Submitted to:

The Critial Period Hypothesis

Ransom A. Myers
Killam Chair in Ocean Studies
Department of Biology
Dalhousie University
Halifax, Nova Scotia
Canada B3H 4J1
email - Ransom.Myers@Dal.Ca

We believe that to make progress on this problem, it is crucial to come to terms with several issues. First, the true abundance of a cohort is never measured without error, and this must be explicitly included in the model. That is, the dynamics of population abundance, must be considered in terms of parameters, i.e. true population abundace, that cannot be observed without error. Cox (1981) makes the useful distinction between models driven by observations and prameter driven models; here we restrict our attention to the latter. Second, population dynamics is inheriently nonlinear, and models must be formulated accordingly. Third, there is not enough data on any one cohort to obtain accurate estimates of density-dependent mortality, and thus the results must be combined among cohorts. Kiefer and Wolfowitz (1956) noted that in estimation situations where the number of parameters increases to infinity, maximum likelihood parameter estimates are not consistent, but by treating parameters as coming from a distribution—that is, as random effects—consisten cy could be obtained. This is the approach taken here. Lastly, even with excellent data, it is rare that definitive conclusions can be reached from any one data set; i.e. it is necessary to combine data across many populations.

We use simulation based metods to obtain maximum likelihood estiamtes for this problem (Mariano, Schuermann, and Weeks 2000). A simulation based method is used to evaluate the integrals that occur in the nonlinear random effects part of the model.

1 Introduction

2 At what life-history stage does density-dependent mortality occur?

Much of fisheries research centers around Hjort's (1914) critial period hypothesis which states "the numerical value of a year class is apparently stated at a very early age, and continues in approximately the same relation to that of other year classes throughout the life of the individuals".

Progress has been limited because the question has not been formulated in a manner that can be formally tested. This question is primarily a statistical question of he relative importance of variation in mortality among yearclasses at different ages.

We consider a population in which each cohort is born during a very narrow time interval, and the population abundance is estimated at discrete ages, a, which correspond to regular surveys. These assessments are assumed to

It is useful to divide mortality into three components: (1) the average mortality independent of population abundance μ_i, (2) the mortality related to the abudance of a yearclass $f_i(N_{y,i})$, and (3) the stochastic component of mortlaity $\varepsilon_{y,i}$. It is useful to examine the abundance of a yearclass, y, at different ages, a. We can write the abundance at the end of time period a as

$$N_{y,a} = N_{y,0} \exp(\sum_{i=1}^{a} -\mu_i - f(N_{y,i}) - \varepsilon_{y,i}).$$

Note that each of the mortality terms, e.g. μ_i, take place between ages $i-1$ and i.

We can now state the strong version of the crictial period hypothesis as follows: The age 0 to a_{crit} is the critical period if

$$\sum_{i=1}^{a_{crit}} Var(\varepsilon_{y,i}) \ll \sum_{i>a_{crit}} Var(\varepsilon_{y,i})$$

and

$$f_a(N_{y,a}) \approx 0 \text{if} a > a_{crit}$$

where the variances are calcualted over yearclasses.

It will be useful to state a weak version of the hypothesis: The age 0 to a_{crit} is the critical period (weak version) if

$$\sum_{i=1}^{a_{crit}} Var(\varepsilon_{y,i}) \ll \sum_{i>a_{crit}} Var(\varepsilon_{y,i})$$

and

$$f_a(N_{y,a}) \text{ is a non decreasing function of } N_{y,a} \text{ if } a > a_{crit}$$

The weak version of the hypothesis is needed because density dependent mortality will generally change the relative relationships among sizes of cohorts even if there is no other variaiton in mortality.

3 The central issue

The central issue, and difficulty, is that it is very difficult to estimate variability in mortality rates. By their very nature, mortality rates require the difference in abundance, which will be mearsured with error. Thus, and method to address the critical period hypothesis must require methods that take into account the estimation error. To estiamte the variability in mortality for different ages, is simply beyound the capacity of most studies of population dynamcis.

Most biologist do not realize the difficult in obtaining estimatines of variances.

4 Example: Norway Spring Spawning Herring

It is useful to examine the longterm and shortterm data for the population. The longterm data is from the Fig. 1 The following is apparent from this data.

- There was a 2 order of magnitude of egg production over the 1973 to 1999 period, which was matched by a similar increase in larval production (although the record was over a shorter time period).
- The trend in the 0+ and recruitment from the VPA is less, but the interannual variability is greater.
-
-

Aging errors will reduce estimated variability in recruitment and cause autocrrelation for catch-at-age analyses (Bradford 1991).

