The Meta-analysis of the Maximum Reproductive Rate for Fish Populations to Estimate Harvest Policy; Why the Estimates Used for the Salem Submission are not Positively Biased

Ransom A. Myers¹ Killam Memorial Chair in Ocean Studies Department of Biology Dalhousie University Halifax, Nova Scotia Canada B3H 4J1

> Ray Hilborn School of Fisheries University of Washington P.O. Box 357980 Seattle, WA 98195 U.S.A.

¹email - Ransom.Myers@@Dal.Ca; telephone 1-902-494-1755

Contents

1	Summary						
2	Introduction						
3	ESSA's Four Concerns3.1Errors in Estimate of Spawner Abundance3.2Inherent difficulties in the interpretation of spawner recruit data3.3Time series bias3.4Lack of similarity with the RIS species	5 5 6 6					
4	Recent Independent Analyses Demonstrate that the Meta-analytic Estimates of Compensation Were Conservative4.1Striped Bass4.2Weakfish	7 7					
5	 A Conservative Model was used to Access Power Plant Impact 5.1 Our Estimates of the Beverton-Holt Compensation Parameter are Conservative	8 8					
6	We carried out the estimates for the distribution of steepness by 3 different methods, and chose the approach that gave the most conservative estimates						
7	We eliminated the largest outliers in the analysis, even though it was a reliable estimate	11					
8	The data often includes plant power plant mortality already, because this was not corrected for, the estimates used are conservative	11					
9	The results were verified when possible by comparing the estimates to those obtained from field experiments	11					
10	The results were verified when possible by an extensive analysis of research survey data	11					
11	Many of the estimates suffer from none of the doubts raised by ESSA	12					
12	Summary	12					

- 14 APPENDIX 2: The Ricker Model and Beverton-Holt Models generally fit the data equally well, but the Ricker Model Givens Much More
Conservative Estimates1814.1 The Beverton-Holt and the Ricker Models fit the data equally well18
- 15 APPENDIX 3: Evidence for Compensatory Mechanisms In Fish Populations 23

1 Summary

This report summarizes results and methods of estimating the variability in the reproductive parameters, in particular the maximum reproductive rate (sometimes called the compensation reserve), for a number of fish species from a meta-analytic perspective.

We summarize that variability in the maximum reproductive rate as the distribution of "steepness" of the spawner recruitment relationship, which provides information on the average rate at which spawning fish can produce replacement spawners at low population sizes if no anthropogenic mortality occurred. To ensure that the statistical methods are as robust as possible, we have pursued parallel model development using different biological and statistical models, and independent computational approaches. The goal is to provide accurate estimates of the maximum reproductive rate that are robust to reasonable variation in biological and statistical assumptions.

2 Introduction

ESSA's objections to the estimates of compensation are wrong, and totally inconsistent with ESSA's own use of such analyses in similar situations. The ESSA report completely ignores extensive efforts to ensure that compensation was not overestimated The extensive analysis used to support the estimates of compensation represents an extensive research that has relieved on the most extensive collection of observational data, experimental data, simulation results, and development of statistical methods that has ever been undertaken for this type of problem. This research has been published in the peer reviewed scientific literature. These steps were necessary because there are statistical processes that may cause the estimated of compensation to be overestimated, as we were very well aware of (Walters 1985; Walters 1990; Myers and Barrowman 1995).

Extraordinary steps were taken to ensure that the estimates of steepness used in the Salem impact assessment are not positively biased. These steps were:

- A conservative model was used in the analysis which always resulted in reduced recruitment in the power plant killed any fish or eggs.
- The model chosen to estimate the parameters of the model produced more conservative estimates, i.e. lower steepness, than the alternatives. This was a key method used to ensure that we did not overestimate compensation in the analysis.
- We carried out the estimates for the distribution of steepness by 3 different methods, and chose the approach that gave the most conservative estimates.
- We eliminated the largest outliers in the analysis, even though it was a reliable estimate. This reduced the estimate of steepness for the bay anchovy by approximately 20%.
- The data often includes plant power plant mortality already (examples of striped bass, shad, alewife, blueback herring, and weakfish).
- The results were verified when possible by comparing the estimates to those obtained from field experiments.
- The results were verified when possible by an extensive analysis of research survey data, in which the potential problems of spawner recruitment data do not occur (Myers and Cadigan 1993a; Myers and Cadigan 1993b) (This is covered in Appendix I of the submission).
- Results from some of the stocks were for the same species as the RIS, and were the subject of experiments. In these cases none of the objections raised by ESSA is even remotely relevant.

Our results have now all been reviewed and published (or accepted to be published) in the peer reviewed scientific literature.

3 ESSA's Four Concerns

3.1 Errors in Estimate of Spawner Abundance

ESSA contends that errors in the estimate of spawner biomass will cause serious overestimation of the compensatory reserve. However, (1) they provide no quantiative estimates of this claim, (2) use an examples that are irrelevant, and (3) ignore this potential problem in their own work.

