Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*

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Abstract: As with other species, frequency-dependent selection during reproduction has long been proposed as an important mechanism in maintaining alternative male reproductive phenotypes in Pacific salmon (*Oncorhynchus* spp.). Jack salmon mature one year earlier than the youngest females in a population and are much smaller than older "adult" males. We tested the hypothesis that mating success of both phenotypes is consistent with the frequency-dependent selection model. By holding male density constant and varying the frequency of adults and jacks in eight separate breeding groups, we found that adult male access to females, participation in spawning events, and adult-to-fry reproductive success increased with their decreasing frequency in a breeding group. Jacks exhibited the same pattern (increasing success with decreasing frequency), although the relationships were not as strong as for adults. Overall, jack and adult males mated with a similar number of females, but jacks sired only 20% of all offspring. Observational data suggested that adult males benefited from sperm precedence associated with their ability to court females and enter the nest first at the time of spawning. Our work provides the first experimental evidence of frequency-dependent selection during mating in the family Salmonidae.

Résumé : Comme on l'a fait chez d'autres espèces, on a longtemps proposé la sélection en fonction de la fréquence durant la reproduction comme mécanisme important pour le maintien des phénotypes reproducteurs mâles de rechange chez les saumons du Pacifique (*Oncorhynchus* spp.). Les madeleineaux mâles atteignent la maturité une année avant les femelles les plus jeunes dans la population et sont beaucoup plus petits que les mâles « adultes » plus âgés. Nous vérifions l'hypothèse qui veut que le succès de la reproduction pour les deux phénotypes soit compatible avec le modèle de sélection en fonction de la fréquence. En maintenant constante la densité des mâles et en faisant varier la fréquence des mâles madeleineaux et adultes dans huit groupes reproducteurs différents, nous observons que l'accès des adultes mâles aux femelles, leur participation aux épisodes de reproduction et leur succès reproductif de l'adulte à l'alevin augmentent en fonction de leur fréquence décroissante dans un groupe reproducteur. Les madeleinaux mâles suivent le même patron (augmentation du succès avec une fréquence décroissante), bien que la relation ne soit pas aussi forte qu'avec les adultes. Globalement, les madeleinaux et les mâles adultes s'accouplent avec un nombre similaire de femelles, mais les madeleinaux n'engendrent que 20 % de l'ensemble des rejetons. Des observations laissent croire que les mâles adultes jouissent d'une préséance spermatique associée à leur habileté à être les premiers à courtiser les femelles et à pénétrer sur les nids au moment de la fraie. Notre travail fournit les premières preuves expérimentales de la sélection en fonction de la fréquence durant la fraie dans la famille des Salmonidae.

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Introduction

Pacific salmon (*Oncorhynchus* spp.) males exhibit alternative reproductive phenotypes. In several species (sockeye: *Oncorhynchus nerka*; coho: *Oncorhynchus kisutch*; and Chinook: *Oncorhynchus tshawytscha*), males that mature one year earlier (termed jacks) than the youngest females in a population are substantially smaller and less sexually dimorphic than older males (hereafter adults). Theoretical models of the evolution and maintenance of alternative life history

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phenotypes in anadromous salmonids include frequency-dependent selection (FDS) during reproduction and polygenic trait thresholds that influence age-at-maturity (Hutchings and Myers 1994; Fleming 1996; Tomkins and Hazel 2007). Evidence for strong heritability in age-at-maturity in Pacific salmon comes from quantitative genetic studies (Hankin et al. 1993; Heath et al. 1994, 2002) and measures at the population level (Hard et al. 1985; Appleby et al. 2003). Physiological traits mediated by environmental conditions have been shown to trigger early male maturation (Vøllestad et al. 2004; Shearer et al. 2006), and growth thresholds for early male maturity can differ among populations of Atlantic salmon (*Salmo salar*, Piché et al. 2008).