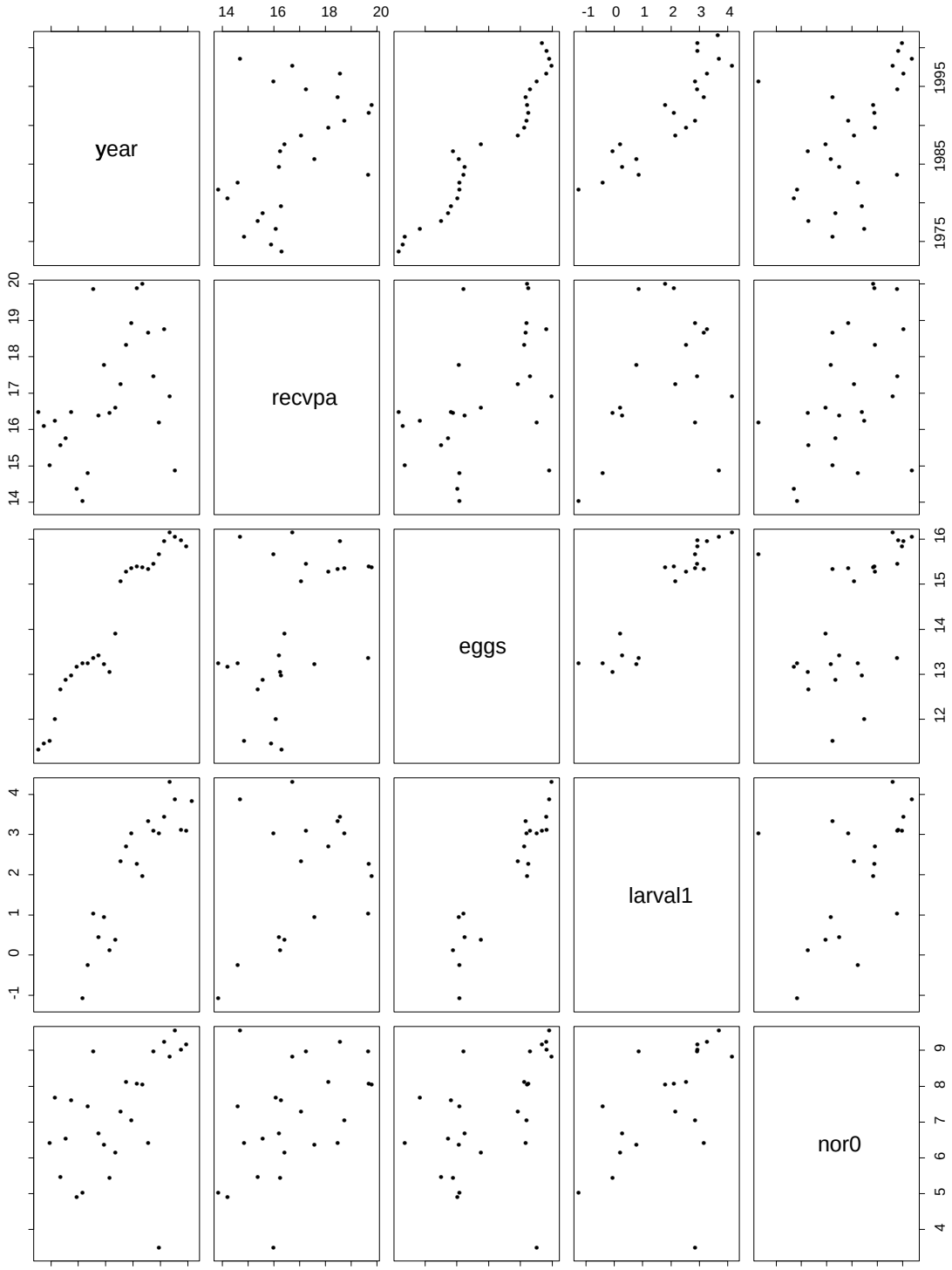

Figure 1: Log transformed data for spawning biomass, larval production, Norway shelf 0+, and recruitment from the VPA for Norwegian spring spawning herring.

The recent acoustic survey data shows a strong correlation among yearclasses Fig. 2. The following appears to be true from these surveys.

- In the early ages (before age 3) there is much wider variation in the numbers at age than in the older years. The strong year classes appear to be consistent among yearclasses.
- This suggests density dependent mortality.
- The correlation among the surveys at age 1 and greater is very high, the correlation with the older ages with the 0+ surveys is lower, but still substantual, and the correlation with the egg

and larval surveys is generally low and variable.

The key issue here is then is the following: Is the ealy juvenile stage the critical period? We will test both the strong and weak hypotheses.