Here we examine these three points, and provide quantitative estimates of the extent of this type of bias.

First, we provide background on this issue. In fitting a regression line using ordinary least squares, the standard assumption is that the independent variable, in this case spawner abundance, is measured without error. The independent variable, in this case recruitment (or in fact the log(R/S)),

Remarkably, ESSA discusses what they view as a potential problem in terms of the Cushing spawner-recruit function, which is essentially a power function. This function was not used at any point in the Salem permit application because it assumes there is infinite compensatory reserve. Since this model was not used in the permit application any discussion of possible bias in a model that was not used is, at best, irrelevalent.

ESSA

3.2 Inherent difficulties in the interpretation of spawner recruit data

ESSA claims that spawner recruitment data cannot be used (although this concern does not apparently apply to their own work, e.g. the Columbia River modeling). These concerns were throughly addressed in the submission. We review them here.

First, we did not rely only upon estimates from spawner recruitment data. In Appendix I, we throughly reviewed many types of data that verified generally our estimates. These include extensive analysis of research survey data, field experiments, and other types of data. In fact, a variety of methods have been used to study and verify compensation mechanisms, these are reviewed in APPENDIX 3 of this report.

One objection that ESSA has is that there may be changes in carrying capacity; however, this does not mean that the steepness cannot be estimated, because they are two separate parameters.

On page 144 of the ESSA report, it is claimed that there are large distortions in the estimates of compensation used. However, ESSA apparently did not read appaerntly read or understand the figure that they use as a basis for their claim. The figure in question showed two things: (1) that estimates of compensation from the Ricker model is always less than those obtained by using the Beverton Holt model and (2) the estimates obtained from the Beverton Holt model can be "ill behaved". This is exactly why the Ricker model was used in the estimates. ESSA's apparently critisies the permit application for using a technique that was not used.

3.3 Time series bias

The basis of ESSA's claim that we overestimated steppeness is the phenomenon of "time-series" bias. This issue was dealt with throughly in the submission, because we had previously carried out the most detailed study of the phenomenon ever carried out Myers and Barrowman (1995).

Unfortunately, it is difficult to correct for time-series bias in practice. Although there are methods to correct for this bias for a very limited number of cases, i.e. for the Ricker model where animals die after reproduction (Walters 1990), simulations have shown that these do not work well in practice (Korman, Peterman, and Walters 1995). This is why we used the approaches described above which produced negatively biased estimates.

In the appendix of this report, we provide quantitative estimates of the source of "time-series bias". We found that 7 of the RIS species, the time-series bias will generally be positive, and on the order of 10%. For the remaining species, bay anchovy, we found that time-series bias, along with positive environmental variation in survival, would probably lead to an underestimate of compensation.

This relative small level of positive bias will be more than compensated by other aspects of the model described above.

3.4 Lack of similarity with the RIS species

ESSA claims that there may be a lack of similarlity between RIS and the species used in the meta-analysis. ESSA's critisisms are grossly misleading for 4 of the the RIS species (Alewife, American shad, stripped bass and blueback herring) because we used data for these species, there was no lack of similarity with those species as claimed by ESSA. For another species, weakfish, we now have good estimates of compensatory reserve from a recent estimate. In this case, the metaanalytic estimates were very conservative (see below). It is true that there exists no data to estimate compensatory reserve for bay anchovy, Atlantic croaker, spot, and white bass ESSA's claim that the data used to infer a prior for steepness for these species may not be appropriate. However, all available data on compensation in the world that could be obtained was used for the analysis, thus, it is unreasonable to believe that the 4 RIS species for which data does not exist, lie completely outside the range of other data.

4 Recent Independent Analyses Demonstrate that the Meta-analytic Estimates of Compensation Were Conservative

Since the filling of the submission, we have two new assessments of RIS species. These assessments show that the values we estimate were conservative.

4.1 Striped Bass

For the striped bass, the alpha increased from 19.4 to 23.6 with the new data. This should have less time-series bias because the series are longer This translates from a z of 0.829 to 0.855. Also, this number has all the present power plant mortality in it, so the actual number is higher.

4.2 Weakfish

The estimate of $\hat{\alpha}$ was 29.6 under the Ricker model and 101 for the Beverton Holt model. The steepness from the Ricker model was 0.88. This is much greater than the modal value of 0.83 (check this) used in the impact assessment.

These results provide strong evidence that the estimates used in the submission are conservative, and underestimate compensation.

5 A Conservative Model was used to Access Power Plant Impact

We used the Beverton-Holt model to access power plant impacts. In this model, power plant mortality will **always** cause a reduction in spawner abundance. This is not true of alternative models, e.g. the Ricker model that ESSA appears to favor or the Shepherd spawner recruitment model. If such a model were used to access power plant impact, it would have generally suggested that power plant impacts would be much less than the model we used.

