

## Using Lifetime Fecundity to Compare Management Strategies: A Case History for Striped Bass

MICHAEL H. PRAGER<sup>1</sup>

National Marine Fisheries Service Southwest Fisheries Center, Post Office Box 271  
La Jolla, California 92038, USA

JOHN F. O'BRIEN

Division of Fish and Wildlife, Rhode Island Department of Environmental Management  
West Kingston, Rhode Island 02892, USA

SAUL B. SAILA

Division of Marine Resources, Graduate School of Oceanography, University of Rhode Island  
Narragansett, Rhode Island 02882, USA

*Abstract.*—To evaluate possible regulatory schemes for restoring the stocks of striped bass *Morone saxatilis* in Rhode Island coastal waters, we constructed a computer simulation model of a cohort's expected lifetime egg production. The model demonstrated that the expected increase in egg production from a proposed increase in minimum legal harvestable size (from 17 to 24 in) also could be achieved by an alternate management regime which, unlike the proposed size increase, would allow continued use of traditional fishing gears. The alternative regime increased the minimum size (but only to 18 in) and simultaneously reduced instantaneous fishing mortality from 0.45 to 0.30. Our findings of equivalence between the two regimes are reasonably robust to errors in population parameters. We then used the simulation model to generate curves of egg production per female recruit under a wide range of regulatory regimes. Such curves can illustrate the potential effects of management measures on depleted stocks.

The decline in the fishery for striped bass *Morone saxatilis* along the Atlantic coast of the United States is a matter of public record. The coastal states have attempted to reverse the decline with various intrastate and interstate management measures. In 1981, the Atlantic States Marine Fisheries Commission (ASMFC) recommended a 24-in total length (TL) minimum size for striped bass caught in coastal areas. The existing size limit in Rhode Island was 16 in fork length (FL), equivalent to about 17 in TL. The possibility of a 24-in limit, however beneficial it might prove to the stocks, raised a difficult fishery management problem in Rhode Island: about 80% of the state's commercial catch for 1981–1983 was taken in the gill- and trap-net fisheries, whose catches are almost all of fish less than 24 in long. The imposition of a 24-in limit would have virtually eliminated these traditional fisheries while allowing others to continue taking striped bass (Boreman 1982). This proposal was considered neither fair nor politically acceptable as a management procedure.

The course of action adopted by the Rhode Is-

land Department of Environmental Management (DEM) was to propose regulations that were considered equivalent to the 24-in limit in restoration potential, but which would allow the continuing participation of the traditional net fisheries on a limited scale. This was accomplished by specifying only a modest increase in minimum size (to 18 in rather than 24 in TL), but simultaneously specifying a reduction in instantaneous fishing mortality ( $F$ ). The reduction was to be achieved through additional closed seasons, gear restrictions, and area closures. We devised an egg production model for comparing these management regimes and used the model to generate expected egg production curves for a wide range of regulatory conditions. This report illustrates, by example, the production of such curves, which form an additional tool for managing depleted stocks.

A prior version of this manuscript was released as Technical Report 84-6 of the University of Rhode Island Graduate School of Oceanography and Technical Report 84-17 of the Oceanography Department of Old Dominion University.

### Description of the Model

As stock replenishment is currently a major goal of Atlantic coast striped bass management, the

<sup>1</sup> Permanent address: Oceanography Department, Old Dominion University, Norfolk, Virginia 23529, USA.

model uses the lifetime egg production of a cohort to compare the effects of different management schemes. We presumed that increased egg production will lead to an increase in stock size. The variables assumed to be subject to management control are the instantaneous fishing mortality  $F$  and the age (years) at first capture  $t_c$ . Although  $t_c$  is not controlled directly, regulating  $l_c$  (the minimum legal size) effectively controls  $t_c$ .