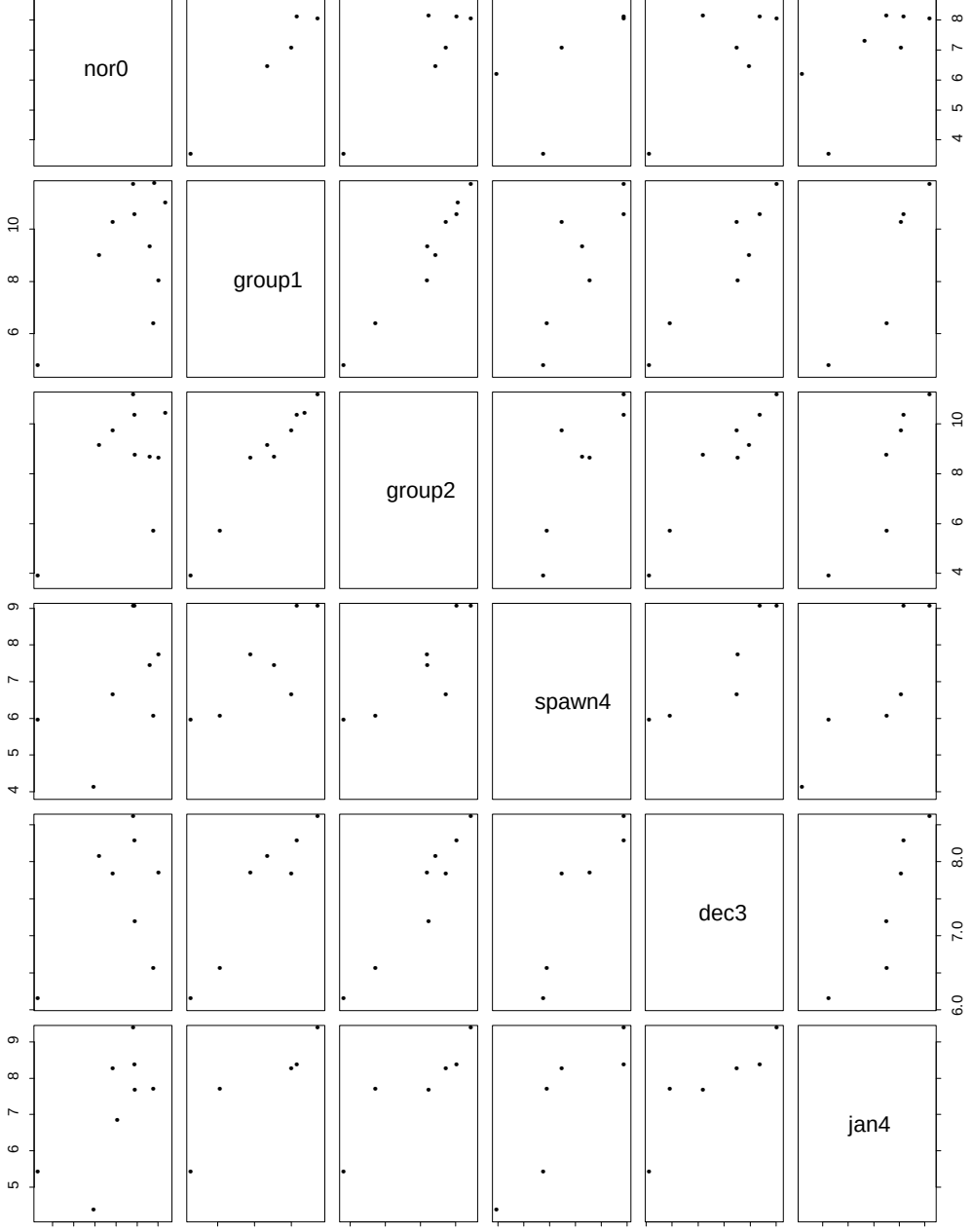

Figure 2: Log transformed data for spawning biomass, larval production, Norway shelf 0+, and recruitment from the VPA for Norwegian spring spawning herring.

5 Other Issues

Here we deal with ages before they are greatly impacted by fishing. It may be that there is compensation at older ages as well. That is, there is some evidence that total mortality is relaitvely constant.

Acknowledgments

References

Bradford, M. J. 1991. Effects of aging errors on recruitment time series estimated from sequential population analysis. Can. J. Fish. Aquat. Sci. **48**: 555–558.

Cox, D. R. 1981. Statistical analysis of time series: some recent developments. Scand. J. Statist. **8**(2): 93–115. With discussion by Gudmundur Gudmundsson, Georg Lindgren, Lennart Bondesson, Erik Harsaae, Petter Laake, Katarina Juselius and Steffen L. Lauritzen, With a reply by the author.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. Rapp. P.-v. Réun. Cons. int. Explor. Mer **20**: 1–228.

Kiefer, J., and Wolfowitz, J. 1956. Consistency of the maximum likelihood estimator in the presence of infinitely many incidental parameters. Ann. Math. Statist. **27**: 887–906.

R. Mariano, T. Schuermann, and M. J. Weeks (Eds.) 2000. Simulation-based inference in econometrics. Cambridge University Press, Cambridge. Methods and applications.