The use of the Ricker or Shepherd model would often result in a situation where power plant mortality of young fish would increase yield to the fishery. While this is perfectly feasible biologically, we believed that it was much more conservative to assume otherwise unless there were good evidence to the contrary.

There is another good reason to use the Beverton-Holt model instead of some of the alternatives. For example, in the ESSA report they refer to the Cushing model as an alternative. We believe that this would be a dangerous and irresponsible model to use in this situation because it has an infinite slope at the origin, i.e. it is impossible to drive a population to extinction. This does not happen with the Beverton Holt model using the method of estimating we used (described in the next section).

The use of the Beverton-Holt cases, for all cases makes our impact estimates inherently conservative because in many cases the Ricker, model fits better (AP-PENDIX 2). In fact, there is no statistical reason in general to prefer one model over the other (APPENDIX 2), and thus by choosing the more conservative one, we will in general be underestimating power plant impacts.

5.1 Our Estimates of the Beverton-Holt Compensation Parameter are Conservative

Since we used the Beverton Holt model for the model dynamics, because it gave conservative model dynamics, it would be reasonable to use the fit of the Beverton Holt model to estimate the model parameters. However, we choose to use a much more conservative approach. That is we estimated the α (the slope at the origin) for the Beverton Holt model from the fit of the Ricker model. We did this, because it produces much more conservative estimates, i.e. it produced lower estimates of the compensation reserve. At the limit of low population size, the slope at the origin has the same meaning for both, but for the same data, the point estimates



for the α for the Beverton-Holt model are always greater than the Ricker (Fig. 1).

Figure 1: A comparison of the slope at the origin estimated from the Ricker model with that estimated from the Beverton-Holt. In order to spread the data out, we have not standardized the slopes: they are in the "raw" units in the database. The cloud of arrows in the upper part of the figure represents cases where the slope at the origin estimated from the Beverton-Holt model is effectively infinite. The dotted line is the one-to-one line.

This is due to two different processes. First, it is possible to estimate "infinite" in the Beverton-Holt model, so that many estimates of the slope at the origin will be infinity. That is, if $K \rightarrow 0$, then $\alpha \rightarrow \infty$ is a perfectly feasible solution. A second reason for the positive bias has to do with the extrapolation to the origin. A simple way to think about this is to convert to $\log(\frac{R}{S})$, and think about the problem as a regression on *S*. On this scale, the Ricker model is

$$\log \frac{R}{S} = \log \alpha - \beta S,\tag{1}$$

so that the log of α is the y-intercept, and the Ricker model is a linear extrapolation.

The Beverton-Holt model may be written as

$$\log \frac{R}{S} = \log \alpha - \log(1 + \frac{S}{K}).$$
⁽²⁾

Note that $-\log(1 + \frac{S}{K})$ is a convex function of *S*, and the model will tend to estimate a higher y-intercept.

The Ricker model has the advantage that the estimates almost always are consistent with the biological constraints when plotted on the z scale.

This produced a much lower estimate of the compensation reserve, typically by about 50% for good data (Myers, Bowen, and Barrowman 1999).

6 We carried out the estimates for the distribution of steepness by 3 different methods, and chose the approach that gave the most conservative estimates

In order to make our estimates even more conservative, we used three approaches to estimate the distribution of steepness (i.e. "priors"), and choose the most conservative option. We developed three alternative quantitative approaches for obtaining estimates of prior distributions: (1) priors based upon information from taxonomically similar populations, (2) priors based upon information from ecologically similar populations, and (3) priors inferred from a quantitative analysis of life-history and environmental data. Overall, we found that option (2) gave the lowest estimates overall, and used these for the impact assessment. This again resulted in lower estimates of the compensation parameters.

7 We eliminated the largest outliers in the analysis, even though it was a reliable estimate

As a further step to ensure the estimates were conservative, we examined the data for outliers and eliminated the most important one. This data set happened to be one of the most reliable data sets in the whole database, but we eliminated because it might not be representative (this data was from the the Ayu from Lake Biwa in Japan) reduced the estimate of steepness for the bay anchovy by 20%.

8 The data often includes plant power plant mortality already, because this was not corrected for, the estimates used are conservative

Many of the data sets used in the analysis already include significant power plant mortality, e.g. the assessment of striped bass, shad, alewife and blueback herring. We did not attempt to correct for this power plant loss, thus this again will make our estimates conservative.

9 The results were verified when possible by comparing the estimates to those obtained from field experiments

In Appendix I of the submission, many examples of field experiments are given that verify the estimates used in the impact assessment. This gives further evidence that the estimates were reasonable and conservative.

10 The results were verified when possible by an extensive analysis of research survey data

ESSA claims that there are inherent problems with interpretation of spawner recruitment data. However, we verified many of our estimates from extensive analysis of research survey data in which the potential problems of spawner recruitment data do not occur (Myers and Cadigan 1993a; Myers and Cadigan 1993b) (This is covered in Appendix I of the submission). Again, this gives more evidence that the estimates were reasonable.

