Sex-biased marine survival and growth in a population of coho salmon

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Examination of historical records for coho salmon in Big Beef Creek, in western Washington, U.S.A., indicated that more adult males than females returned to spawn, and that the mean length of the females exceeded that of males. Sex-biased survival and faster growth among females are unusual among salmonids but preceded in some other coho salmon populations. To help determine the stage of life at which sex-biased mortality might occur, the sex-linked GH-Y pseudogene was used to determine the sex of smolts emigrating from Big Beef Creek in 1995–1997. In each of the 3 years the sex ratio was indistinguishable from 50 : 50, indicating similar survival rates in fresh water, and implying that the male and female coho salmon follow different foraging strategies when they are at sea. The female strategy apparently results in greater mortality, but benefits survivors with greater size. The male strategy appears to allow greater survival at the cost of reduced size.

Key words: behavioural ecology; foraging strategies; growth hormone; Salmonidae; sex determination; sexual dimorphism.

INTRODUCTION

Sexual dimorphism is common in animals and is thought to result from combinations of sexual selection and variable parental investment (Pough et al., 1989). Both mechanisms act to produce sexual dimorphism in size and shape in Pacific salmon Oncorhynchus spp. (Groot & Margolis, 1991) and Atlantic salmon Salmo salar L. (Fleming, 1996). In salmonids, female body size is positively correlated with several attributes presumed to increase reproductive success: fecundity and egg size (Beacham & Murray, 1993), success in territorial competition (van den Berghe & Gross, 1989; Foote, 1990) and egg burial depth (van den Berghe & Gross, 1984; Crisp & Carling, 1989).

Although there is considerable variation among populations, adult male salmon are typically larger than conspecific females of the same age within populations, for example chum, O. keta (Walbaum) (Beacham & Murray, 1985) and sockeye, O. nerka (Walbaum) (Blair et al., 1993). Increased size benefits male salmon by increasing their access to potential mates through intrasexual competition (Fleming & Gross, 1994; Quinn & Foote, 1994) and female choice (Foote, 1989). However, males may vary more in size than females of a given age, e.g. pink salmon, O. gorbuscha (Walbaum) (Beacham & Murray, 1985) and may also mature at an age younger than the youngest females.

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(Gross, 1985; Fleming, 1996). Such males are often referred to as jacks if they have migrated to sea or mature parr if they mature prior to seaward migration. Selection for increased size at maturity thus appears to differ between males and females.

In the typical coho salmon, *O. kisutch* (Walbaum), population, all females and most males spend about a year and a half at sea and the jacks spend only a half-year at sea (Sandercock, 1991). Gross (1985) interpreted the occurrence of jacks as evidence of a mixed evolutionarily stable strategy in which a certain number of such small (i.e. young) males reproduce successfully, even in the presence of larger (older) males, by sneaking underneath spawning adults to fertilize some of the eggs released by the female. Gross (1985) described a pattern of disruptive selection on male size in which medium-sized males may be at a selective disadvantage, being too small to fight successfully with the large males for access to mates, and too large to sneak spawning opportunities successfully. Thus sexual selection seems to favour jacks and also large males.

However, Holtby & Healey (1990) provided evidence that coho salmon populations varied in the relative size of males and females, and in the sex ratio of adults. In some populations, notably Carnation Creek, British Columbia, the sex ratio was male-biased and males were smaller than females, whereas in other populations the sex ratio was equal and males were larger. Holtby & Healey (1990) interpreted the inverse correlation of male size and frequency as evidence that males in some populations follow a more risk-averse foraging strategy than females, increasing the probability that a male will survive to reproductive age, at the cost of reduced size. Sexual selection on male body size was hypothesized to be reduced in such populations. Sex-specific foraging strategies have been demonstrated in some fishes [e.g. American plaice, *Hippoglossoides platessoides* (Fabricius) (Swain, 1997); and masu salmon, *O. masou* (Brevoort) (Nagata & Irvine, 1997)].

It is unclear at which point in the life cycle the mortality and growth of females might exceed that of males. Nielsen (1990) observed no difference in the sex ratio or size of males and females in a sample of juvenile coho salmon from a small stream in Washington and Pearcy (1992) concluded that most marine mortality of coho salmon takes place in the first few months at sea, but most growth takes place later.

