

What Can We Learn about Mortality from Sex Ratio Data? A Look at Lumpfish in Newfoundland

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Abstract.—Sex ratio data can provide information about mortality rates, which may be especially useful for sex-specific fisheries when little other information is available. In this paper, we develop a theory and methods relating sex ratio to mortality rates and apply them to data for lumpfish *Cyclopterus lumpus* on the southern Newfoundland Shelf. If the sexes have different mortality rates, and the rates as well as recruitment are constant with age and time, the sex ratio of the population provides an estimate of the ratio of the instantaneous mortality rates of the sexes. If a cohort can be followed over time, changes in the sex ratio provide an estimate of the ratio of the survival rates of the sexes or the difference in the instantaneous mortality rates. With the latter approach, it is not necessary for the sexes to have equal catchabilities in the survey nor for recruitment to be constant over time. This approach involves fewer assumptions and is of greater general interest, but it requires that cohorts be identified either by aging or tagging the fish. For lumpfish, we used sex ratio data from a research survey to estimate the change in the mortality rate of females, which are the subject of a sex-specific roe fishery. Unfortunately, it is not possible to follow cohorts of lumpfish over time because lumpfish caught in the survey are not aged. Nonetheless, the sex ratio (females : males) decreased progressively from approximately 2.24 in 1985 to 1.09 in 1994. We attribute the decline to a doubling of the mortality rate of female lumpfish caused by the fishery, and our analysis probably underestimates the true change because of failures of assumptions. Our results are consistent with those of other work on lumpfish in Newfoundland and indicate that there is cause for serious concern about the effects of the fishery on lumpfish stocks.

Data on sex ratios of adult fish populations are often easily obtained and may exist for fisheries where little other information is available. It is valuable to be able to use such data to generate information about the effects of a fishery. Such an approach is most applicable for sex-specific fisheries (e.g., Smith and Jamieson 1991; Zhou and Shirley 1995; Rago et al. 1998; Watanabe and Yamasaki 1999; Kennelly and Scandol 2002).

Kelker (1940, 1943) first noted that changes in sex ratio, along with estimates of harvest, could be used to estimate population size in situations in which the sexes experience different mortality rates. The method was treated statistically by Chapman (1954, 1955) and later extended to include estimation of mortality rates by Lander (1962) and Chapman and Murphy (1965). Numerous extensions of the method have been developed since that time. The approach is a specific form of a class of methods now generally known as change-in-ratio methods, which have had a storied history (Paulik and Robson 1969) and are

summarized in Seber (1982) and Williams et al. (2002).

In this paper, we develop a mathematical theory relating mortality rates to sex ratio in the absence of information about harvest and demonstrate its utility in making inferences about changes in mortality rates. We apply the theory to sex ratio data for lumpfish *Cyclopterus lumpus* taken from a groundfish survey on the southern Newfoundland Shelf (St. Pierre Bank, Northwest Atlantic Fisheries Organization Division 3Ps) to examine changes in the mortality rate of female lumpfish.

Lumpfish in Atlantic Canada are exploited exclusively for their roe by a gill-net fishery that began in 1969 to provide a substitute for sturgeon caviar (Collins 1976, 1979). Although numerous studies have been done on aquaculture of the species and the characteristics of the larval and juvenile stages, rather little research attention has been given to adult lumpfish or the effects of the fishery. As a result, there is currently scant information available for assessing lumpfish stocks (FRCC 2003). Nonetheless, the sex-specific nature of the fishery provides opportunities for stock assessment.

Lumpfish move inshore to spawn in spring and summer (Collins 1976). Females depart for deeper

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water after depositing their eggs, leaving males to defend the egg masses (Collins 1979). The fishery effort is concentrated on the inshore spawning areas, and prespawning females are taken to extract their roe (FRCC 2003). Small numbers of males are caught in the fishery but are released because they have no commercial value. Anecdotal information indicates that the survival of released males is high. Therefore, if the exploitation rate of the females increases over time, we would expect to see a progressive change in the sex ratio of lumpfish captured in the research survey. This change in sex ratio would be partially obscured by incoming recruits, which would not have been subjected to the differential mortality of the fishery. Thus, we would have an even more sensitive way to detect changes in the relative mortality of females and males if we could identify recruits in the survey data and remove them from consideration.

