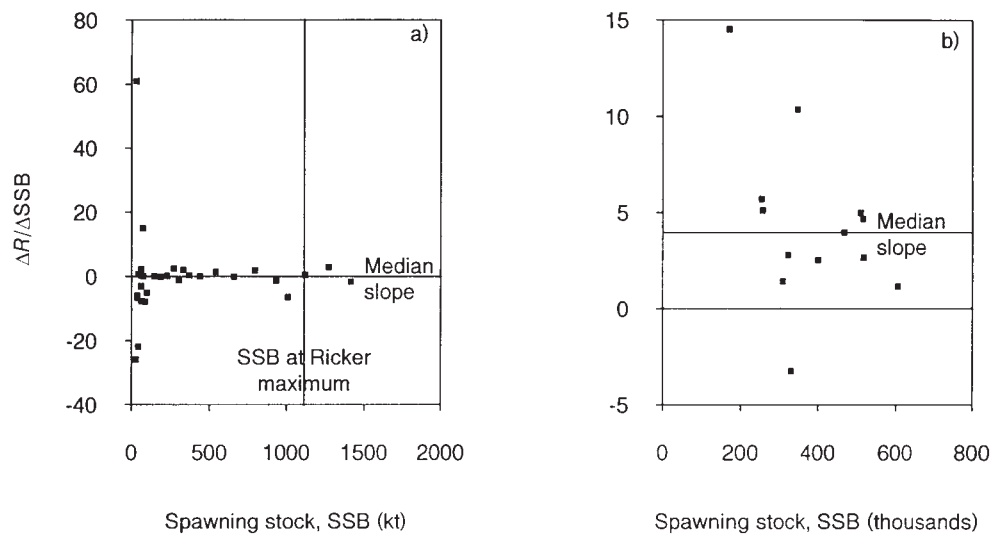
states hypothesis. However, these tests cannot show which hypothesis causes rejection. The derivatives test does distinguish between these two alternatives because it could only reject the null hypothesis against the stock recruitment paradigm.

Under the stock recruitment paradigm, the derivative of R with respect to SSB is positive for low SSB. If a stock had a dome-shaped stock recruitment relationship, and observations occurred on both sides of the dome, $\Delta R/\Delta$SSB would have both positive and negative values. The derivatives test may then falsely fail to reject the null hypothesis. To address this possibility, the test was repeated after censoring the data. For those stocks for which the fitted Ricker model had its maximum within the range of the SSBs, I excluded observations of $\Delta R/\Delta$SSB to the right of the maximum. This did not materially alter the results for the marine spawning bony fishes (Table 2).

The above tests were also carried out on each of four orders of marine spawning bony fishes (those with sufficient data): Pleuronectiformes, Clupeiformes, Gadiformes, and Perciformes. For none was the null hypothesis rejected.

A probabilistic hypothesis

For the marine spawning bony fish stocks, this test failed to reject the null hypothesis against a positively sloped relationship between SSB and R. A further alternative hypothesis, which I will refer to as the probabilistic hypothesis, would not be rejected by the derivatives test. The probabilistic hypothesis proposes that stocks switch between recruitment states stochastically, with the probability of switching from a high to a low recruitment state increasing as SSB declines. This hypothesis is consistent with concepts of risk described by Francis (1993) and is broadly within the stock recruitment paradigm.

To test this hypothesis the recruitment states model was fitted to each stock by sum of squares, as described above. I compared the SSB for the first recruitment after a downwards switch, to the distribution of SSBs in the previous high recruitment state period. The SSB at the switch was expressed as a

sample quantile of the set of high recruitment state SSBs. Only stocks that exhibited downwards switches were included. If the probabilistic hypothesis were true, quantiles below 0.5 (the median) would be expected. In 64 out of 123 instances, the quantile was below 0.5. Assuming a binomial distribution under a random null hypothesis, this result is not significant.

Data quality and power of tests

Recruitment data contain measurement error and process error. Measurement error refers to the difference between the true value and the measured or estimated value. For the present purposes SSB is considered to have only measurement error. Process error is the deviation from a particular postulated model owing to unmodelled effects (i.e., the lack of fit that would remain if there were no measurement error). Environmental effects are often considered to cause process error around a stock recruitment relationship. Process error can generally be assumed to contribute the greater part of the relatively high variances displayed by recruitment time series. However, in stock and recruitment data, measurement error has the potential to be troublesome because it may not be random.