Trade-offs between sexual selection and other forms of natural selection may also shape the frequency of alternative phenotypes in a population. Jacks benefit from higher survival to maturity owing to their reduced time spent at sea or from reduced predation or other forms of ecological selection during reproduction (Quinn et al. 2001). Nevertheless, jacks often represent a small portion of breeding populations of sockeye, coho, and Chinook salmon (Myers et al. 1998; Appleby et al. 2003; Carlson et al. 2004). This may partly reflect disadvantages of small size and reduced access to females during reproduction (Carlson et al. 2004). Surprisingly, the natural relative mating success of jack and adult male Pacific salmon has received very little attention. Van Doornik et al. (2002) estimated the effective proportion of coho salmon jacks in two naturally spawning populations to be 35%, compared with only 2% in a hatchery population. Gross (1985) indirectly estimated mating success in coho salmon jacks at 66% that of older males. The only direct evaluation of jack mating success in Pacific salmon comes from Foote et al. (1997), who used genetic markers and quantified the relative success of seven sockeye salmon jacks in 3.5 m by 3.5 m cages and found highly variable breeding success (3% to 97%; average = 42%) relative to that of older males.

Pacific salmon adult males fight for primary access to females and thus the ability to engage in courtship and spawn with them. Losers often establish "satellite" positions downstream of the courting pair, from which they attempt to "sneak" spawn, and may be excluded from breeding opportunities altogether. The smaller jacks very rarely challenge larger males for courtship opportunities and instead compete for lower positions in hierarchies or hide and wait for opportunities to sneak spawn. Just as adults are not obligate consorts, jacks are not obligate sneakers. Jack Chinook salmon will court and spawn with females in the absence of larger males, and when doing so exhibit high fertilization success (Berejikian et al. 2000; Berejikian and Tezak 2005).

Some fishes display genetically based reproductive polymorphisms that are maintained by FDS (Dijkstra et al. 2008; Hurtado-Gonzales and Uy 2009). FDS favors the rare form, wherein the fitness of one form decreases as it becomes relatively more frequent in the population. Male intrasexual competition, which is very intense in Pacific salmon, has recently been proposed as an important mechanism causing frequency dependence in other taxa (van Doorn et al. 2004). Gross (1985) predicted that increases in the number of jack coho salmon would reduce their proximity to the female and decrease their fitness.

Hutchings and Myers (1988) tested the relationship between sneaker male (mature male parr Atlantic salmon) frequency and mating success, but did not control for male density and therefore could not distinguish between the effects of density and frequency dependence (see Bleay et al. 2007).

In the present study, we quantified jack and adult male Chinook salmon breeding behavior, their proximity to females prior to and during spawning, and conducted DNA-based pedigree analyses to obtain measures of their adult-to-fry reproductive success. We tested for FDS by varying the ratio of jack and adult males in eight separate breeding groups to quantify the effects of jack and adult male frequencies on access to breeding opportunities, participation in observed spawning events, and individual reproductive success. Male density was held constant to avoid confounding frequency dependence with density dependence, and as such this represents the first experimental test of FDS on alternative life history strategies in a salmonid.

Materials and methods

Adult spring Chinook salmon were obtained from the Trask River Hatchery, located on the Trask River, Oregon. Twelve females and 32 males were collected and transported on each of two dates (5 and 12 September 2007) in an oxygenated transport tank to the Oregon Hatchery Research Center, located on Fall Creek approximately 3 h from the Trask River Hatchery. Upon arrival, the fish were held overnight in 4 m diameter tanks supplied with Fall Creek water. The following day, each adult Chinook salmon was anesthetized (MS-222: tricaine methanesulfonate), weighed (nearest g), measured for fork length and postorbital–hypural (POH) length (nearest mm), and externally tagged with a uniquely numbered Petersen disc tag. A portion of the anal fin was removed and preserved in 100% nondenatured alcohol for genetic analysis. This procedure was repeated the next year (3 and 10 September 2008).

Six female and 16 male Chinook salmon were stocked into each of two replicate spawning channels on 6 and 13 September 2007 and two additional channels on 4 and 11 September 2008. The nearly 3:1 male to female sex ratio was established to mimic natural operational sex ratios (ratio of sexually active males to sexually active females). Even when sex ratios are nearly equal, the operational sex ratio can be much greater than one because of the longer breeding duration of males (cf. Hamon et al. 1999). We intentionally varied the number of jack and adult males among the four channels within each year (Table 1). Females from Oregon coast Chinook salmon populations mature at age-3 or older; therefore jacks mature at age-2 (Hankin et al. 1993). The body sizes of jacks (age-2) and adult males (age-3 and age-4) stocked into each section are also shown (Table 1). At the time of stocking, we considered males less than 430 mm POH to be jacks based on Hankin et al. (1993). All fish of this size were morphologically characteristic of jacks (no pronounced secondary sexual characteristics), and subsequent scale analyses indicated that agreement between scale age and size-based determination of male phenotype was 98.4% (126 out of 128 total males).