Theory of Sex Ratios

Static Sex Ratios

Assume that after some early life history period of duration t_r , the mortality rate becomes constant with age and does not change over time. The number of animals present at time t ($t \geq t_r$) in a group with a homogeneous mortality rate is given by the usual relationship

$$N_t = N_r e^{-Z(t-t_r)}, \quad (1)$$

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 total mortality rate per year.

At the time of recruitment, t_r , the sex ratio is defined to be R_0 . Letting Z_m and Z_f represent the mortality rates for males and females, respectively, which are considered to be constant over age and time, the sex ratio (females : males) at any age $t \geq t_r$, R_t , is given by

$$R_t = R_0 e^{(Z_m - Z_f)(t-t_r)}. \quad (2)$$

If we assume that reproduction occurs continuously throughout the year at a constant level, the overall sex ratio in the population of animals of age $\geq t_r$, \bar{R} , is given by

$$\bar{R} = R_0 \frac{\int_{t_r}^{\infty} e^{-Z_f(t-t_r)} dt}{\int_{t_r}^{\infty} e^{-Z_m(t-t_r)} dt} = R_0 \frac{Z_m}{Z_f}. \quad (3)$$

Thus, when R_0 is 1.0, the ratio of females to males

of age $\geq t_r$ is equal to the ratio of the instantaneous mortality rate of males to that of females and does not depend on the value of t_r . Under the same assumptions, in the case where only animals of age $\geq t_c$ are sampled (as in a survey), for $t_c \geq t_r$, the overall sex ratio for animals of age $\geq t_c$, \tilde{R}_c , is given by

$$\tilde{R}_c = \frac{Z_m}{Z_f} e^{(Z_m - Z_f)(t_c - t_r)}. \quad (4)$$

Fisher (1930) asserted that natural selection would favor females that produced equal numbers of progeny of each sex, such that the sex ratio at birth should be 1.0. Furthermore, he stated that selection should operate in this way even if there is a difference in the mortality rates of the sexes after the parental care period (if one exists). Since R_0 is usually defined at a young age, it should be reasonable to assume that $R_0 = 1.0$ in most cases. This assumption is consistent with abundant empirical evidence, though some protogynous species are obvious exceptions. We make the assumption that $R_0 = 1.0$ throughout the rest of this paper.

In temperate and polar regions the assumption of continuous recruitment is not realistic, as reproduction generally occurs annually during a restricted season. Although recruitment could be spread out over an extended period of time, we assume here that all recruitment occurs quickly in an annual pulse. Hence, the sex ratio can be expected to fluctuate throughout the year and will be closest to 1.0 immediately following the recruitment of young animals having a sex ratio close to 1.0 (Figure 1).

We represent the age structure for each of the sexes in the population by a geometric series (the discrete analog of the exponential model), such that

$$\frac{N_{t+1}}{N_t} = e^{-Z}. \quad (5)$$

The overall sex ratio at time $\alpha = 0$, \tilde{R}_0 , which is defined to be just after recruitment occurs, is given by

$$\tilde{R}_0 = \frac{1 + e^{-Z_f} + e^{-2Z_f} + \dots}{1 + e^{-Z_m} + e^{-2Z_m} + \dots}, \quad (6)$$

which simplifies to

$$\tilde{R}_0 = \frac{1 - e^{-Z_m}}{1 - e^{-Z_f}}, \quad (7)$$

where the tilde indicates annual pulsed recruitment

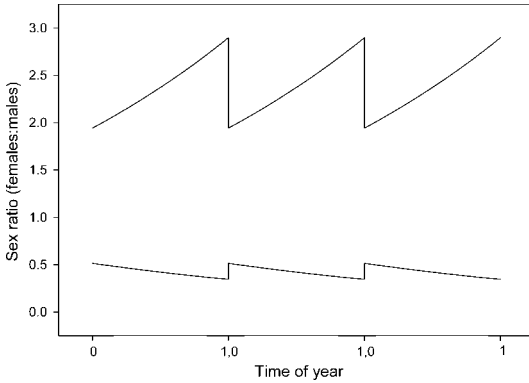


FIGURE 1.—Seasonal change in the overall sex ratio when recruitment occurs annually in an instant and is constant among years, new recruits have a sex ratio of 1.0, and mortality rates above the age of recruitment are constant with respect to age and time. On the x -axis, 0 indicates the instant just after recruitment and 1 the instant just prior to recruitment. In the upper curve, the mortality rate for males is 0.7/year, that for females 0.3/year; in the lower curve, the mortality rate for males is 0.3/year, that for females 0.7/year.

and the subscript denotes the fraction of the year that has elapsed since recruitment (the simplification of equation 6 is shown in Appendix 1). Note that equation (7) is approximately equal to equation (3) when Z_m and Z_f are both small.