11 Many of the estimates suffer from none of the doubts raised by ESSA

Results from some of the stocks were for the same species as the RIS, and were the subject of experiments. In these cases none of the objections raised by ESSA is even remotely relevant. This is particularly true of the estimates for shad, alewife, and blueback herring. In each case, we had situations where there were very large changes in abundance, often semi-experimentally, with excellent estimates of spawner abundance, i.e. direct counts of spawners going upstream. In these cases, the allegations made by ESSA about the data are not even remotely relevant.

12 Summary

To be written.

References

- Abdussamad, E. M., and Thampy, D. M. 1994. Cannibalism in the tiger shrimp, *Penaeus monodon* Fabricius in nursery rearing phase. J. Aquacult. Trop. 9(1): 67–75.
- Aku, P. M. K., and Tonn, W. M. 1997. Changes in population structure, growth, and biomass of cisco (*Coregonus artedi*) during hypolimnetic oxygenation of a deep, eutrophic lake, Amisk Lake, Alberta. Can. J. Fish. Aquat. Sci. 54(9): 2196–2206.
- Auvinen, H. 1995. Intra- and interspecific factors in the dynamics of vendace (*Corgonus albula* L. Finnish Fish. Res. **15**: 87–96.
- Buckel, J. A., and Stoner, A. W. 2000. Functional response and switching behavior of young-of-the-year piscivorous bluefish. Journal of Experimental Marine Biology and Ecology 245(1): 25–41.

- Buynak, G. L., Hale, R. S., and Mitchell, B. 1992. Differential growth of young-of-year gizzard shad in several Kentucky reservoirs. N. Am. J. Fish. Manage. 12: 656–662.
- Close, T. L., and Anderson, C. S. 1992. Dispersal, density dependent growth, and survival of stocked steelhead fry in Lake Superior tributaries. N. Am. J. Fish. Manage. 12: 728–735.
- Cowan, J. H., Rose, K. A., Houde, E. D., Wang, S. B., and Young, J. 1999. Modeling effects of increased larval mortality on bay anchovy population dynamics in the mesohaline Chesapeake Bay: Evidence for compensatory reserve. Mar. Ecol. Prog. Ser. 185: 133–146.
- Coward, K., and Bromage, N. 1995. Density-dependent inhibition of spawning in the substrate-spawning cichlid, *Tilapia tholloni* (Sauvage). Proceedings Of The Fifth International Symposium On The Reproductive Physiology Of Fish, The University Of Texas At Austin: 184.
- Crisp, D. P. 1993. Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. Journal of Applied Ecology 30(4): 759–771.
- DeAngelis, D. L., Godbout, L., and Shuter, B. J. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. Ecological Modelling 57: 1–2.
- Dettmers, J. M., and Wahl, D. H. 1999. Evidence for zooplankton compensation and reduced fish growth in response to increased juvenile fish density. Hydrobiologia **400**: 115–121.
- Dittel, A. I., Hines, A. H., Ruiz, G. M., and Ruffin, K. K. 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. Bulletin of Marine Science 57: 902–916.
- Docker, M. F., and Beamish, F. W. H. 1994. Age, growth, and sex ratio among populations of least brook lamprey, *Lampetra aepyptera*, larvae: An argument for environmental sex determination. Environmental Biology of Fish 41(1): 191–205.
- Dong, Q., and DeAngelis, D. L. 1998. Consequences of cannibalism and competition for food in a smallmouth bass population: An individual-based modeling study. Trans. Am. Fish. Soc. 127(2): 174–191.

- Eggleston, D. B., Lipcius, R. N., and Hines, A. H. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85: 1–2.
- Elliott, J. M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. 3. The role of territorial behaviour. J. Anim. Ecol. 59(3): 803–818.
- Elliott, J. M. 1994. Quantitative Ecology and the Brown Trout. Oxford University Press, Oxford.
- Elliott, J. M., and Hurley, M. A. 1998. Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a lake district stream. J. Anim. Ecol. 67(2): 280–286.
- Fox, M. G., and Flowers, D. D. 1990. Effect of fish density on growth, survival, and food consumption by juvenile walleyes in rearing pond. Trans. Am. Fish. Soc. 119: 112–121.
- Goodyear, C. P. 1980. Compensation in fish populations. *In* Biological monitoring of fish. *Edited by* C. H. Hocutt and J. R. Stauffer. Lexington Books, D. C. Heath and Co., pp. 253–280.
- Hassell, M. P. 1978. Arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey.
- Heard, W. 1978. Probable case of streambed overseeding 1967 pink salmon, Oncorhynchus gorbuscha, spawners and survival of their progeny in Sashin Creek, southeastern Alaska. Fish. Bull. 76: 569–582.
- Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press, Vancouver, BC, Canada, pp. 119–230.
- Hecht, T., and Appelbaum, S. 1988. Observations on intraspecific aggression and coeval sibling cannibalism by larval and juvenile *Clarias gariepinus* (Clariidae: Pisces) under controlled conditions. Journal of Zoology 214: 21–44.
- Hobbs, R. C., and Botsford, L. W. 1989. Dynamics and age-structured prey with density- and predation-dependent recruitment: the Dungeness crab and a nemertean egg predator worm. Theoret. Pop. Biol. **36**: 1–22.
- Holm, J. C., Refstie, T., and Boe, S. 1990. The effect of fish density and feeding regimes on individual growth rate and mortality in rainbow trout (*On*-

corhynchus mykiss). Aquaculture 89: 225–232.