Each meandering spawning channel measured 8 m wide by 65 m long and contained a mixture of substrates ranging

Table 1. Stocking date, jack frequency, and average (standard deviation in parentheses) postorbital–hypural (POH) length (mm) of Chinook salmon males stocked into each of the four stream channels in 2007 and 2008.

Channel	Stocking date	Jack frequency	POH Adult	Jack	Spawnings observed	Fry collected (sampled)
2007						
A	12 Sept.	8	604 (42)	369 (19)	9	3010 (301)
B	12 Sept.	4	603 (40)	388 (11)	12	5972 (641)
C	5 Sept.	6	541 (61)	394 (24)	2	5198 (572)
D	5 Sept.	5	607 (42)	397 (21)	3	3682 (363)
2008						
A	10 Sept.	6	583 (20)	400 (18)	6	—
B	10 Sept.	4	554 (39)	391 (29)	10	—
C	3 Sept.	10	604 (42)	401 (20)	11	—
D	3 Sept.	8	561 (36)	400 (19)	14	—

Note: The number of adult males in each section equaled 16 minus the number of jacks. Six females were stocked into each section. The total number of spawning events observed and the number of fry collected from each channel (number sampled for DNA pedigree analyses in parentheses) are also shown.

from coarse sand to large cobbles. Each channel contained several meanders, pool–riffle sequences, and large woody debris, placed in such manner that each channel was a very close replicate of the others. Shade cloth was suspended above the streams. Water was diverted from Fall Creek, through a settling pond and then to each channel to provide approximately 0.043 $m^3 \cdot s^{-1}$ per channel. Airlift pumps were used to partially recirculate water through the channels to create a total flow of approximately 0.06 $m^3 \cdot s^{-1}$ in each channel.

Behavioral observations were conducted from dawn to dusk in each channel from the time the fish were introduced until the last female in each channel was no longer sexually active (i.e., no longer nest building). We scanned each of the stream channels multiple times each day to document the activity of each female, and we conducted focal sampling of females that were constructing nests and preparing to spawn. When a female was determined to be constructing a nest, we characterized the male dominance hierarchy surrounding the female. The "dominant" male had primary access to the female, exhibited courtship behaviors (crossing over and quivering), and chased off other males positioned either downstream or upstream of the female. "Satellite" males held positions typically downstream of the courting pair, were frequently chased by the dominant male, and would occasionally sneak into the nest pocket prior to and during spawning. The satellite maintaining closest proximity to the female was designated "S1", the second closest was "S2", and so on. We included males that hid or adopted what have been referred to as "sneaker" tactics (Gross 1985; Healey and Prince 1998) as satellites, because males would often switch between fighting and sneaking behaviors within the same hierarchy. Dominant and satellite males were determined to have participated in a "hierarchy", and the number of hierarchy participations was tabulated for each male over the course of the spawning season.

We attempted to observe as many actual spawning events as possible and record the males that participated in each event and their order of nest entry at the time of spawning. Only instances in which females crouched in the nest pocket, gaped, were accompanied by at least one gaping male, and covered their eggs with a rapidly increased rate of digging (Berejikian et al. 2000) were considered actual spawning events. These were discriminated from false spawning events in which females do not engage in egg covering. We tabulated the frequency of spawning participations for each male and categorized them by rank order of nest entry (1 = first to enter, 2 = second to enter, etc.).

In 2007, channels C and D were stocked and monitored first. The pace of spawning was quicker than we had anticipated, and we did not continuously observe nesting females for long enough periods of time and as a result we missed observing some spawning events. However, in channels A and B (i.e., the second group of fish stocked in 2007), and in all four channels in 2008, we are certain we observed all spawning events that occurred between dawn and dusk because no nesting females were subsequently observed cover digging or constructing new nests (see Berejikian et al. 2007 for details on digging frequencies in Chinook salmon) without our having observed a spawning. Much spawning occurred at night in both channels that was not observed. Thus, the behavioral data reflect only daytime activity, and the reproductive success estimates reflect breeding that occurred throughout the study (day and night).