In describing the model, we start with the final formulation. Let  $E$  represent the number of eggs produced by a cohort during its lifetime. For our purposes, we can approximate  $E$  by the formula

$$E = \sum_{t=t_r}^{t_\infty} N_t k_t; \quad (1)$$

$t$  is age, which ranges from  $t_r$  (an age below that of first reproduction) to  $t_\infty$  (an age greater than the maximum age in the population);  $N_t$  is the female population size at age  $t$ ; and  $k_t$  is the mean fecundity at age  $t$  adjusted for the proportion of females that are mature. To obtain  $N_t$  in equation (1), we assume the exponential mortality function

$$N_t = N_{(t-1)} \exp(-Z_t); \quad (2)$$

$Z_t$  is the instantaneous rate of total mortality and  $N_t$  is initialized to an arbitrary  $N_r$  at  $t = t_r$ . Further, we use the customary form that

$$Z_t = F_t + M; \quad (3)$$

i.e.,  $Z$  is composed of age-specific fishing mortality  $F_t$  and age-invariant natural mortality  $M$ .

We determined  $F_t$  in equation (3) as follows. Let  $F$  be the fishing mortality allowed through the fishing regulations and  $l_t$  the length at age  $t$ . Then

$$F_t = 0, \quad \text{if } l_t \leq l_c; \quad (4a)$$

$$F_t = F(l_t - l_c) / [l_t - l_{(t-1)}], \quad \text{if } l_{(t-1)} < l_c < l_t; \quad (4b)$$

$$F_t = F, \quad \text{if } l_{(t-1)} \geq l_c. \quad (4c)$$

That is, the fishing mortality is interpolated linearly during the year in which the cohort becomes vulnerable. This is, in effect, knife-edge recruitment beginning at an interpolated age.

The model also requires an age-length relationship because  $k$  and  $F$ , although expressed in terms of age in equations (1), (3), and (4), are known in terms of length. Growth is assumed to follow the von Bertalanffy growth function

$$l_t = L_\infty \{1 - \exp[-K(t - t_0)]\}; \quad (5)$$

$L_\infty$  is the asymptotic length;  $K$  is a growth coefficient;  $t_0$  is age at zero length.

The fecundity at age  $k_t$  is derived from a length-fecundity relationship

$$k_t = g(l_t); \quad (6)$$

$g$  is an appropriate length-fecundity model. In our application,  $g$  was a polynomial fecundity model for striped bass, as described below in equation (7).

Given parameters for equations (2) through (6), we can calculate the cohort fecundity  $E$  for any combination of  $F$  and  $t_c$ .

#### Use of the Model: Case History

The model was used first to calculate the cohort fecundity  $E_1$  under a baseline management regime of the existing  $F$  and the proposed  $l_c$  (regime 1). Next, the  $l_c$  of an alternative management scheme was substituted into the model in order to calculate the resulting cohort fecundity  $E_2$ . Finally,  $F$  was systematically decremented until a combination of  $l_c$  and  $F$  was obtained that gave  $E_2 \geq E_1$ . This combination we called regime 2.

Before applying the model, certain parameters and relationships were specified. About half the Rhode Island striped bass harvest is taken from the Chesapeake Bay stock and half from the Hudson River stock (Saila et al. 1983); however, published parameter estimates were not usually available for each stock. Therefore, we used the following values and equations.

(a) Growth parameters were those of O'Brien and Sisson (1982), determined from samples of the Rhode Island commercial landings. The values used were  $K = 0.102/\text{year}$ ,  $L_\infty = 149.2 \text{ cm}$ , and  $t_0 = 0.232 \text{ year}$ .

(b) We used the length-fecundity relationship of Goodyear (1984):

$$k_t = 941.2 + 569.3T + 68.5T^2; \quad (7a)$$

$$T = 0.00856l_t - 6.008. \quad (7b)$$

Here,  $l_t$  is fork length in millimeters, and  $k_t$  is measured in thousands of eggs. This equation, which incorporates a correction for the proportion of fish that are mature at length, is based on observations of Chesapeake Bay fish. We were unable to locate fecundity information for the Hudson River stock.

(c) Values for  $t_r$  and  $t_\infty$  were set at 3 years and 25 years, respectively;  $N_r$  was initialized at 10,000 fish. Because the model was used to compare various management schemes (rather than to com-