The level of measurement error in the salmonid (SSB, R) data is considerably lower than that in the marine fish data. The former were mostly obtained by fairly reliable counting processes, whereas the latter were mostly obtained by virtual population analyses (VPA) or related methods. VPA essentially sums the estimated numbers of fish from each cohort that are caught in successive years, making adjustment for losses through natural mortality. Error in the estimated numbers of fish caught, ageing, natural mortality, and numbers of residual uncaught fish in cohorts all lead to measurement error in SSB and R. This may be random, systematic (bias), autocorrelated, or with correlated time trends (e.g., Pope 1972; Ulltang 1977; Sims 1982, 1984; Sampson 1988; Hildén 1988; Lapointe et al. 1989; Bradford and Peterman 1989; Bradford 1991; Lapointe et al. 1992).

For the salmonid data, both the sum of squares test and the

derivatives test rejected the null hypothesis in favour of the stock recruitment paradigm and were therefore both powerful enough to overcome the process plus measurement error.

For the marine spawning bony fish data, the sum of squares test rejected the null hypothesis in favour of the recruitment states hypothesis and so was also powerful enough to overcome the process plus measurement error. Spurious trends in R as described by Lapointe et al. (1989) could potentially have caused a false rejection of the null hypothesis. This seems quite unlikely because (*i*) the p value was so low and (*ii*) the ratios of the estimated high state mean recruitment to the low state mean recruitment were typically greater than could be accounted for by the effects described by Lapointe et al. (the lower quartile of this ratio was 1.76).

For the marine spawning bony fish data, the derivatives test failed to reject the null hypothesis. The critical question is whether the test was powerful enough to overcome the process plus measurement error. Systematic error in SSB and R would not reduce the power of the test. The sign of an estimated slope would not be changed by a constant bias in R or in SSB.

Spurious correlated time trends in SSB and R (Lapointe et al. 1989) could potentially increase or decrease the chance of rejecting the null hypothesis. In the hypothetical case where the recruitment to a stock was constant and no other error existed, a spurious correlated trend in R and SSB, caused by VPA estimation error, may cause spurious positive values in $\Delta R/\Delta SSB$, leading to a false rejection. Alternatively, if there was a positive relationship between R and SSB and if the SSB time series followed a monotonic trend, then this could be obscured by an unlucky contrary spurious trend in R and SSB. Obscuring would be much less likely than false positive values of $\Delta R/\Delta SSB$ because it would require an improbable concurrence of size and timing of error and could only occur when SSB was largely monotonic. Failure to reject the null hypothesis because of spurious correlated time trends seems highly unlikely.

The chance of rejecting the null hypothesis by the derivatives test would not be reduced by spurious autocorrelation in R (Bradford 1991). Spurious autocorrelation tends to bring successive R values towards each other. Although this would tend to reduce individual slope estimates, it would not systematically change their signs.

Random error in both SSB and R is likely to be the main problem for the derivatives test. Differencing aggravates the effects of random error. However, process error in R is the main source of error for most stocks. For the set of 31 salmonid stocks, the test was powerful enough to overcome process error (measurement error is small). It seems reasonable to presume that the very much larger dataset of marine spawning bony fish stocks (153 less two 1 year maturity stocks) would have adequate power to reject the null hypothesis if the stock recruitment paradigm were valid. Medians are used to reduce the negative impact of error on the power of the test.

Consider a hypothetical realisation under a null hypothesis model (with random error). The intermediate statistic (median slope for a stock) would vary around zero. Values would tend to be near zero, and on average, half would be above zero. Now consider adding a positively sloped relationship to the model for each stock. Positive quantities would be added at every observation of slope. Hence, the median slope would increase for every stock. Because many median slopes had been near zero, the number that would be increased to exceed zero would readily become significant.

Conclusions

The first of two alternative hypotheses explaining recruitment, the stock recruitment paradigm, is that R is on average determined by SSB and at low levels of SSB is positively related to SSB. The second, the recruitment states hypothesis, is that a stock can occupy one of several distinct states for successive periods and that R varies about a different constant mean in each of these states.

In a meta-analysis of a set of datasets containing marine spawning bony fish and salmonid stocks, the null hypothesis that each year's recruitment was an independent random event was rejected for both categories of species. Two different tests gave results that could be consistently interpreted for both categories of species. For the salmonids, the data significantly supported the stock recruitment paradigm. For the marine spawning bony fishes, the data significantly supported the recruitment states hypothesis. An explanation for this difference probably lies in the substantial differences between the spawning and recruitment processes of the salmonids and the marine spawning bony fishes.