- Jones, G. P. 1987. Competitive interaction among adults and juveniles in a coral reef fish. Ecology 68: 1534–1547.
- Korman, J., Peterman, R. M., and Walters, C. J. 1995. Empirical and theoretical analyses of correction of time-series bias in stock-recruitment relationships of sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 52: 2174–2189.
- Koslow, J. A., Bell, J., Virtue, P., and Smith, D. C. 1995. Fecundity and its variability in orange roughy: Effects of population density, condition, egg size, and senescence. J. Fish Biol. 47(6): 1063–1080.
- LeCren, E. D., Kipling, C., and McCormack, J. 1972. Windermere: effects of exploitation and euthrophication on the salmonid community. Can. J. Fish. Aquat. Sci. 29: 819–832.
- Lindholm, J. B., Auster, P. J., and Kaufman, L. S. 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod, *Gadus morhua*. Mar. Ecol. Prog. Ser. 180: 247–257.
- Lorenzen, K. 1996. A simple von Bertalanffy model for density-dependent growth in extensive aquaculture, with an application to common carp (*Cyprinus carpio*). Aquaculture **142**: 191–205.
- MacCall, A. D. 1981. The consequences of cannibalism in the stockrecruitment relationship of planktivirous pelagic fishes such as Engraulis. IOC Workshop Report 28: 201–220.
- Mathur, D., McCreight, P. L., and Nardacci, G. A. 1979. Variations in fecundity of white crappie in Conowingo Pond, Pennsylvania. Trans. Am. Fish. Soc. 108(6): 548–554.
- Michaletz, P. H. 1997. Factors affecting abundance, growth, and survival of age-0 gizzard shad. Trans. Am. Fish. Soc. *126*(1): 84–100.
- Millar, R. B., and Myers, R. A. 1990. Modelling environmentally induced change in size at age for Atlantic Canada cod stocks. International Council for the Exploration of the Sea C.M. **1990/G:24**.
- Morman, R. H. 1987. Relationship of density to growth and metamorphosis of caged larval sea lampreys, *Petromyzon marinus L.*, in Michigan streams. IOC Workshop Report 28: 201–220.

- Myers, R. A., and Barrowman, N. J. 1995. Time series bias in the estimation of density-dependent mortality in stock-recruitment models. Can. J. Fish. Aquat. Sci. **52**: 223–232.
- Myers, R. A., Bowen, K. G., and Barrowman, N. J. 1999. The maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. 56: 2404–2419.
- Myers, R. A., and Cadigan, N. G. 1993a. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. **50**: 1576–1590.
- Myers, R. A., and Cadigan, N. G. 1993b. Is juvenile natural mortality in marine demersal fish variable? Can. J. Fish. Aquat. Sci. **50**: 1591–1598.
- Nikolsky, G., Bogdanov, A., and Lapin, Y. 1973. On fecundity as a regulatory mechanism in fish population dynamics. Rapp. P.-v. Réun. Cons. int. Explor. Mer 164: 174–177.
- Nordeide, J. T., Fossa, J. H., Salvanes, A. G. V., and Smedstad, O. M. 1994. Testing if year-class strength of coastal cod, *Gadus morhua* L., can be determined at the juvenile stage. Aquaculture and Fisheries Management 25: 101–116.
- Owens, R. W., and Noguchi, G. E. 1998. Intra-lake variation in maturity, fecundity, and spawning of slimy sculpins (*Cottus cognatus*) in southern Lake Ontario. Journal of Great Lakes Research 24(2): 383–391.
- Partridge, D. G., and DeVries, D. R. 1999. Regulation of growth and mortality in larval bluegills: implications for juvenile recruitment. Trans. Am. Fish. Soc. 128(4): 625–638.
- Rangeley, R. W., and Kramer, D. L. 1998. Density-dependent antipredator tactics and habitat selection in juvenile pollock. Ecology *79*(3): 943–952.
- Rice, J. A., Crowder, L. B., and Holey, M. E. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: A recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116: 703–718.
- Salojarvi, K. 1991. Compensation in a whitefish (*Coregonus lavaretus* L.S.L.) population maintained by stocking in Lake Kallioinen, Northern Finland. Finnish Fish. Res. 12: 65–76.
- Sandercock, F. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). *In* Pacific Salmon Life Histories. *Edited by* C. Groot and L. Margolis. UBC

Press, Vancover, pp. 395–446.