At any time of the year α , the overall sex ratio for the population of animals of age $\geq t_r$, \tilde{R}_α , is given by

$$\tilde{R}_\alpha = \tilde{R}_0 e^{\Delta Z \alpha}, \quad 0 \leq \alpha \leq 1, \quad (8)$$

where $\Delta Z = Z_m - Z_f$ (Appendix 2). In the case where only animals of age $\geq t_c$ are sampled, for $t_c \geq t_r$, the overall sex ratio for animals of age $\geq t_c$, \tilde{R}_{α,t_c} , is given by

$$\tilde{R}_{\alpha,t_c} = \tilde{R}_0 e^{\Delta Z(\alpha + t_c - t_r)}, \quad (9)$$

where t_c can take on integer values $\geq t_r$.

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 natural logarithms of both sides of equation (9), we have

$$\log_e(\tilde{R}_{\alpha,t_c}) = \log_e(\tilde{R}_0) + \Delta Z(\alpha + t_c - t_r), \quad (10)$$

which describes a straight line with a regression coefficient that estimates ΔZ . Using the definitions of \tilde{R}_0 and ΔZ , we obtain two equations in two unknowns that 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 the sex ratio can be made throughout much of the year for two or three years (e.g., Hoenig and Lawing 1983).

Dynamic Sex Ratios

Suppose that the expected catch rate of animals older than age t_c in a research survey is

$$E(C_{it}) = q_{it} N_{it}, \quad i \in \{m, f\}, \quad (11)$$

where $E(C)$ is the expected catch, i refers to the sex ($m = \text{male}$, $f = \text{female}$), t refers to the year, q is the catchability coefficient, and N is the abundance. If a survey is conducted starting in year 0 and follows the same cohorts of animals over time, then the ratio of expected survey catches in year t , R_t , is

$$R_t = \frac{E(C_{f,t})}{E(C_{m,t})} = \frac{q_{f,t} N_{f,0} e^{-Z_f t}}{q_{m,t} N_{m,0} e^{-Z_m t}}. \quad (12)$$

We will assume that the ratio $q_{f,t}/q_{m,t}$ does not change over time. Since we are following the same cohorts over time, the ratio of initial abundances is also constant over time and we can write equation (12) as

$$R_t = q^* \frac{e^{-Z_f t}}{e^{-Z_m t}} = q^* e^{(Z_m - Z_f)t}. \quad (13)$$

where q^* is a nuisance parameter that subsumes the catchability coefficients and initial abundances. It is significant that we are not assuming that we know the initial relative abundances of the sexes or that the catchabilities remain constant over time. However, we do assume that q^* is constant, such that the ratio of the catchabilities remains constant over time.

If we plot the logarithm of R_t versus time, we get a linear relationship with a slope equal to the expected difference in mortality rates ($Z_m - Z_f$). In fact, Hoenig et al. (1990) showed that this is a logistic regression model, a specific form of a generalized linear model that can account for small sample sizes and zeros.

A special case of this (Paulik and Robson 1969; Seber 1982) entails comparing the sex ratio in a pair of adjacent years, such that

$$\frac{R_2}{R_1} = e^{Z_m - Z_f} = \frac{S_f}{S_m}, \quad (14)$$

where S_i is the survival rate for sex i , or

$$\log_e \left(\frac{R_2}{R_1} \right) = Z_m - Z_f. \quad (15)$$

Ecologists view the ratio of the survival rates of two groups of animals as a measure of the relative fitness of the two groups (e.g., Manly 1985).

The change in the sex ratio over time for a cohort or group of cohorts provides an estimate of the difference in the instantaneous mortality rates or the ratio of survival rates. To implement this technique, the animals caught in the survey must be divided into two groups, the cohort(s) being followed and the new recruits. Alternatively, the method can be applied to the sex-specific returns over time from a batch of animals tagged in a particular year (Hoenig and Lawing 1983).

