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What can we learn about lumpfish mortality from sex ratio data?

by

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ABSTRACT

Under certain assumptions, the ratio of females to males in the "virgin" population (before exploitation begins) can be used to estimate the ratio of mortality rates of males to females (i.e., Z_m/Z_f). Changes in sex ratio over time of a cohort of animals provides an estimate of the difference in mortality rates. Thus, if one compares the sex ratio in a survey at time i with the sex ratio of the same cohorts at time i+1 one can estimate $Z_m - Z_f$. This latter approach is appealing because only minimal assumptions are made about catchabilities: the ratio of catchabilities of females:males remains constant over time but the catchabilities are not assumed equal or constant over time. However, it is necessary to remove the recruitment from the survey results at time i+1 to follow a group of cohorts and get unbiased estimates. Lumpfish sex ratio data for 3Ps are available from groundfish surveys. The survey catches have always been skewed towards females. However, the ratio of females to males has decreased over the years 1979 to 1994 indicating that the mortality rate of females has increased relative to that of the males. If recruits could be identified in the trawl data and removed from consideration, one might get some useful information on relative mortality rates and on changes in mortality rates of females over time.

RÉSUMÉ

Selon certaines hypothèses, le rapport des femelles aux mâles au sein de la population «vierge» (avant exploitation) peut servir à évaluer le rapport du taux de mortalité chez les mâles et les femelles (soit Zm/Zf). Les fluctuations du rapport des sexes d'une cohorte d'animaux, sur une période donnée, permettent d'estimer les différences au niveau des taux de mortalité. Ainsi, si l'on compare le rapport des sexes établi à la suite d'un relevé effectué à un moment i avec le rapport des sexes des mêmes cohortes pour le moment i+1, on peut évaluer Zm - Zf. Cette méthode est intéressante parce qu'elle ne nécessite que quelques hypothèses au sujet du potentiel de capture : le rapport de capturabilité des femelles et des mâles demeure constant avec le temps, mais la capturabilité n'est pas considérée comme étant égale ou constante avec le temps. Toutefois, il faut faire abstraction du recrutement dans les résultats du relevé au moment i+1 pour suivre un groupe de cohortes sans biaiser les résultats. Les données sur le rapport des sexes de la lompe dans la sous-division 3Ps peuvent être extraites des relevés du poisson de fond. Les prises effectuées au cours des relevés ont toujours penché en faveur des femelles. Cependant, le rapport des femelles aux mâles a diminué entre 1979 et 1994, ce qui indique que le taux de mortalité des femelles a augmenté par rapport à celui des mâles. S'il était possible de déterminer le nombre de recrues parmi les captures et de les soustraire des données, on pourrait obtenir des informations utiles sur les rapports de mortalité relative et la variation du taux de mortalité des femelles en fonction du temps.

Introduction

Lumpfish are exploited exclusively for roe and the survival rate of released males is apparently high. Therefore, if the exploitation rate on the females becomes high we would expect to see a progressive change in the sex ratio in our surveys. This change in the sex ratio would be partially obscured by incoming recruits which would not have been subjected to the differential mortality of the fishery. Therefore, we would expect to have an even more sensitive way to detect changes in relative mortality, and to quantify the ratio of the survival rates, if we could identify recruits in the survey data and remove them from consideration. Unfortunately, at this time I do not know the growth rate of lumpfish and cannot adjust the survey results. However, it is worthwhile analyzing the existing data to see what kinds of inferences can be made with and without the recruitment data.

Theory of sex ratios

The theory in this section is developed more fully in Hoenig et al. (1983 and 1990). Part of the theory is an application of change-in-ratio methodology described by Paulik and Robson (1969) and Seber (1982).

overall sex ratio

Assume that, after some early life history period of duration t_r, the mortality rate has become constant so that the number of animals present at time t_r is given by the usual relationship

$$N_t = N_r \exp(-Z(t - t_r)) \tag{1}$$

where N_t is the number of animals at time t, N_r is the number present at time t_r, and Z is the instantaneous mortality rate. Assume also that at the time of recruitment, t_r, the sex ratio is 1:1. If the sex ratio is different from 1:1 at time t_r then all formulae for the sex ratio must be multiplied by the intial sex ratio at the time of recruitment. Let Z_m and Z_f represent the mortality rates for males and females (considered constant over age and time). Then the sex ratio at any age $t \geq t_r$ is given by

$$R_{age=t} = \frac{\text{females}}{\text{males}} = \exp\{(Z_m - Z_f)(t - t_r)\} \tag{2}$$