- Schlosser, I. J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. Oecologia **113**: 260–268.
- Schoenherr, A. A. 1977. Density dependent and density-independent regulation of reproduction in the gila topminnow, *Poeciliopsis occidentalis*. Ecology 58: 438–444.
- Shelbourne, J. E. 1957. The feeding and condition of plaice larvae in good and bad plankton patches. J. Mar. Biol. Assoc. UK. **36**: 539–552.
- Shepherd, J. G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40: 67–76.
- Shepherd, J. G., and Cushing, D. H. 1980. A mechanism for density-dependent survival of larvalfish as the basis for a stock-recruitment relationship. J. Cons. Int. Explor. Mer **39**: 160–167.
- Tonn, W. M., Holopainen, I. J., and Paszkowski, C. A. 1994. Densitydependent effects and the regulation of crucian carp populations in singlespecies ponds. Ecology 75(3): 824–834.
- Tupper, M., and Boutilier, R. G. 1995. Effects of conspecific density on settlement, growth and post-settlement survival of a temperate reef fish. Journal of Experimental Marine Biology and Ecology 191: 209–222.
- van Der Veer, H. W. 1986. Immigration, settlement and density- dependent mortality of a larval and early post-larval O-group (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29: 223–236.
- Walters, C. J. 1985. Bias in the estimation of functional relationships from time series data. Can. J. Fish. Aquat. Sci. **42**: 147–149.
- Walters, C. J. 1990. A partial bias correction factor for stock-recruitment parameter estimation in the presence of autocorrelated environmental effects. Can. J. Fish. Aquat. Sci. 47: 516–519.
- Whoriskey, F. G., and FitzGerald, G. J. 1985. Sex, cannibalism and sticklebacks. Behav. Ecol. Sociobiol. *18*(1): 15–18.
- Winters, G. H., Wheeler, J. P., and Stansbury, D. 1993. Variability in the reproductive output of spring-spawning herring in the Northwest Atlantic. ICES J. Mar. Sci. 50(1): 15–25.

13 APPENDIX 1: (send as a separate file)

14 APPENDIX 2: The Ricker Model and Beverton-Holt Models generally fit the data equally well, but the Ricker Model Givens Much More Conservative Estimates

14.1 The Beverton-Holt and the Ricker Models fit the data equally well

This analysis will consider the five most commonly used spawner-recruitment models. Let R be recruitment, E(R) be the expectation of R, and S be spawner abundance. We consider the models:

Cushing
$$E(R) = \alpha S^{\beta}$$

Ricker $E(R) = \alpha S e^{-\beta S}$
Beverton-Holt $E(R) = \frac{\alpha S}{1 + (S/K)}$
Shepherd $E(R) = \frac{\alpha S}{1 + (S/K)^{\gamma}}$

For the Ricker and Beverton-Holt models, the parameter α has dimensions of recruitment per unit spawner abundance and gives the slope of the function at S = 0. This parameter is crucial to setting the limits of overfishing (?). Note that this parameter must be positive. The "Shepherd Function", first proposed by Maynard Smith and Slatkin (1973), is a generalization of the Beverton-Holt model and is discussed in Bellows (1981). 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 (Shepherd 1982).

A critical factor for the practical selection of a recruitment model is its behaviour at low population sizes, in particular, the slope at the origin. We would like any model to behave in a reasonable manner at low population sizes. Using this criterion gives a very strong preference for the use of the Ricker or Beverton-Holt model. The Ricker model almost always gives a biologically plausible estimate of the slope at the origin. The Beverton-Holt often does, although unreasonable estimates are not uncommon (see next section). The Cushing model will almost always estimate an infinite slope at the origin, with the rare exception of a zero slope estimate. The Shepherd model has similar difficulties: if $\gamma = 1$, the Beverton-Holt model is recovered; if $\gamma < 1$, survival is estimated to be infinity as $S \rightarrow 0$; if $\gamma > 1$, the derivative of survival as $S \rightarrow 0$ will always be zero. Therefore, for $\gamma \leq 1$, the Shepherd model may be unreliable for the use of extrapolation of low population sizes.

These arguments give us *a priori* reasons to prefer the Ricker or Beverton-Holt model.



Figure 2: Boxplots of the difference in maximized log likelihoods of the Ricker and Beverton-Holt models for each species. Positive differences means that the alternative to the Ricker model is superior. The boxplots show the limits of the middle half of the data (the white line inside the box represents the median). The upper quartile and lower quartile provide the outline of the box. Whiskers are drawn to the nearest value not beyond 1.5*(inter-quartile range) from the quartiles; points beyond are drawn individually as outliers. The numbers in the pararentheses are the number of stocks used in the analysis.