Walters (1985) pointed out that time series effects could bias estimates of relationships between SSB and R when they were treated as independent observations. Here it is shown that other time series effects can cause hypothesis tests on (SSB, R) time series data to be potentially misleading. If there were periods for which mean R was low, for reasons other than low SSB, these would cause low SSB and would produce an apparent relationship between SSB and R. Conclusions that typically R is positively related to SSB (e.g., Myers and Barrowman 1996; Iles 1994) may be subject to this times series effect. A test that was based on estimates of the derivative of R with respect to SSB avoided this time series difficulty. For the marine spawning bony fishes, the null hypothesis could not be rejected by this test. For the salmonids, rejection was highly significant.

An extensive literature exists on how best to manage fisheries to maintain adequate SSB levels so as to ensure good recruitment (e.g., Beddington and Cooke 1983; Gabriel et al. 1989; Anonymous 1990*a*, 1990*b*; Quinn et al. 1990; Clark 1991; Francis 1993; Mace and Sissenwine 1993; Thompson 1993; Myers et al. 1994). Management strategies that apply calculated reference points to constrain annual catch, fishing mortality, spawning stock biomass, or spawning stock biomass per recruit have been discussed as means to achieve this. My results show that these discussions are relevant to salmonids, but not to marine spawning bony fishes. The power of the derivatives test is clearly not adequate to reject the stock recruitment paradigm everywhere. It could be true for a small number of stocks if estimation error is severe or at spawning stock biomasses below most of those observed in the meta-dataset. However, the general result for marine spawning bony fish stocks is that periods of low recruitment appear to be environmentally induced and unavoidable. Managing such stocks is perhaps comparable to managing water in hydroelectric dams. Periods of low recruitment (like periods of drought) may not be able to be averted by prudent management.

Acknowledgement

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Appendix

Fish stocks used in this analysis (from Myers et al. 1995).

Marine spawning bony fish	
American plaice, NAFO 3LNO	Herring, Iceland (spring spawners)
American plaice, NAFO 5YZ	Herring, Iceland (summer spawners)
Northern anchovy, California	Herring, northern Irish Sea
Blue whiting, northern ICES	Herring, Norway (spring spawners)
Blue whiting, southern ICES	Herring, North Sea
Capelin, Iceland	Herring, North Strait of Georgia
Cod, NAFO 1	Herring, northwest coast of Vancouver Island
Cod, NAFO 2J3KL	Herring, Prince Rupert district
Cod, 3M	Herring, Queen Charlotte Islands
Cod, NAFO 3NO	Herring, southern central Baltic
Cod, NAFO 3Pn4RS	Herring, southeast Alaska
Cod, NAFO 3Ps	Herring, southern Strait of Georgia
Cod, NAFO 4TVn	Herring, southwest coast of Vancouver Island
Cod, NAFO 4VsW	Herring, ICES VIa (north)
Cod, NAFO 4X	Herring, ICES VIa (south) and VIIb,c
Cod, NAFO 5Y	Herring, Yellow Sea or Huanghai Sea
Cod, NAFO 5Z	Greater lizardfish, East China Sea
Cod, Baltic areas 22 and 24	Mackerel, NAFO 2 to 6
Cod, Baltic areas 25–32	Horse mackerel, western ICES
Cod, Celtic Sea	Mackerel, western ICES
Cod, Faroe Plateau	Atlantic Menhaden, U.S. Atlantic
Cod, Iceland	Gulf Menhaden, Gulf of Mexico
Cod, Irish Sea	Norway pout, North Sea
Cod, Kattegat	Peruvian anchoveta, northern–central stock Peru
Cod, northeast Arctic	Pacific cod, eastern Bering Sea
Cod, North Sea	Pacific cod, Hecate Strait
Cod, Skaggerak	Pacific halibut, Pacific
Cod, ICES VIId	Plaice, ICES VIId
Cod, ICES VIIa	Plaice, ICES VIIe
Greenland halibut, northeast Arctic	Plaice, Celtic Sea
Greenland halibut, ICES V and XIV	Plaice, Irish Sea
Grey mullet, Taiwan	Plaice, Kattegat
Haddock, NAFO 4TVW	Plaice, North Sea
Haddock, NAFO 4X	Plaice, Skagerrak
Haddock, NAFO 5Z	Pacific mackerel, southern California
Haddock, Faroe Plateau	Pollock or saithe, NAFO 4VWX5
Haddock, Iceland	Pollock or saithe, Faroe
Haddock, northeast Arctic	Pollock or saithe, Iceland
Haddock, North Sea	Pollock or saithe, northeast Arctic
Haddock, VIa	Pollock or saithe, North Sea
Common hake, Chile: females in northern zone	Pollock or saithe, ICES VI
Hake, ICES IVa,VIa,VII,VIIIa, and VIIIb	Redfish, ICES V and XIV
Peruvian hake, Peru	Redfish, Iceland
Pacific hake, western U.S. + Canada	Redfish, northeast Arctic
Hake, ICES VIIIc and IXa	Redhake, NAFO Gulf of Maine, northern Georges Bank
Common hake, Chile: south-central zone	Red hake, NAFO southern New England
Herring, Baltic areas 22 and 24	Rock sole, Pacific
Herring, Baltic areas 25–29, 32 plus Gulf of Riga	Anchovy, South Africa
Herring, Baltic area 30	S.A. Hake, South Africa 1.6
Herring, NAFO 4-5	A. Hake, South Africa South Coast
Herring, NAFO 4R (fall spawners)	Cape horse mackerel, South Africa 1.3–1.5
Herring, NAFO 4R (spring spawners)	Southern African pilchard, South Africa
Herring, NAFO 4T (fall spawners)	Southern African pilchard (N), South Africa
Herring, NAFO 4WX	Pacific sardine, California
Herring, Bothnian Bay	Japanese sardine, Japan-E.
Herring, central coast of B.C.	Spanish sardine, Chile: north zone
Herring, Downs stock	Spanish sardine, ICES VIIIc–IXa
Herring, eastern Bering Sea	Yellow sea bream, East China Sea
Herring, Georges Bank	Sandeel, northern North Sea
Herring, Gulf of Finland	Sandeel, Shetland
Herring, Gulf of Maine	Sandeel, southern North Sea
Herring, Gulf of Riga	Sandeel, ICES VIa