We now consider what happens if cohorts cannot be followed over time and instead view the population composition over time (i.e., we view the cohorts we are trying to follow plus whatever recruitment occurs over the time of the study). Clearly, an influx of recruits with a sex ratio close to 1.0 will be averaged in with the older cohorts that exhibit skewed sex ratios. Thus, the observed sex ratio will be closer to 1.0 than it would be if recruits were eliminated. This will tend to bias the estimate of differential mortality toward a smaller difference between the sexes.

In theory, it may be possible to take account of this dilution of the sex ratio, especially if something is known about the longevity of the species. If the species is long-lived and many age groups are 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, it may be simpler and more satisfactory to find a way to age the animals so that recruits can be removed from consideration. In this case, the use of changes in sex ratios becomes especially attractive because we can eliminate the effects of recruitment variability on the estimation of relative mortality rates.

Now consider what happens to a population at equilibrium if the mortality rate of females increases suddenly and remains at the higher level thereafter (e.g., interest in a fishery suddenly increases due to market incentives). The overall sex ratio will eventually reflect the new mortality rate, but it will take time for the population to achieve the new equilibrium. It is instructive to look at the transition of the sex ratio in such a situation. For example, one year after the fishing season in which the fishing mortality of females changes, the sex ratio in the population is given by

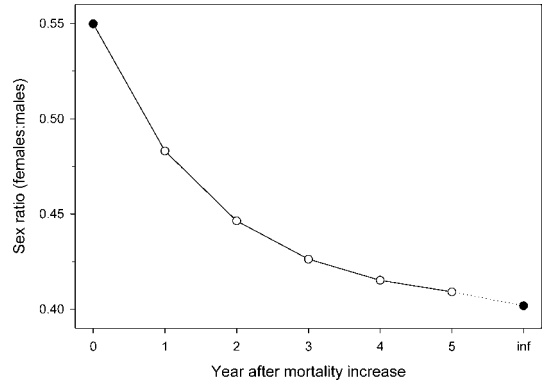


FIGURE 2.—Evolution of the sex ratio over time when there is a sudden and permanent increase in the female mortality rate. Before time 0, the female mortality rate is 0.4/year; after time 0, it is 0.6/year; the male mortality rate is constant at 0.2/year. Solid circles represent equilibrium points, open circles transitional points. The left-most data point is the equilibrium sex ratio under the initial conditions. The sex ratio converges asymptotically to the new equilibrium following the increase in the female mortality rate.

$$\begin{aligned} {}^1\tilde{R} &= \frac{1 + e^{-Z_{fn}} + e^{(-Z_{fn}-Z_{fo})} + e^{(-Z_{fn}-2Z_{fo})} + \dots}{1 + e^{-Z_m} + e^{-2Z_m} + e^{-3Z_m} + \dots} \\ &= \frac{1 - e^{-Z_m}}{1 - e^{-Z_{fo}}} (1 + e^{-Z_{fn}} - e^{-Z_{fo}}), \end{aligned} \quad (16)$$

where the subscripts *fo* and *fn* refer to the old and new mortality rates for females, respectively. At this point, the recruiting cohort has not experienced the new mortality rate, the cohort that recruited the previous year has experienced only the new mortality rate, and all other cohorts have experienced a combination of the old and new mortality rates. Similarly, after two years of fishing at the new level, the sex ratio in the population would be

$$\begin{aligned} {}^2\tilde{R} &= [1 + e^{-Z_{fn}} + e^{-2Z_{fn}} + e^{(-2Z_{fn}-Z_{fo})} + e^{(-2Z_{fn}-2Z_{fo})} \\ &\quad + \dots] / (1 + e^{-Z_m} + e^{-2Z_m} + e^{-3Z_m} + \dots) \\ &= \frac{1 - e^{-Z_m}}{1 - e^{-Z_{fo}}} [1 + e^{-Z_{fn}} + e^{-2Z_{fn}} - e^{-Z_{fo}} \\ &\quad - e^{(-Z_{fn}-Z_{fo})}]. \end{aligned} \quad (17)$$

We can repeat this process and derive expressions that allow us to follow the evolution of the sex ratio over time (Figure 2). Eventually, the sex ratio will reach a new equilibrium. Using the same logic employed to simplify equation (6) (Appendix 1), the ratio of the new equilibrium sex ratio, \tilde{R}_n , to the old equilibrium sex ratio, \tilde{R}_{old} , will be an

TABLE 1.—Lumpfish sex ratio (females : males) data from a research survey on the southern Newfoundland Shelf. Data are from Stansbury et al. (1995); no data were available for 1984.