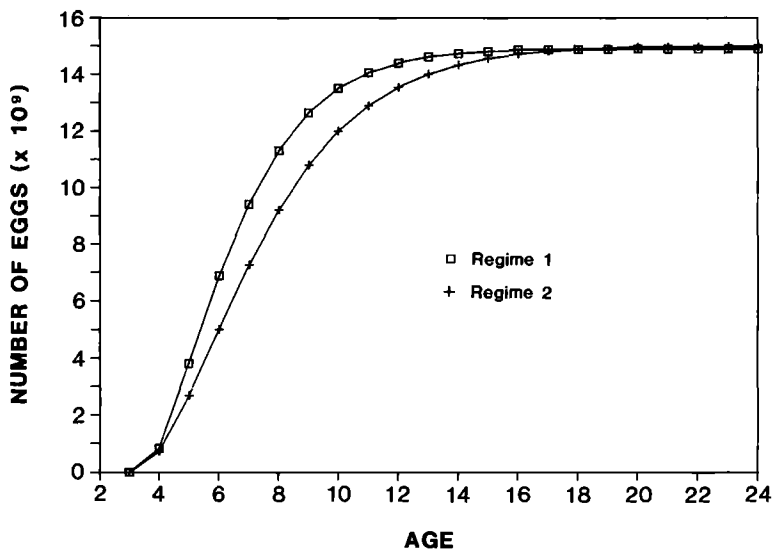


FIGURE 1.—Cumulative cohort fecundity of striped bass at various ages (years) under two management regimes. Regime 1:  $F$  (fishing mortality) = 0.45;  $l_c$  (minimum legal length) = 24 in total length. Regime 2:  $F$  = 0.30,  $l_c$  = 18 in.

pute absolute fecundities of cohorts), it was possible to initialize  $N$ , arbitrarily without disturbing the validity of the outcome.

(d) We set  $M$  to 0.15/year, following Kohlenstein (1980). This value originally was reported from tagging studies in California (Chadwick 1968), and it is used because no reliable value for either Atlantic coast stock could be located. We set  $F$  to 0.45/year, a midrange value from the estimates of Boreman (1982), and decremented it by 0.05/year per iteration.

(e) We set  $l_c$  for regime 1 at 22.5 in FL, equivalent to the recommended (24 in TL) size limit.

### Results

Under regime 1 (with the recommended 24-in TL size limit and  $F$  = 0.45), the calculated cohort egg production  $E_1$  was  $1.5 \times 10^{10}$  eggs. We then decreased  $L_c$  to 18 in TL (equivalent to 16.8 in FL), which had been identified by DEM as a socially preferable alternative to the ASMFC recommendation. The model indicated a 46% drop in cohort egg production:  $E_2 = 8.1 \times 10^9$  eggs. Upon decreasing  $F$ , the simulated egg production recovered; the total egg production  $E_2$  of  $1.5 \times 10^{10}$  eggs was achieved again at an  $F$  of 0.30 (Figure 1, regime 2).

### Sensitivity Analysis

We analyzed the robustness of our results to errors in the population parameters  $M$ ,  $t_0$ ,  $K$ ,  $L_\infty$ ,

and  $F$ . For this analysis, we defined the quantity  $D = 100(E_2 - E_1)/E_1$ . That is,  $D$  is the change (in percent) between egg production under regime 1 and that under regime 2. For the original parameter values described above,  $D = 0.55\%$ , which is not significant.

We systematically varied each parameter, increasing and decreasing it by 1, 10, and 25% in turn. To examine the effects of error in  $F$ , we varied  $F$  for regime 1 and assumed that  $F$  for regime 2 was a constant percentage (67%) of that for regime 1. The results for each trial are listed in Table 1. These results indicated that the methodology is robust to errors in  $M$  (largest  $|D|$  = 4.8%), reasonably robust to errors in  $F_1$  (largest  $|D|$  = 15.8%), reasonably robust to errors in  $K$  (largest  $|D|$  = 9.3%), not very robust to errors in  $L_\infty$  (largest  $|D|$  = 27.3%), and extremely robust to errors in  $t_0$  (largest  $|D|$  = 0.6%).

### Discussion

The Department of Environmental Management had planned to propose a decrease of 0.15 in  $F$  along with its revised minimum size. The lifetime fecundity model, by suggesting the same decrease in  $F$ , provided an objective basis for DEM's proposal in the context of interstate management of striped bass.