It would be very useful if one model consistent fit and predicted recruitment better for a given taxonomic group (Fig. ??). Unfortunately, this is rarely the case; for most species neither the Ricker nor the Beverton-Holt models consistently fit the data better (Fig. 6) or are superior at predicting recruitment (Fig 7). However, there are species are better suited by a particular model. For example, the populations of coho salmon appear to favor the Beverton-Holt model, whereas freshwater brook trout are fit better by the Ricker. Similar results are found when prediction accuracy is considered (Fig. 7). The fits and perdition accuracy in figures 6 and 7 are for the models fit under the gamma assumption of recruitment variability. Similar results were obtained for the fit under the lognormal assumption.



Figure 3: Boxplots of the difference in root mean squared prediction accuracy of the gamma Ricker and gamma Beverton-Holt models for each species. See the legend of Fig. 2 for an explanation of the boxplots.

15 APPENDIX 3: Evidence for Compensatory Mechanisms In Fish Populations

In this appendix we describe some of the compensatory mechanisms that cause survival, growth, or fecundity to increase at low abundance (see also (Goodyear 1980), examples of which are presented in Table 1. We also describe how they are studied in practice. Increased survival at low abundance has been observed due to a variety of mechanisms. Predators may reproduce more rapidly, or migrate into an area, when prey are abundant (numerical response), or may become conditioned to seek the more abundant prey (functional response) (Hassell 1978). In many fish populations, cannibalism acts in a compensatory manner because the large number of parents from which large broods arise may constitute a large pool of predators (MacCall 1981). In addition to predation, parasites, disease and limited food availability typically have a greater suppressive effect when the population is large than when the population is small. Parasites and disease usually spread more rapidly when population density is high than when it is low. At high population abundance, starvation may increase because of competition for limited food resources (Nordeide, Fossa, Salvanes, and Smedstad 1994). Many fish species exhibit territorial behavior or have spatial requirements that can lead to density-dependent mortality (Elliott 1994) or emigration to areas of low survival (Crisp 1993).

Although such territorial behavior is associated with food utilization, it often results in higher predation mortality and immigration as well as decreased somatic growth for individuals without territories. At higher population sizes, competition for food normally translates into slower growth and, in turn, into a delay in sexual maturity and a decrease in the number of eggs or offspring produced (LeCren, Kipling, and McCormack 1972; Schoenherr 1977; Jones 1987). Because growth is indeterminate in fish, and age at sexual maturity and fecundity are very elastic parameters, fish can generate very large compensatory responses through changes in growth and fecundity. Faster growing individuals also tend to reach sexual maturity at an earlier age and to produce more eggs per spawning than slower growing fish. Both younger age at maturation and increased eggs per spawning result in higher life time egg production (Nikolsky, Bogdanov, and Lapin 1973). An increased percentage of sexually mature individuals in the younger ages can cause a significant increase in reproduction because the younger age groups usually consist of large numbers of fish.

Different compensatory factors often interact. For example, slower growth

caused by food scarcity may leave a particular life stage of a fish vulnerable to predation for a longer period of time and hence result in higher mortality. Immigration and emigration act as safety valves to reduce numbers at times of peak density, and to increase them when environmental resources are abundant relative to population numbers. The stress of more intense competition due to crowding may cause behavioral or physiological changes in individual organisms that result in lower survival or lower reproductive capacity.

Although compensation affects survival, growth, reproduction and movement, the greatest factor is almost always survival during early ages. We will discuss this in more detail in later chapters.

mechanisms									
life-history	habitat	species	study	affects	reference				
stage									
functional feeding response of predators									
juv.	pelagic, estuary	bluefish	field, exp.	S	Buckel and Stoner (2000)				
adult	benthic	clam	lab.	S	Eggleston et al. (1992)				
limited refuge from predation									
juv.	demersal, ocean	cod	field	S,G	Tupper and Boutilier (1995)				
juv.	demersal, estuary	blue crab	exp.	S	Dittel et al. (1995)				
juv.	demersal	cod	lab	S	Lindholm et al. (1999)				
juv.	demersal	plaice	field	S	van Der Veer (1986)				
juv.	pelagic,ocean	pollock	field, exp.		Rangeley and Kramer (1998)				
cannibalism									
juv.	demersal	tiger shrimp	lab	S	Abdussamad and Thampy (1994)				
adult-egg	pelagic	anchovy	field	S	MacCall (1981)				
juv.	demersal	cod	field	S	Nordeide et al. (1994)				
adult-egg	demersal, estuarine	stickleback	field	S	Whoriskey and FitzGerald (1985)				
juv.	pelagic,lake	smallmouth bass	sim. model	S	Dong and DeAngelis (1998)				
larvae, juv.	demersal, lake	sharptooth catfish	lab	S	Hecht and Appelbaum (1988)				
juv		crucian carp	field, exp.	S	Tonn et al. (1994)				
parasitism									
adult	demersal, ocean	Dungeness crab	field, theory	S	Hobbs and Botsford (1989)				
food limitation	(general)								
larvae	pelagic	plaice	field	S	Shelbourne (1957)				
larvae	pelagic	bloater	field	S,G	Rice et al. (1987)				
larvae	pelagic, ocean	general	theory	S,G	Shepherd and Cushing (1980)				
post egg	pelagic, lake	vendace	field	G	Auvinen (1995)				
post egg	pelagic, lake	vendace	field, exp.	G	Salojarvi (1991)				
juv, adult	demersal, ocean	cod	field	G	Millar and Myers (1990)				
adult	demersal, ponds	common carp	exp.	G	Lorenzen (1996)				
fry	stream bed	steelhead salmon	field, exp.	G	Close and Anderson (1992)				
juv.	pelagic, pond	walleye	field, exp.	G	Fox and Flowers (1990)				
juv	pelagic, lake	gizzard shad	field	G	Buynak et al. (1992)				
larvae	stream bed	sea lamprey	field, exp.	G	Morman (1987)				
larvae, juv.	pelagic	bay anchovy	sim. model	S,G	Cowan et al. (1999)				
juv.	pelagic, lake	smallmouth bass	sim. model	S,G	DeAngelis et al. (1991)				
juv.	pelagic, lake	gizzard shad	field, exp.	S,G	Dettmers and Wahl (1999)				
juv.	pelagic, lake	rainbow trout	lab	S,G	Holm et al. (1990)				
larvae	pelagic, lake	gizzard shad	field	S,G	Michaletz (1997)				
adult	benthic	slimy sculpin	field	G,R	Owens and Noguchi (1998)				
juv.	stream	creek chub	field	S,G,M	Schlosser (1998)				