Year	No. of males	No. of females	Sex ratio ^a	Months of survey
1979	171	1,255	1.99	Jan–Mar
1980	441	617	0.34	Jan–Mar
1981	27	182	1.91	Jan–Mar
1982	4	6	0.41	Apr–Jun
1983	101	464	1.52	Apr–Jun
1984				
1985	1,519	3,121	0.72	Jan–Mar
1986	1,036	3,399	1.19	Jan–Mar
1987	3,521	5,112	0.37	Jan–Mar
1988	731	1,175	0.47	Jan–Mar
1989	1,072	2,292	0.76	Jan–Mar
1990	2,612	2,485	-0.05	Jan–Mar
1991	2,157	3,131	0.37	Jan–Mar
1992	1,097	1,484	0.30	Jan–Mar
1993	996	847	-0.16	Jan–Jun
1994	825	1,311	0.46	Apr–Jun

^a Log_e transformed.

estimate of the ratio of the annual mortality rates of females:

$$\frac{\tilde{R}_n}{\tilde{R}_{old}} = \frac{1 - e^{-Z_f}}{1 - e^{-Z_m}} \quad (18)$$

If the catchability coefficient for males differs from that for females, then the transitional sex ratios observed in a research survey will be biased by the factor q_f/q_m . However, equation (18) will still provide a valid estimate of the ratio of the total mortality rates at two times if the population has achieved equilibrium.

Application to Lumpfish

We apply the above concepts to data for lumpfish from the southern Newfoundland Shelf. The Department of Fisheries and Oceans Canada (DFO) conducted a research trawl survey in the area every year from 1979 to 1994. All lumpfish that were captured were measured and had their sex determined (Table 1), but the fish were not aged. Sex ratio data were not available for 1984.

A linear regression shows that there is a clear downward trend in the sex ratio (females : males) over the period 1985–1994 (Figure 3). We use an ordinary linear regression rather than a weighted regression because we believe that the variability in the data are due more to year effects than to random error. The ordinary linear regression is unbiased but does not minimize the variance. The data for the earlier period, 1979–1983, are consistent with the trend observed for the later years.

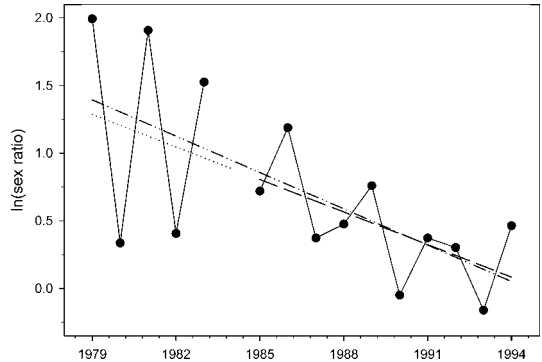


FIGURE 3.—Natural logarithm of the lumpfish sex ratio over time in a groundfish survey on the southern Newfoundland Shelf. The dashed line is a regression fitted to the data for 1985–1994. The dot-and-dash line is a regression fitted to all of the data (1979–1994). The dotted line is an extrapolation of the 1985–1994 regression, showing that the data from the early years of the survey are consistent with the trend seen in the later years despite their variability.

However, the observed sex ratios are much more variable and the total number of lumpfish captured was much lower before 1984 than after 1984 (Figure 3). It is not clear why the catches were so low during the early years of the survey, but this indicates that the early years may have been different in some way from those after 1984. Thus, although it would be valuable to determine the sex ratio as far back as possible, we restrict our analysis to the period 1985–1994.

The observed sex ratio should not change over time if (1) the survey occurred at the same time each year relative to the timing of recruitment and the timing of the fishery, (2) the ratio of the instantaneous mortality rates remained constant, and (3) the magnitude of recruitment remained constant. The actual timing of the DFO trawl survey has varied somewhat over the years but without trend (Table 1). Such variation does not necessarily bias estimates of the sex ratio based on survey catches, and the data do not demonstrate a consistent effect of timing on sex ratio estimates for the period we examined (Table 1). Therefore, we treat any variability in the sex ratio induced by variability in the timing of the survey as a random effect.