The major assumptions of the lifetime fecundity model are (a) constant  $M$  over the period  $t, \leq t \leq t_\infty$ ; (b) knife-edge gear selection with subsequent

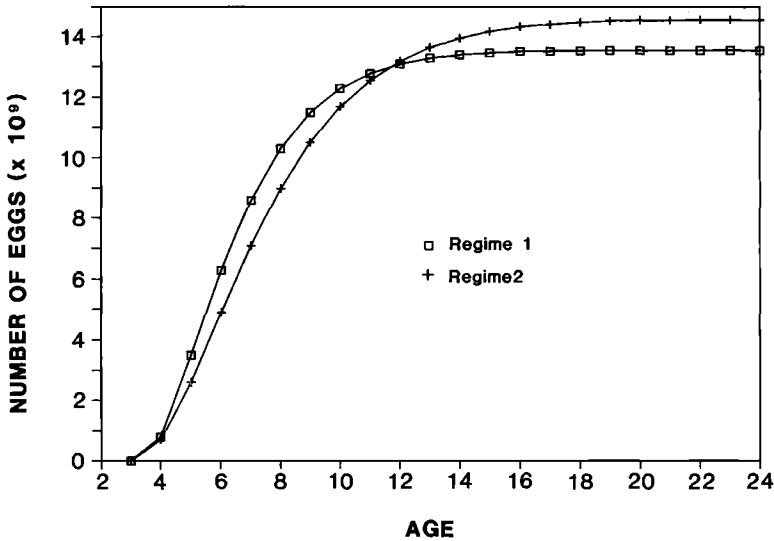


FIGURE 2.—Cumulative cohort fecundity of striped bass at various ages (years) with added instantaneous handling mortality of 0.05/year for undersized fish. Management regimes are as in Figure 1.

constant  $F$ ; (c) growth according to the von Bertalanffy growth function with parameters as cited; (d) a closed population (no immigration or emigration); and (e) length-specific fecundity, following equations (7a) and (7b).

Violation of any of these assumptions would have minor consequences, in part because the assumptions are applied to each management regime. However, if  $M$  (for example) were to vary with changes in  $F$  or  $l_c$ , the model would not yield an accurate comparison of regimes unless the variation in  $M$  were taken into account. One such case follows.

An assumption made implicitly by equations

TABLE 1.—Sensitivity analysis showing change in striped bass egg production (%) from regime 1 to regime 2 with changed population parameters.

| Percent change in parameter | Parameter <sup>a</sup> |       |            |        |       |
|-----------------------------|------------------------|-------|------------|--------|-------|
|                             | $M$                    | $F_1$ | $L_\infty$ | $K$    | $t_0$ |
| None                        | 0.55                   | 0.55  | 0.55       | 0.55   | 0.55  |
| 1                           | 0.18                   | 0.05  | 1.28       | 0.94   | 0.54  |
| -1                          | 0.72                   | 0.85  | -0.31      | -0.12  | 0.58  |
| 10                          | -1.11                  | -3.3  | 9.09       | 5.74   | 0.52  |
| -10                         | 1.95                   | 4.20  | -9.42      | -5.02  | 0.25  |
| 25                          | -3.07                  | -8.95 | 27.09      | 15.76  | 0.64  |
| -25                         | 4.77                   | 9.28  | -27.29     | -14.68 | 0.44  |

<sup>a</sup>  $M$  is natural mortality;  $F_1$  is fishing mortality under regime 1;  $L_\infty$  is asymptotic length;  $K$  is the Brady growth coefficient;  $t_0$  is age at zero length.

(4a–4c) is that handling mortality in landing and releasing undersized fish is negligible. However, handling mortality is expected with any gear, although its magnitude is difficult to determine. Chadwick (1968) found that fishing mortality was correlated with natural mortality in a California striped bass population; he inferred the presence of handling mortality. Because fish above the legal size are no longer subject to handling mortality, regime 2 (with lower  $t_c$ ) allows less mortality in excess of that modeled; thus, its modeled egg production is likely to be more accurate. By contrast, the egg production of regime 1 may be somewhat overestimated. To quantify this phenomenon, we simulated another cohort to which we applied an instantaneous handling mortality of 0.05/year for  $t \leq t_c$ . The cohort under regime 2 produced about  $1.45 \times 10^{10}$  eggs; under regime 1, it produced about  $1.35 \times 10^{10}$  eggs (about 7% fewer) (Figure 2).