If reproduction occurs continuously and at a constant level, the overall sex rato, $\bar{R}$, in the population of animals above the age t_r is given by

$$\bar{R} = \frac{\text{females}}{\text{males}} = \frac{N_r \int_{t_r}^{\infty} \exp\{-Z_f(t - t_r)\}dt}{N_r \int_{t_r}^{\infty} \exp\{-Z_m(t - t_r)\}dt} = \frac{Z_m}{Z_f}\ . \tag{3}$$

Thus, the ratio of females to males above the age t_r is equal to the ratio of the instantaneous mortality rates of males to females and does not depend on the value of t_r (provided the sex ratio is 1:1 at age t_r).

If the gear used to sample the population does not catch animals younger than age t_c for $t_c \geq t_r$ then the overall sex ratio for animals greater than or equal to age t_c is given by

$$\bar{R}_c = \frac{Z_m}{Z_f} \exp\{(Z_m - Z_f)(t_c - t_r)\} \tag{4}$$

Of course, in temperate regions, reproduction generally occurs annually during a restricted season although recruitment could be spread out over an extended period of time. Hence, the sex ratio can be expected to fluctuate and is closest to 1.0 immediately following the recruitment of a pulse of young animals having a sex ratio close to 1.0 (Figure 1). We represent the age structure for one of the sexes in the population by a geometric model instead of the exponential models such that

$$\frac{N_{t+1}}{N_t} = \exp(-Z) \ . \tag{5}$$

The overall sex ratio at time of the year $\alpha = 0$, defined to be just after recruitment occurs, is given by

$$\tilde{R}_o = \frac{\text{females}}{\text{males}} = \frac{1 + \exp(-Z_f) + \exp(-2Z_f) + \ ...}{1 + \exp(-Z_m) + \exp(-2Z_m) + \ ...}$$

$$= \frac{1 - \exp(-Z_m)}{1 - \exp(-Z_f)} \tag{6}$$

where the tilda indicates annual reproduction and the subscript o denotes the fraction of the year that has elapsed since recruitment. At time of year = α, the overall sex ratio is given by

$$\tilde{R}_\alpha = \tilde{R}_o \exp(\Delta Z \, \alpha), \qquad 0 \leq \alpha \leq 1 \tag{7}$$

where $\Delta Z = Z_m - Z_f$. More generally, it can be shown that the sex ratio at any time of the year α, when the youngest age group caught is t_c, is given by

$$\tilde{R}_{\alpha,t_c} = \tilde{R}_o \exp\{\Delta Z \, (\alpha + t_c)\} \tag{8}$$

where t_c can take on values 0, 1, 2, ...

According to this model, sex ratio data at two or more times of the year are sufficient to estimate Z_m and Z_f. Taking logarithms of the previous expression, we have

$$\log_e(\tilde{R}_{\alpha,t_c}) = \log_e(\tilde{R}_o) + \Delta Z \, (\alpha + t_c) \tag{9}$$

which describes a straight line with regression coefficient estimating ΔZ. Using the definitions of $\tilde{R}_o$ and ΔZ gives two equations in two unknowns which can be solved simultaneously for Z_m and Z_f. In practice, this method is likely to require too strong an adherence to the assumption of instantaneous recruitment unless estimates of sex ratio can be made throughout much of the year for two or three years.

change in sex ratio over time

Suppose the expected catch rate of animals with age $\geq t_c$ in the surveys is

$$C_{it} = q_{it} N_{it} \quad , i \in \{m,f\} \tag{10}$$

where i refers to the sex {m = male, f = female}, t refers to the year, C is the expected catch, q is the catchability coefficient and N is the abundance. Suppose that we start our surveys in year 0 and follow the same cohorts of animals over time. Then the ratio of expected catches in year t, R_t, is

$$R_t = \frac{C_{f,t}}{C_{m,t}} = \frac{q_{ft} N_{f0} \exp(-Z_f t)}{q_{mt} N_{m0} \exp(-Z_m t)} \ . \tag{11}$$

We will assume that the ratio of q_{ft}/q_{mt} does not change over time. Since the ratio of initial abundances is also a constant, we can write the above equation as

$$R_t = q^* \frac{\exp(-Z_f t)}{\exp(-Z_m t)} = q^* \exp\{(Z_m - Z_f)t\}. \tag{12}$$

Here, q* is a nuisance parameter that subsumes the catchabilities and the initial abundances. It is significant that we are not assuming that we know the initial relative abundances of the sexes nor are we assuming that the two sexes have equal catchabilities nor are we assuming that the catchabilities remain constant over time. All we assume is that the ratio of catchabilities remains constant over time.