Appendix (*concluded*).

Summer founder, Middle Atlantic Bight	Whiting, Celtic Sea
Yellowtail flounder, southern New England	Whiting, Irish Sea
Silver hake, NAFO 5Ze	Whiting, North Sea
Silver hake, Mid Atlantic Bight	Whiting, ICES VIId
Silk Snapper, zone B: Cuba	Whiting, ICES VIa
Sole, Celtic Sea	Walleye pollock, eastern Bering Sea
Sole, Irish Sea	Walleye pollock, Gulf of Alaska
Sole, North Sea	Walleye pollock, Japan: Pacific coast of Hokkaido
Sole, ICES VIII	Walleye pollock, East Kamchatka
Sole, ICES VIId	Walleye pollock, west Bering Sea
Sole, ICES VIIe	Widow rockfish, western U.S. <$E +> Canada
Sprat, Baltic areas 22–32	Yellowtail flounder, NAFO 3LNO
False trevally, Gulf of Thailand	Yellowtail flounder, NAFO 5Z
White hake, NAFO 4T	Yellowfin sole, eastern Bering Sea

Salmonid stocks

Chinook salmon, wild Canadian coastwide	Sockeye salmon, Bristol Bay, Alaska
Chum salmon, central Alaska	Sockeye salmon, Chilko River, B.C.
Chum salmon, central coast, B.C.	Sockeye salmon, Columbia River, Washington
Chum salmon, Fraser River, B.C.	Sockeye salmon, Egegik, Alaska
Chum salmon, Hooknose Creek, B.C.	Sockeye salmon, Horsefly River, B.C.
Chum salmon, Johnstone Strait	Sockeye salmon, Karluk River, Alaska
Chum salmon, north coast, B.C.	Sockeye salmon, Kvichak River, Alaska
Chum salmon, Queen Charlotte Islands, B.C.	Sockeye salmon, Naknek–Kvichak, Alaska
Chum salmon, West Coast Vancouver Island, B.C.	Sockeye salmon, Nushagak, Alaska
Chum salmon, Minter Creek, Washington	Sockeye salmon, Pinkut Creek, B.C.
Pink salmon, Sashin Creek, Little Port Walter, Alaska	Sockeye salmon, Rivers Inlet, B.C.
Pink salmon, Prince William Sound, Alaska	Sockeye salmon, Skeena River, B.C.
Pink salmon, central B.C.	Sockeye salmon, Stellako River, B.C., Canada
Pink salmon, Hooknose Creek, B.C.	Sockeye salmon, early Stuart complex, B.C.
Sockeye salmon, Adams complex, B.C.	Sockeye salmon, Ugashik, Alaska
Sockeye salmon, Birkenhead River, B.C.	