For lumpfish on the southern Newfoundland Shelf, the decline in the sex ratio over the period 1985–1994 implies either an increase in female mortality or a decline in recruitment. The survey catches of male lumpfish, which we assume suffer negligible fishing mortality, show a downward

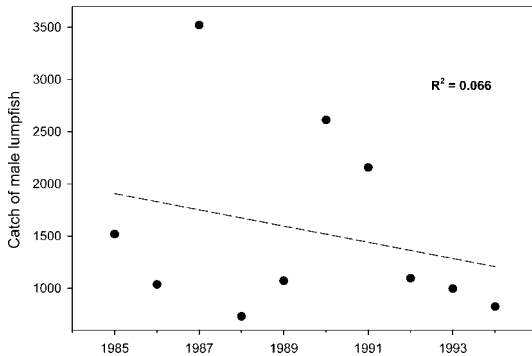


FIGURE 4.—Catch of male lumpfish in a groundfish survey on the southern Newfoundland Shelf, 1985–1994. The dashed line is a linear regression.

trend over time (Figure 4). The predicted survey catch for 1994 was 37% lower than the predicted survey catch for 1985. This pattern is consistent with the idea that recruitment has declined over the period of interest. However, the catches are highly variable and show little trend over time ($r = -0.26$, $P = 0.47$), so the case for a decline in recruitment is not compelling.

If we assume that the sex ratio in 1985 was at equilibrium, then the estimated sex ratio (~ 2.24) represents $(1 - e^{-Z_m}) / (1 - e^{-Z_f})$ (from equation 7). If the sex ratio in 1994 (~ 1.09) was also at equilibrium, its value represents $(1 - e^{-Z_m}) / (1 - e^{-Z_f})$. The ratio of these sex ratios, $1.09/2.24$, is an estimate of the ratio of the annual total mortality rates of females at the two times (as in equation 18). Thus, it appears that the mortality rate for females in 1994 was twice what it was in 1985. This will be an underestimate to the extent that male lumpfish are killed in the fishery. If equilibrium had not been reached in 1994, increases in the mortality rate would not yet be reflected in the sex ratio and the approach will underestimate the change.

Discussion

We have developed a theory and methods that relate sex ratios to mortality rates. Sex-specific differences in mortality rates, such as might be driven by a sex-specific fishery, are fairly common. These differences are reflected in the sex ratio of the population at equilibrium and can be used to make inferences about the effects of fisheries. Where appropriate, we suggest that these ideas be employed in the early stages of fisheries stock assessments.

Our analysis of lumpfish sex ratio data from the

southern Newfoundland Shelf groundfish survey indicates that the mortality rate of females in this area rose considerably over the period 1985–1994. Had we compared the sex ratio in 1994 with that in the early 1980s, the estimated increase in female mortality would have been even greater. We believe that the increase in female mortality was driven by increasing effort in the lumpfish roe fishery. Effort shifted to the lumpfish fishery when stocks of Atlantic cod *Gadus morhua* experienced drastic declines in the late 1980s and early 1990s. These declines ultimately resulted in the imposition of a moratorium on Atlantic cod in 1993 (FRCC 2003).

While variation in the timing of the research survey is likely to reduce its effectiveness in providing an index of abundance (FRCC 2003), it appears that the sex ratio data based on survey catches are reliable for the time period examined here. No other research has been conducted on the utility of the groundfish survey for estimating the relative abundance or sex ratio of lumpfish. Given the variation in the survey timing, there is potential for the seasonality of the lumpfish spawning migration to influence the observed sex ratios. More detailed information about spawning patterns is needed to address this concern and could be acquired through implementation of an index fishermen program (FRCC 2003). The research survey methods were changed in 1995, including a major gear alteration as well as timing, such that our results may not be directly comparable to those of more recent years. However, the approach we have used here could be applied to data for those years to determine whether the trend has continued. This approach could also be used with data collected through an index fishermen program.

More compelling results about mortality rates could be obtained if the lumpfish in the survey were aged. The lack of age data prevented us from monitoring recruitment over time. While we cannot be certain that recruitment did not decline, the evidence for such a decline in the catch rates of male lumpfish is weak. In addition to being able to monitor recruitment, age data would allow us to follow cohorts over time and apply equation (13) in a straightforward manner.

Age data would also make it possible to estimate sex-specific growth rates and to try other techniques used in stock assessments, including (1) catch curve analysis for estimating total mortality rates, (2) open-population index-removal estimation of population size (Collie and Sissenwine 1983), (3) open-population change-in-ratio esti-

mation of population size (Lander 1962; Chapman and Murphy 1965), and (4) incorporation of landings data into open-population change-in-ratio estimation of mortality rates (Chapman and Murphy 1965). Recent advances in techniques for aging lumpfish using otoliths (Albert et al. 2002) should be helpful in this regard.