If we plot the logarithm of R_t versus time, we get a linear relationship with slope equal to the difference in mortality rates (Z_m - Z_f). In fact, Hoenig et al. (1990) showed that this is a logistic regression.

A special case of this (discussed by Paulik and Robson (1969) and Seber (1982)) is when we compare the sex ratio in a pair of adjacent years. Then,

$$\frac{R_2}{R_1} = \exp(Z_m - Z_f) = \frac{S_f}{S_m} \tag{13}$$

or

$$\log_e \frac{R_2}{R_1} = Z_m - Z_f \tag{14}$$

where S_i is the survival rate for sex i.

The point is that change over time in the sex ratio in a (group of) cohort(s) provides an estimate of the difference in the instantaneous mortality rates (or an estimate of the ratio of survival rates).

effect of recruitment on sex ratio

The previous section deals with what can be determined by following a cohort (or group of cohorts) over time. If the animals can be aged, then one could divide the animals caught in the surveys into two groups: the cohorts that we're following, and the new recruits. Alternatively, one could tag a group of fish and look at changes in the sex ratio in the tag returns over time (this is obviously expensive). These approaches allow us to estimate the difference in survival rates.

If we cannot age or tag the fish (apparently the current situation for lumpfish), then the survey results will give biased results. This is because the influx of new recruits with the "initial sex ratio" dilutes the changes in the sex ratio that have been occurring due to differential mortality. It may be possible, in theory, to take account of this dilution, especially if something is known about the longevity of the species (with many age groups present the effect of recruiting one more age group will tend to be less than if there are only a few age groups present). However, this is not likely to be satisfactory and may be more trouble than if one simply determined a way to obtain approximate ages of the fish. Also, by eliminating new recruits, we eliminate the effects of recruitment variability on the estimation of mortality rates which makes the use of sex ratios especially attractive.

Artifacts of sampling

In this section, we note that there are a number of ways in which misleading results can be obtained. The interpretation of a steady-state sex ratio, such as observed in a virgin population or in a population subject to a constant exploitation rate for a long period of time, is far more difficult than the interpretation of changes in sex ratio. To interpret the overall sex ratio, we must assume that recruitment is constant, the age at first capture is the same (this is likely to be a problem if the sexes grow at different rates), and that the catchabilities of the two sexes are the same. The survey must cover the entire area inhabited by the stock or else there must not be any spatial segregation by sex. Finally, the mortality rates are assumed to not vary over time or with age.

The interpretation of changes in sex ratio are far less problematic. Nonetheless, there are certain potenial problems that must be investigated. In particular, the survey must cover the entire area inhabited by the stock or there must not be a pattern of spatial segregation that changes over time. Recruitment is assumed to occur all at once but if recruitment occurs over a period of years then only fully recruited cohorts should be considered.

Application to lumpfish in 3Ps

Sex ratio data from groundfish surveys from 1979 to 1994 (from Stansbury et al. 1995) are presented in Table 1. Two things stand out immediately. First, the catches of lumpfish in the surveys in the early years (1979 - 1983) were much lower than in later years (there was no survey in 1984). Thus, it appears that the early surveys may have been different in some way from later surveys and this could and should be investigated. Table 5 in Stansbury et al. (1995) is a good starting place. Second, the sex ratio has shown a progressive change over time starting with a high predominance of females and ending up with a more nearly equal sex ratio (Figure 2, top).

As pointed out earlier, interpretation of an overall sex ratio is rather difficult because of the many factors that could affect the sex ratio. If all the assumptions could be met, then a population dominated by females would imply that females have a lower mortality rate than males. However, examination of the length frequency plots from the research surveys reveals that the smaller females (30-35 cm) are largely absent whereas the modal size for males is around 30-35 cm. Therefore, the skewed sex ratio observed in the surveys may well be an artifact of sampling. Clearly, aging data would be very useful in establishing whether or not the same age groups for each sex are present in the survey catches.