To quantify individual reproductive success of Chinook salmon spawning in 2007, emergent fry were removed from the stream channels by seining and electroshocking on 29 and 30 January 2008. All channels were sampled again on 25 February 2008, and the channels were dewatered to ensure that all fry were collected. We counted the total number of fry from each channel and subsampled at a similar rate among channels (Table 1). Subsampled fry received a lethal dose of MS-222, and their caudal fins were preserved in 100% nondenatured alcohol for DNA pedigree analyses. Fry offspring were not collected from Chinook salmon spawning in 2008 because eggs from individual nests were intention-

ally excavated when the eggs were at the eyed stage of development as part of a related study to estimate fertilization success of males at different positions in the hierarchy. Thus, we have adult-to-fry reproductive success estimates for four separate breeding groups at four jack–adult ratios from the 2007 spawning season, but not from 2008 (Table 1). Hereafter, we refer to the different jack–adult ratios shown (Table 1) as "jack frequencies" and present the number of jacks within each breeding group (the number of adults is always 16 minus the number of jacks).

Genomic DNA was extracted from the adult and offspring tissue samples and subjected to polymerase chain reactions (PCR) to amplify eight microsatellite loci: Ogo4 (Olsen et al. 1998); Oki100 (K.M. Miller, Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada, unpublished data); Omm1080 (Rexroad et al. 2001); Ots3M (Greig and Banks 1999); Ots9 (Banks et al. 1999); and Ots211, Ots212, and Ots213 (Greig et al. 2003). A fragment analysis was conducted on the PCR products using an Applied Biosystems 3100 genetic analyzer, and Genescan and Genotyper software (Applied Biosystems) was used to determine the genotypes of every individual for each locus. Offspring that were unable to be genotyped for four or more loci were dropped from further analyses. The genotypes of the offspring were then compared with those of the adults using the computer program CERVUS 3.0 (Kalinowski et al. 2007) to determine the parentage of each fry. Parentage assignments had to meet the 95% confidence level to be included in further analyses.

The number of focal sampling observations made on male hierarchies surrounding 46 of the 48 nesting females stocked into the spawning channels in 2007 and 2008 (two females died prior to spawning) ranged from 58 to 198 ($N = 878$). Therefore, within each breeding group, we calculated the proportion of observations in which each male was observed in the dominant and satellite positions in prespawning male hierarchies. We also calculated the proportion of actual spawning observations in which each male spawned as the first, second, third, fourth, or fifth to enter the nest and the total number of spawning participations. The prespawning hierarchy proportions and actual spawning proportions were angular (arcsine square-root) transformed to improve normality. The ability of individuals to achieve each status within a prespawning hierarchy and to participate in spawning events was analyzed by two factor analyses of variance (ANOVAs) with male phenotype (jack or adult) and jack frequency as the main effects. Separate ANOVAs were conducted for each year. We calculated the average rank order of nest entry at spawning for each phenotype within a breeding group. Similar patterns were evident among breeding groups (see Results), so we used a t test on the combined data to compare the rank order of nest entry between jack and adult males. In 2007, individual reproductive success was calculated as the number of fry per male spawner and expressed as a proportion of the total number of fry produced in its respective channel. Angular transformed proportions were analyzed by the same ANOVA model as the behavioral measures. A regression analysis was performed to test for a linear relationship between the average reproductive success of each phenotype within a breeding group and its frequency.

Results

Adult males competed primarily among themselves to establish dominance and attain courtships with nesting females. Adult males also competed among themselves and with jacks for satellite positions in the hierarchies. Adult males attained the dominant position in prespawning male hierarchies more frequently than jacks in both 2007 and 2008 (Table 2). Adult males were observed significantly more often than jacks in the first satellite (S1) position in 2008, but not in 2007 (Table 2). Jacks were significantly more often observed in the S2 position in 2007 and S3 position in 2008 (Table 2). There were no significant interactions between jack frequency and male phenotype on participation at any level within the prespawning hierarchies (Table 2).