An underlying assumption in the application of a lifetime cohort fecundity model is that the cumulative egg production  $E$  is a good measure of a cohort's reproductive contribution. While useful, it is not a complete measure as it omits the age structure of the reproduction, which may affect the population in several ways. First, the reproduction under regime 1 is concentrated at earlier ages than under regime 2 (Figure 3), which theoretically would lead to faster growth of the population under regime 1 (Cole 1954). A quantifi-

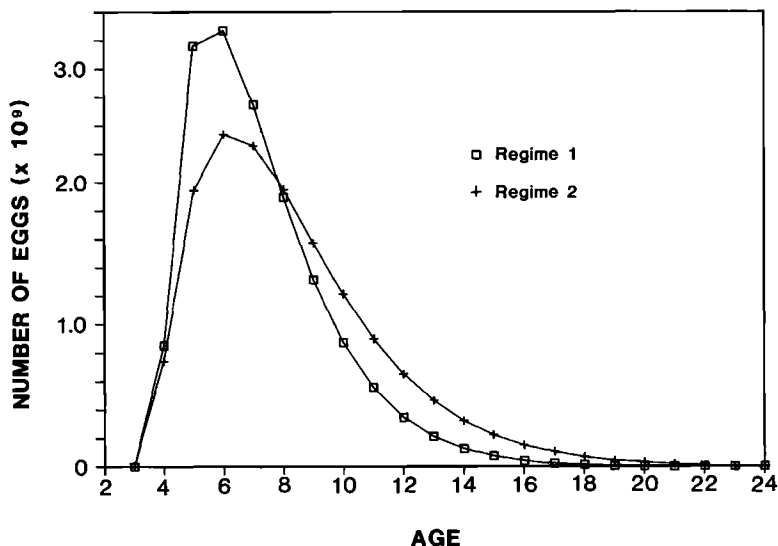


FIGURE 3.—Age-specific (years) cohort fecundity of striped bass under the same two management regimes as in Figures 1 and 2.

cation of this effect would require an estimate of the survival from the egg stage (which varies widely). On the other hand, any increase in viability of eggs spawned by older females would act in the opposite direction. Moreover, the reproduction of a cohort under regime 2 is more evenly distributed among age-classes. Such an age structure could increase stability in recruitment; for example, if spawning were over a longer season, larvae would be less vulnerable to environmental extremes. A broader age structure in the population also should allow the fishery to better cope with a series of poor year classes.

Two common criteria used in managing fish stocks are yield per recruit (YPR) and optimum yield (OY) or other variants of maximum sustainable yield (MSY). In managing severely depleted stocks (as the Chesapeake Bay stock of striped bass seems to be), these models are insufficient. Most parameterizations of the MSY-derived models assume equilibrium conditions, which are neither realistic nor desirable in managing depleted stocks. The concept of OY, however (as presented in Roedel 1975), seems accommodating enough to encompass almost any management methods or objectives.

Yield-per-recruit analysis does not place recruitment within its set of manageable parameters, nor does it attempt to maintain a minimum stock size in order to prevent recruitment overfishing. (However, eumetric fishing regimes generally yield

a relatively high stock size.) The sole criterion used is maximum harvest of biomass from each cohort. This is not a sufficient objective if stock replenishment is necessary.

When managing a stock thought to be in a state of recruitment overfishing, therefore, a resource manager needs information in addition to that provided by MSY or YPR analyses. We suggest that the estimated egg production of a cohort can provide such useful information. When egg production is divided by the initial cohort number, we can express the resultant quantity as "eggs per recruit" (EPR):

$$EPR = E/N_r \quad (8)$$

This formulation removes the effect of the initial number  $N_r$  from the results. It must be realized that EPR cannot be maximized as can yield per recruit; EPR is a monotonically increasing function of stock size and weight. Calculation of EPR can give a more complete picture of the expected effects of various combinations of  $F$  and  $t_c$ . It provides an additional rational basis for management of any fish stock regulated by  $F$  and  $t_c$ . This point is illustrated in Figure 4, a series of EPR curves for striped bass under a range of  $F$  and  $t_c$  regimes.