On the other hand, change in sex ratio over time from heavily dominated by females to more nearly equal is strong evidence of an increase in mortality of females relative to that of males. This is true even though the effects of recruitment were not removed from the survey data. Presumably the annual recruitment has had a constant sex ratio over time so if the overall sex ratio is changed while the recruitment ratio remained constant then the females must be have experienced an increase in mortality.

Although it is not valid to estimate time-specific differences in survival rate because we cannot eliminate the recruitment, it may be instructive to do so anyway as long as we recognize that the results are biased. This is done in Table 1 and the results are shown in Figure 2 (bottom). The estimates of S_m/S_f are highly variable. This is not surprising considering that some of the sample sizes (in the early years) are quite low, and that this procedure is not protected from the influence of variable recruitment because recruitment is not eliminated from the the data. Nonethess, we are left with a median estimate of S_m/S_f of 0.9 which is somewhat interesting. The females, which are exploited, appear to have a mortality rate which is slightly lower than that of the unexploited males. However, the data also suggest that in the pre-exploitation days the females had a mortality that was much less than that of the males. Hence, the mortality rate of the females appears to have changed considerably. Obviously, the uncertainties in the analysis need to be cleared up.

Discussion

The change-in-ratio estimator of relative survival rates (or differences in instantaneous mortalities) can be made workable by resolving questions about the survey coverage and the growth rates of lumpfish. Specifically, the following is recommended:

1) The area covered by the surveys over time should be reviewed to resolve why the numbers of lumpfish in the early surveys is low (some of this may be answerable based on information in Table 5 of Stansbury et al. 1995);

2) The spatial distribution of males and females, by size group, should be studied to determine the likelihood of biased estimates of sex ratio from the surveys. In particular, it should be determined why small females (30-35 cm) are not taken in the trawl survey;

3) Estimates of growth rates of males and of females should be obtained so that it can be determined which ages are taken in the trawl survey and so recruits can be eliminated from survey results.

It should be pointed out that, if these problems with the survey are resolved, there are three other options potentially available for assessing the lumpfish stocks. The first is to try catch curve analysis to estimate total mortality rate by looking at the decline in survey catches of a group of cohorts over time. The second option is to try an open population model for change-in-ratio estimation of population size developed by Chapman and Murphy (1965) (and by Lander 1962). That is, the change in sex ratio caused by the known removal (catch) can be used to estimate the absolute abundance if recruitment can be eliminated and natural mortality can be accounted for. The third approach is to use an open population version of index removal estimation (e.g., Collie and Sissenwine 1983 or Conser 1995). This approach says that the recruited population this year is equal to the recruited population last year minus the catch plus the recruits all discounted by natural mortality; given indices of recruitment and recruited biomass and absolute value of catch one can solve for population abundance. Although I can not prove it at this point, it seems that lack of information on spatial stock structure might be more of a problem for estimating absolute population size than for estimating changes in mortality rates and relative mortality rates.

Prospects for improved assessment of lumpfish stocks appear good.

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Table 1. Lumpfish sex ratio data and calculation of biased estimates of relative survival. Data are from Stansbury et al. (1995).

pair of years	number of males	number of females	R = males/females	R2/R1 = Sm/Sf
79	171	1255	.1363	5.24
80	441	617	.7147	
80	441	617	.7147	.21
81	27	182	.1484	
81	27	182	.1484	4.49
82	4	6	.6667	
82	4	6	.6667	.33
83	101	464	.2177	
85	1519	3121	.4867	.62
86	1036	3399	.3048	
86	1036	3399	.3048	2.26
87	3521	5112	.6888	
87	3521	5112	.6888	.90
88	731	1175	.6221	
88	731	1175	.6221	.75
89	1072	2292	.4677	
89	1072	2292	.4677	2.25
90	2612	2485	1.0511	
90	2612	2485	1.0511	.66
91	2157	3131	.6889	
91	2157	3131	.6889	.93
92	1097	1484	.7392	
92	1097	1484	.7392	1.59
93	996	847	1.1759	
93	996	847	1.1759	.53
94	825	1311	.6293	
median			.6293	.90