The purpose of this study was to examine long-term data on the body size and sex ratio of coho salmon at Big Beef Creek (BBC), Washington (47°39' N, 122°46' W) because they appeared to match the pattern of male-biased sex ratio and small-bodied males described by Holtby & Healey (1990). The coho salmon population of BBC has been monitored by the Washington Department of Fish and Wildlife (WDFW) over the past 20 years, making data available to determine the patterns of size and sex ratio. In addition, to help determine the stage of life at which sex-biased mortality might occur, we used the sex-linked GH-Ψ pseudogene (Du et al., 1993) to determine the sex of smolts emigrating from BBC in spring of 1995, 1996, and 1997. A male-biased sex ratio among the smolts would indicate either a biased sex ratio among the embryos or male-biased survival during the year spent in the stream; an equal sex ratio would indicate male-biased survival at sea.
MATERIALS AND METHODS

WDFW HISTORICAL RECORDS OF BIG BEEF CREEK COHO SALMON

WDFW records list the number of adult (one winter, two summers at sea) coho returning to spawn at BBC each fall from 1976 until 1993. From 1978 until 1993, jacks (one summer only at sea) were recorded also. From 1979 to 1993, samples of each sex and age class were measured (fork length) each year. Mean fork length of each age class and standard deviation were reported. Variance and range (minimum and maximum) of length were not listed in the WDFW reports. Because WDFW records are available only through the fall 1993 spawning run, our historical review ends at that point.

After summarizing the records from all available WDFW reports (Blankenship & Tivel, 1980; Seiler et al., 1981, 1984, 1988a, b, 1989, 1991a, b, 1992a, b, 1993a, b, 1994, 1995; D. Seiler, WDFW, Olympia, WA, U.S.A., unpublished data), one-tailed paired t-tests were used on the annual mean values to determine (a) if adult (non-jack) males were smaller than females from 1979–1993, and (b) if adult (non-jack) males were more numerous than females from 1976–1993.

SEX DETERMINATION IN COHO SALMON SMOLTS

WDFW staff mark all BBC smolts with coded wire tags and signal the presence of the tags by removing the adipose fin, thus tissue collection simply involved retaining the clipped adipose fins in 100% ethanol. Adipose fins were sorted by the data on which the smolts were removed from the trap at the mouth of the creek. The GH-Ø pseudogene is sex-linked in coho salmon, occurring only in males (Du et al., 1993). A protocol developed by Forbes et al. (1994) was modified to assay the GH-Ø pseudogene in smolts emigrating from BBC in spring of 1995, 1996, and 1997. Smolts to be sexed were selected from throughout their migration period, late April to late May of each year.

It is possible that phenotypic sex is environmentally labile in coho salmon, and the genetic sex detected by the GH-Ø pseudogene assay does not strictly indicate phenotypic sex (see Craig et al., 1996 for evidence of environmental sex determination in O. nerka). However, in laboratory tests with 40 adult BBC coho, the genetic sex marker GH-Ø matched the phenotypic sex of all individuals correctly (Spidle, unpublished data). Therefore, if environmental sex determination occurs in BBC coho salmon, it is a relatively rare phenomenon.

DNA was isolated by standard phenol–chloroform extraction (Hoelzel & Green, 1992). The smolt DNA was used as template for a low stringency polymerase chain reaction (PCR) using GH-II primers (sequences given in Forbes et al., 1994) to amplify both the GH-II gene and also the GH-Ø pseudogene. Each 10 μl PCR contained 0.5 U Promega Taq polymerase, 1 μl Promega 10 × PCR buffer, 1 μl unquantified template DNA, MgCl₂ to 4 mM, and primers to 0.5 μM. The PCR profile consisted of 30 cycles as follows: 45 s at 94°C, 45 s at 62°C, and 45 s at 72°C.

One microlitre of the PCR product was placed into a 10-μl HinfI restriction digest. Because the GH-II PCR product does not have a HinfI site, and the GH-Ø pseudogene does, only males will show a restriction pattern following electrophoresis (3 h at 5 V cm⁻¹ on a 2.5% agarose/TBE gel; Fig. 1). Restriction digests were visualized by post-staining the gels for 30–60 min in a bath of 1 × SYBR Green (Molecular Probes, Beaverton, OR, U.S.A.), and scanning on a Molecular Dynamics FluorImager 575.

RESULTS

WDFW HISTORICAL RECORDS OF BIG BEEF CREEK COHO

Since records have been kept, female coho salmon at BBC have been consistently larger than males of the same age (Fig. 2). On average, the annual mean female length exceeded that of males by 4.6 cm or 8.6% (paired t-test, t=7.30, P=3.92 × 10⁻⁶). It is interesting to note that the trend of BBC adult males being
smaller than females stands across year to year fluctuations in size of adult coho salmon, and across the long-term trend of decreasing coho salmon size (Fig. 2).

It was also found that male coho have consistently outnumbered females of the same age (Fig. 3). The sex ratio of adult coho salmon (no jacks) averaged 1.21 : 1 (male : female) each year over the period of record (paired $t$-test; $t=5.59$, $P=4.1 \times 10^{-5}$). In addition, over the years with complete records, there were substantial numbers of jacks, averaging 24.0% of the total return and 35.9% of the male return on an annual basis. In these years the sex ratio was 1.91 : 1 (male : female) over all age classes.