Table 1 Examples of compensatory mechanisms affecting survival (S), growth (G), reproduction (R), and movement (M).

mechanisms					
life-history	habitat	species	study	affects	reference
stage					
food limitation	(territorial behav	viour)			
juv.	stream bed	coho salmon	field	S	Sandercock (1991)
juv.	demersal, ocean	cod	field	S,G	Tupper and Boutilier (1995)
larvae	pelagic, lake	bluegill	field	S,G	Partridge and DeVries (1999)
territorial beh	aviour				
juv.	stream bed	brown trout	field	S,G,M	Elliott (1990)
dispersal					
fry	stream bed	brown trout	field, exp.	S,M	Crisp (1993)
competition fo	r refugia				
juv,adult	pelagic, lake	cisco	field	S,G,M	Aku and Tonn (1997)
suffocation cau	ised by crowding				
eggs	demersal	herring	field		
larvae	stream bed	pink salmon	field	S	Heard (1978)
overturning of	egg nests				
adult-eggs	streams	pink salmon	field	S	Heard (1991)
spawning inhil	bition				
adult	pelagic	tilapia	lab	R	Coward and Bromage (1995)
adult	pelagic, lake	brown trout	field	R	Elliott and Hurley (1998)
sex determinat	tion				
larvae	stream bed	least brook lamprey	field	R	Docker and Beamish (1994)
maturity					
adult	pelagic, lake	brown trout	field	R	Elliott and Hurley (1998)
fecundity					
adult	pelagic, ocean	orange ruffy	field	R	Koslow et al. (1995)
adult	pelagic, lake	white crappie	field	R	Mathur et al. (1979)
adult	benthic	slimy sculpin	field	G,R	Owens and Noguchi (1998)
adult	pelagic, ocean	Atlantic herring	field	R	Winters et al. (1993)

Common name	Scientific name
Atlantic herring	Clupea harengus harengus
Anchovy	Engraulis sp.
Bay anchovy	Anchoa mitchilli
Bloater	Coregonus hoyi
Blue crab	Callinectes sapidus
Bluefish	Pomatomus saltatrix
Bluegill	Lepomis macrochirus
Brown trout	Salmo trutta
Cisco	Coregonus artedi
Clam	Macoma balthica
Cod	Gadus morhua
Coho salmon	Oncorhynchus kisutch
Common carp	Cyprinus carpio
Creek chub	Semotilus atromaculatus
Crucian carp	Carassius carassius
Dungeness crab	Cancer magister
Gizzard shad	Dorosoma cepedianum
Herring	Clupea harengus
Least brook lamprey	Lampetra aepyptera
Northern anchovy	Engraulis mordax
Orange ruffy	Hoplostethus atlanticus
Pink salmon	Oncorhynchus gorbuscha
Plaice	Pleuronectes platessa
Pollock	Pollachius virens
Sea lamprey	Petromyzon marinus
Sharptooth catfish	Clarias gariepinus
Slimy sculpin	Cottus cognatus
Smallmouth bass	Micropterus dolomieui
Sockeye salmon	Oncorhynchus nerka
Steelhead salmon	Oncorhynchus mykiss
Stickback	Gasterosteus aculeatus
Tiger shrimp	Pemaeus monodon
Tilapia	Tilapia tholloni
Rainbow trout	Oncorhynchus mykiss
Vendace	Corgonus albula
Walleye	Stizostedion vitreum
White crappie	Pomoxis annularis

Table 2. Latin names of species listed in Table 1.Common nameScientific name