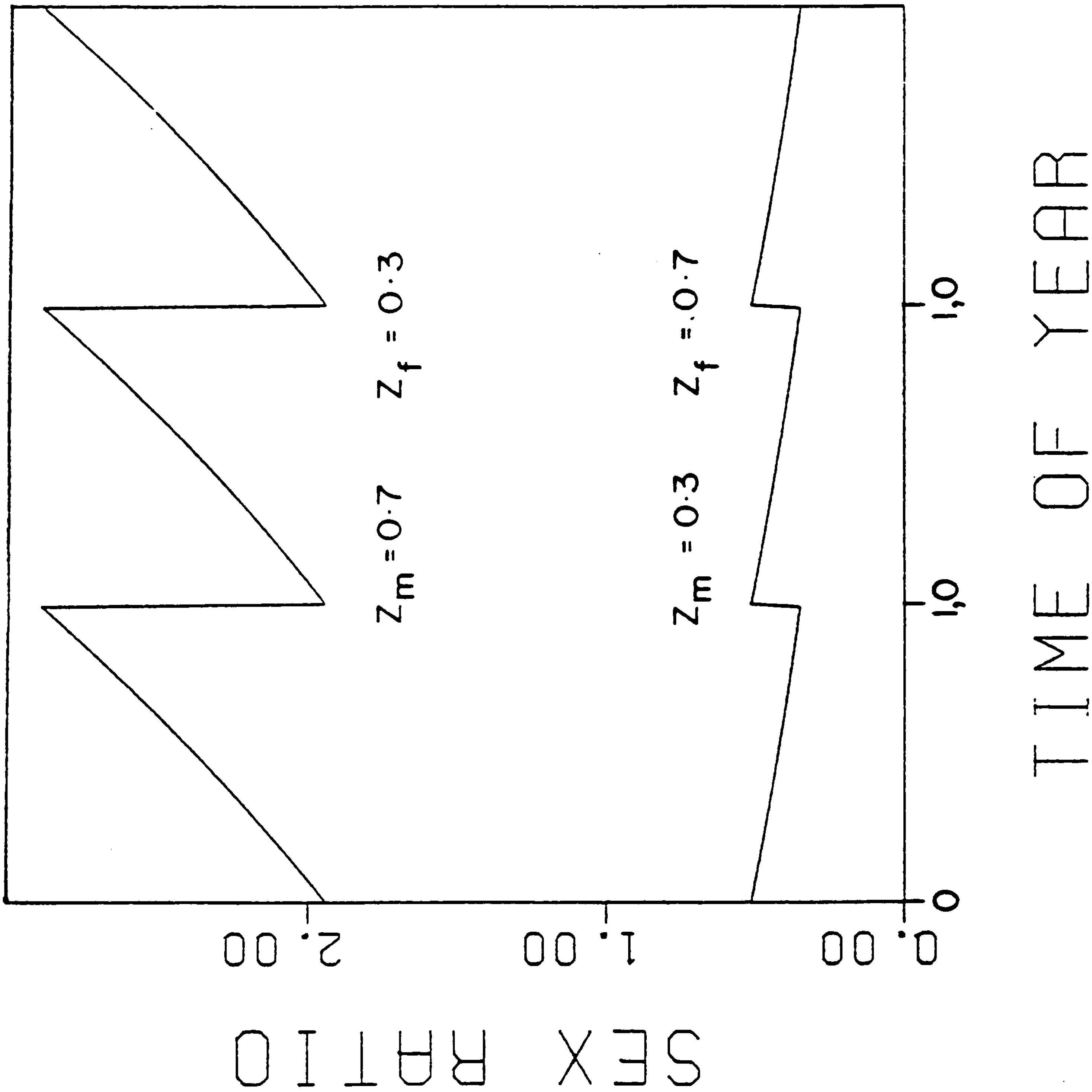

Figure 1. Seasonal change in sex ratio when the sex ratio at age of recruitment is 1.0, recruitment is constant and annual, and mortality rates above the age of recruitment are constant (with respect to age and time).