SEX DETERMINATION IN SMOLTS

A total of 312 coho salmon smolts collected in 1995–1997 was sexed. Within each year the sex ratio was indistinguishable from 50% (Table I; overall $\chi^2=0.10$, $P=0.75$).
DISCUSSION

It has been demonstrated that coho salmon smolts leave Big Beef Creek at an equal sex ratio, but when they return, the sex ratio is heavily skewed towards males, and that these males are smaller than females of the same age. These results fit the model proposed by Holtby & Healey (1990) to explain the structure of some coho salmon populations. They hypothesized that in some populations, males forage in a more risk-averse manner than females, and therefore grow more slowly but survive at a higher rate. Whether this is due to foraging in different areas, as seen in American plaice (Swain, 1997) and masu salmon (Nagata & Irvine, 1997) or different feeding behaviour is unclear.

There is no direct information on sex-specific distribution or behaviour of coho salmon at sea, but Holtby & Healey (1990) reported that the sex ratio of coho salmon caught with trolling gear (i.e. with baited hooks or lures) became more female-biased late in their final summer at sea. This mortality was not sufficient to explain the surplus of males returning to streams but was taken to indicate more aggressive feeding by females. Based on coded wire tag records (D. Seiler, WDFW, Olympia, WA, U.S.A., unpublished data), BBC coho salmon experience an estimated average natural mortality of about 80% and a fishing
mortality of about 77% on the remainder surviving to their second summer (i.e. large enough to be kept legally). Even if it were substantially female biased, the fishing mortality alone seems insufficient to explain the surplus of adult males. When the jacks are considered, the surplus of males in BBC was even more extreme. Although they spent a year less at sea than the adult salmon, the jacks probably experienced much of the natural mortality that takes place at sea (Pearcy, 1992).

Rapid growth rate has been hypothesized to be partly responsible for the phenomenon of jacking (Rowe & Thorpe, 1990; Berglund, 1992). It is therefore possible that the fastest growing males at BBC are diverted down the pathway of jacking, and do not reach 3 years of age. Our comparison of the length of age 3 males and age 3 females may therefore be biased by exclusion of the fastest growing males. Holtby & Healey (1990) reported the jack frequency for three creeks which show excess female mortality, as observed at BBC, and for three creeks which do not (summarized in Table II).

Of the three creeks with excess female mortality, one had a higher rate of jacking than was found in BBC, and two had a lower rate of jacking than BBC (Table II). Of the three creeks with equal mortality by sex, Waddell Creek had a similar rate of jacking to BBC, Minter had a lower rate, and Hooknose had a greater rate (Table II). Big Beef Creek, therefore, does not appear to have an exceptional amount of jacking relative to other populations of coho salmon. In the absence of an excess of jacking, we conclude that the size discrepancy observed across sexes within a year class at BBC resulted from a genuine difference in growth between the sexes, rather than from the diversion of rapidly growing males to early maturation.

It was beyond the scope of this study to determine the mechanisms underlying the patterns of growth and survival of salmon at sea but possibilities include sex-specific differences in foraging depth, diel activity period, spatial distribution and responses to predators. Nielsen (1990) found no differences in foraging behaviour of juvenile male and female coho salmon in streams but the examination of marine foraging would seem to be a fruitful topic for further research.

<table>
<thead>
<tr>
<th>Creek</th>
<th>% of males returning as jacks</th>
<th>% of coho returning as jacks</th>
<th>Excess of female mortality?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Beef Creek*</td>
<td>35.9</td>
<td>24.0</td>
<td>+</td>
</tr>
<tr>
<td>Carnation Creek†</td>
<td>49.8</td>
<td>35.0</td>
<td>+</td>
</tr>
<tr>
<td>Waddell Creek‡</td>
<td>32.5</td>
<td>18.7</td>
<td>−</td>
</tr>
<tr>
<td>Deer Creek‡</td>
<td>13.6</td>
<td>10.8</td>
<td>+</td>
</tr>
<tr>
<td>Flynn Creek‡</td>
<td>20.4</td>
<td>16.1</td>
<td>+</td>
</tr>
<tr>
<td>Minter Creek‡</td>
<td>22.9</td>
<td>12.8</td>
<td>−</td>
</tr>
<tr>
<td>Hooknose Creek‡</td>
<td>63.2</td>
<td>47.2</td>
<td>−</td>
</tr>
</tbody>
</table>

*This study; †Holtby & Healey (1990) averaged over two freshwater age classes; ‡Holtby & Healey (1990).

+/−, Excess female mortality occurs/does not occur.
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References