Our interpretation of the sex ratio data as indicating an increase in the mortality rate of females is supported by two other independent studies. Myers et al. (1995) examined the catches of lumpfish recorded in the logbooks of a limited number of cooperating fishermen from around Newfoundland. They showed substantial declines in catch per unit effort (CPUE) of lumpfish in all areas examined over the years 1989–1994. Neis et al. (1999) conducted extensive interviews of fishermen on the northeastern coast of the island to assess changes in CPUE of lumpfish. They showed declines in CPUE of upwards of 90% between 1980 and 1996, with the declines accelerating during the 1990s. Neis et al. (1999) also concluded that fishing effort had increased substantially and reported that the fishermen they interviewed attributed the decline in CPUE to this increase in effort.

Summarizing survey data through 1994, Stansbury et al. (1995) concluded that it was “very likely” that lumpfish were being overexploited in Newfoundland. The Department of Fisheries and Oceans Canada attempted to ameliorate the effects of the lumpfish fishery through successive gear and effort restrictions from 1993 to 1997. Since 1997, the only management changes have been irregular adjustments to the length of the season, primarily in response to market considerations (J. Perry, Fisheries and Oceans Canada, personal communication). The latest DFO regional stock status report (DFO 2002) notes the substantial decline in landings and survey abundance indices but attributes the declines to factors other than fishing. Unfortunately, no attempt has been made to formally assess the stock or evaluate the effectiveness of management measures (DFO 2002), despite the analyses and recommendations of Hoenig (1995), Myers et al. (1995), Stansbury et al. (1995), and Neis et al. (1999). Given the paucity of information about lumpfish and the apparent steep decline in the stocks, continued exploitation is not precautionary. We believe it is prudent to pursue the approach employed here or other methods to at least preliminarily assess the stocks.

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Appendix 1: Simplification of Equation (6)

The number of animals at any age $t + 1$ is related to the number at the previous age, t , by the relationship (from equation 5 in the text)

$$N_{t+1} = N_t e^{-Z}$$

Thus, the total number of animals in the population, T , is the sum over all ages, such that

$$T = N(1 + e^{-Z} + e^{-2Z} + \dots), \quad (A1.1)$$

where N is the number of recruits, which is assumed to be constant over time.

The sex ratio at time $\alpha = 0$ is the quotient of the sum of the females, T_f , and the sum of the males, T_m :

$$\tilde{R}_0 = \frac{T_f}{T_m} = \frac{1 + e^{-Z_f} + e^{-2Z_f} + \dots}{1 + e^{-Z_m} + e^{-2Z_m} + \dots}$$

Appendix 2: Derivation of Equation (8)

The sex ratio at time of year α ($0 \leq \alpha \leq 1$) is

$$\tilde{R}_\alpha = \frac{e^{-Z_f \alpha} + e^{-Z_f(1+\alpha)} + e^{-Z_f(2+\alpha)} \dots}{e^{-Z_m \alpha} + e^{-Z_m(1+\alpha)} + e^{-Z_m(2+\alpha)} \dots}$$

Factoring out the constants gives

For each T , multiplying each side by e^{-Z} gives

$$(e^{-Z})T = N(e^{-Z})(1 + e^{-Z} + e^{-2Z} + \dots) \quad \text{or}$$

$$Te^{-Z} = N(e^{-Z} + e^{-2Z} + \dots). \quad (A1.2)$$

Subtracting (A1.2) from (A1.1) gives

$$T - Te^{-Z} = N$$

or

$$T = \frac{1}{1 - e^{-Z}}$$

Thus,

$$\tilde{R}_0 = \frac{1 - e^{-Z_m}}{1 - e^{-Z_f}}$$

$$\tilde{R}_\alpha = \frac{e^{-Z_f \alpha}}{e^{-Z_m \alpha}} \cdot \frac{1 + e^{-Z_f} + e^{-2Z_f} \dots}{1 + e^{-Z_m} + e^{-2Z_m} \dots}$$

From equation (6) in the text, the quotient on the far right is \tilde{R}_0 . Thus,

$$\tilde{R}_\alpha = e^{(Z_m - Z_f)\alpha} \tilde{R}_0 = \tilde{R}_0 e^{\Delta Z \alpha}$$