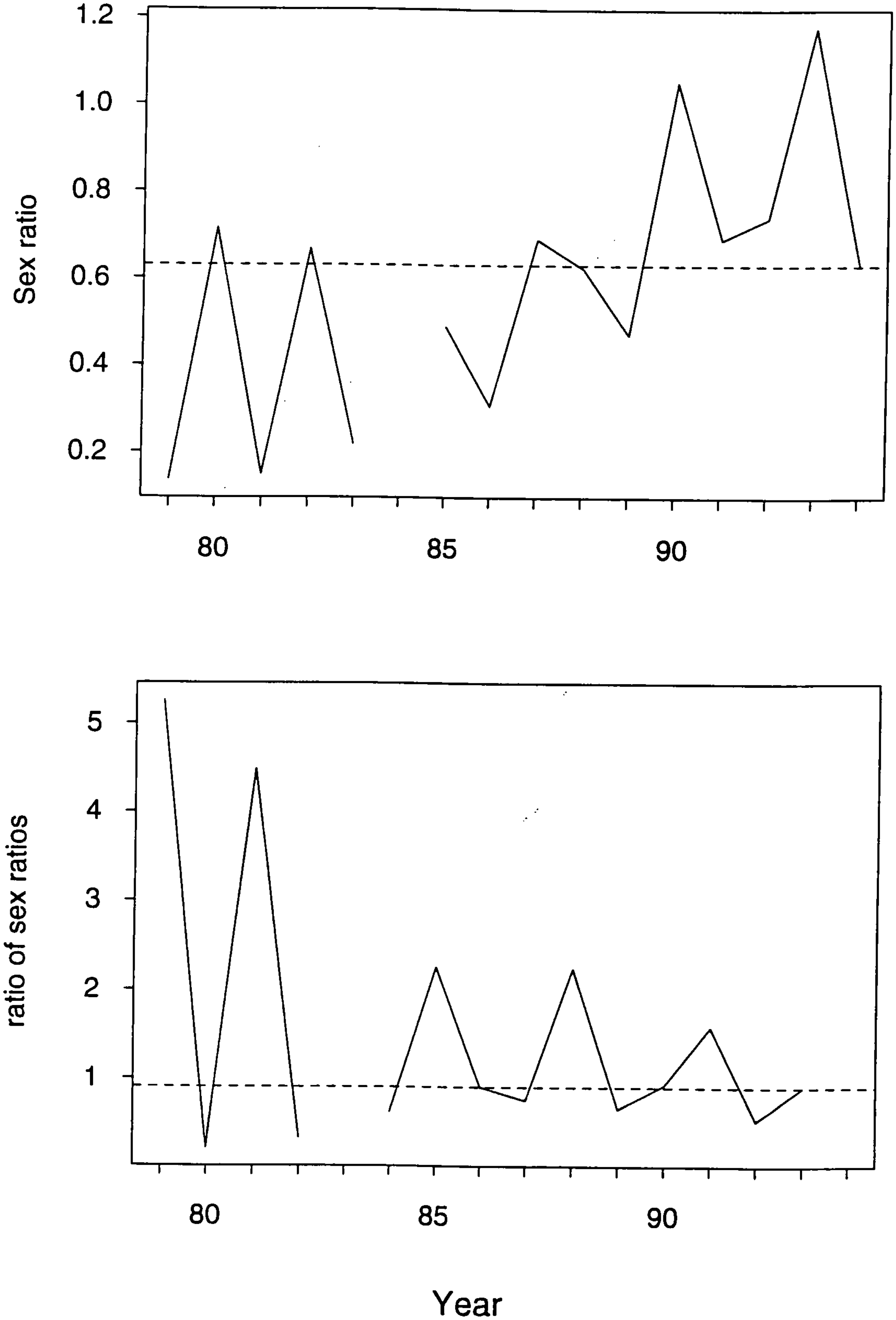

Figure 2 (top). Sex ratio over time of lumpfish in groundfish surveys in NAFO region 3Ps (data from Stansbury et al. 1995). Ordinate is number of males caught in survey divided by number of females; abscissa is the survey year. Horizontal line gives the median of the estimates. (bottom). Estimates of ratio of annual survival rates (S_m/S_f) over time. Estimates are computed from pairs of estimates of sex ratio for adjacent years without correcting for the influence of recruitment. Abscissa is survey year for the first year in the pair of surveys. Horizontal line gives the median of the estimates.