Eggs-per-recruit curves such as these show the expected long-term results of a policy. For quantification of short-term results (before the age distribution has stabilized), a Leslie matrix model using the fecundity relationships cited here might

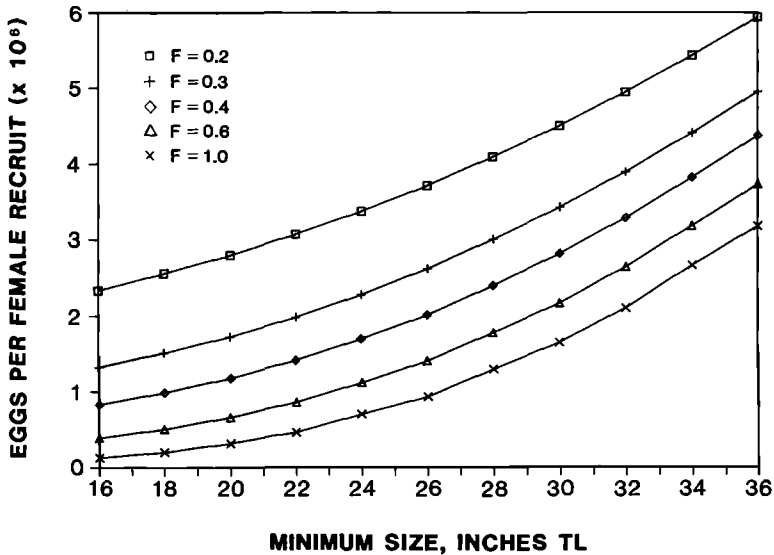


FIGURE 4.—Eggs-per-female-recruit curves for striped bass under a range of possible fishing regulations. TL is total length;  $F$  is instantaneous fishing mortality.

be an appropriate tool. Such an analysis would be most important in the case of an existing population with a preponderance of larger fish.

A peripheral aspect of EPR computation is that it does not depend on determination of the stock-recruitment function. For a depleted stock, all recognized curves will be in a region of significant positive slope. The logical conclusion is that increased egg production will lead to a higher expected value of recruitment. The manager may not be able to observe higher recruitment in any given case because of the confounding influences of environmental variability and imperfect knowledge of spawning stock size and fecundity (Kohlenstein 1980; Walters and Ludwig 1981; Goodyear and Christensen 1984). The imperfection of our knowledge, however, should never stop us from taking the most rational actions possible. The concept of EPR is suggested as an additional useful tool in this effort.

#### Acknowledgments

John Boreman started us thinking about this problem by suggesting egg production as an appropriate quantity to examine. The manuscript was read and improvements were suggested by John Hoinig, John McConaugha, Louis Rugolo, and three anonymous reviewers. Any remaining errors are the authors'. The University of Rhode Island, Old Dominion University, and the Southwest Fisheries Center provided technical support.

#### References

- Boreman, J. 1982. Potential impact of the state/federal recommendations for striped bass management on the commercial fisheries in Rhode Island. National Marine Fisheries Service, Northeast Fisheries Center, Laboratory Reference Document 82-05, Woods Hole, Massachusetts.
- Chadwick, H. K. 1968. Mortality rates in the California striped bass population. *California Fish and Game* 54:228-246.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103-137.
- Goodyear, C. P. 1984. Analysis of potential yield per recruit for striped bass produced in Chesapeake Bay. *North American Journal of Fisheries Management* 4:488-496.
- Goodyear, C. P., and S. W. Christensen. 1984. On the ability to detect the influence of spawning stock on recruitment. *North American Journal of Fisheries Management* 4:186-193.
- Kohlenstein, L. C. 1980. Aspects of the population dynamics of striped bass (*Morone saxatilis*) spawning in Maryland tributaries of Chesapeake Bay. Doctoral dissertation. Johns Hopkins University, Baltimore, Maryland. (Johns Hopkins Applied Physics Laboratory, Publication JHU PPSE T-14.)
- O'Brien, J. F., and R. T. Sisson. 1982. Striped bass stock assessment in Rhode Island waters. A summary of the 1981 sampling season. Rhode Island Department of Environmental Management, Division of Fish and Wildlife, Annual Progress Report AFC-4-1, West Kingston.
- Roedel, P. M., editor. 1975. Optimum sustainable yield

- as a concept in fisheries management. American Fisheries Society Special Publication 9.
- Saila, S. B., M. C. Fabrizio, M. H. Prager, and C. E. Button. 1983. Discrimination of stocks of striped bass, *Morone saxatilis*, with special reference to the Rhode Island trap fishery. Final report to Rhode Island Department of Environmental Management, West Kingston.
- Walters, C. J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Canadian Journal of Fisheries and Aquatic Sciences 6:704-710.