Jacks used a number of different tactics to maintain positions in hierarchies and position themselves for spawning. Jacks often mimicked female coloration patterns (dark lateral stripe), hid under logs or in side channel pools, held positions in very shallow water downstream from nests where larger males appeared reluctant to chase them, and held positions alongside or downstream of larger males. From these peripheral positions, they periodically darted into the nest to position themselves for spawning. Jacks did court females, but it was very infrequent and typically occurred shortly after females had spawned or were still hours away from their next spawning event when adult males less vigorously defended females.

We observed a total of 67 spawning events (Table 1), 27 (40%) of which involved a single male participant, while the remainder included from two to five participants. Participation in prespawning hierarchies was a significant predictor of participation in observed spawning events ($P < 0.05$ for all linear regressions; Fig. 1). In 2007, there was a significant interaction effect between male phenotype and jack frequency on spawning participation (Table 2). Jack participation in spawning events decreased and adult male participation increased with increasing jack frequency (Fig. 2). The interaction term was not significant in 2008 (Table 2, Fig. 2). However, in the group containing four jacks in 2008, all jacks were dead by 14 September before 80% of the observed spawning events had occurred. The premature deaths were caused by injuries from one adult male that repeatedly chased, bit, and shook all of the jacks. We did not observe comparably violent aggression or premature jack deaths to this extent in the other seven breeding groups. Although the statistical analyses of spawning success in 2008 include the breeding group with four jacks, it is important to recognize that the greater spawning success of adult males in this group reflects the absence of jacks and a different mechanism affecting reproductive success than in the other seven breeding groups.

Adult males participated in a significantly greater number of spawning events than jacks in 2008, but not in 2007 (Table 2). Adult males were significantly more often observed as the first to enter the nest during spawning than jacks in both years (Table 2). In fact, jacks were observed as the first male to enter the nest on only two occasions. There were no significant differences between jack and adult males in their spawning frequency as the second or third

Table 2. Tests for effects of male phenotype and jack frequency by male phenotype interactions on behavioral measures of breeding success.

	Phenotype			Phenotype × frequency	
	F	*P*	Greater	*F*	*P*
2007					
Spawning participations	0.013	0.910	NS	7.03	**0.013**
First to enter	4.78	**0.037**	Adult	0.85	0.364
Second to enter	1.13	0.297	NS	11.10	**0.002**
Third to enter	2.57	0.120	NS	0.46	0.502
Total courtships	10.48	**0.002**	Adult	0.43	0.729
Dominant	13.89	**<0.001**	Adult	0.28	0.841
S1	0.85	0.359	NS	0.68	0.571
S2	5.74	**0.020**	Jack	1.77	0.164
S3	2.27	0.137	NS	1.45	0.237
2008					
Spawning participations	9.84	**0.003**	Adult	1.99	0.126
First to enter	9.13	**0.004**	Adult	0.64	0.591
Second to enter	2.37	0.130	NS	0.52	0.669
Third to enter	0.03	0.873	NS	3.64	**0.018**
Total courtships	35.85	**<0.001**	Adult	0.20	0.894
Dominant	35.01	**<0.001**	Adult	0.47	0.707
S1	9.49	**0.003**	Adult	0.35	0.790
S2	17.26	0.512	NS	2.15	0.105
S3	12.23	**0.001**	Jack	0.98	0.409

Note: *F* tests and *P* values from the analyses of variance (ANOVAs) for the main effect of male phenotype (jack or adult male) and the interaction between jack frequency and male phenotype are shown. The phenotype with the greater mean value is shown where there were significant effects ($P < 0.05$, in bold; NS = nonsignificant). The total spawning participations and order of nest entry in 2007 include analysis of breeding groups that contained four or eight jacks. The groups that contained five or six jacks were excluded because too few spawning events were observed (see Table 1). S1, closest satellite position; S2, second closest position; S3, third closest position.

Fig. 1. Frequency of participation in observed spawning events plotted against frequency of participation in prespawning hierarchies. Each point represents a different male and each symbol represents a different breeding group. In 2007, solid triangles = four jacks and open triangles = eight jacks. In 2008, open circles = four jacks, solid diamonds = six jacks, solid circles = eight jacks, and open diamonds = ten jacks. All six correlation coefficients were significant ($P < 0.05$). Analyses from channels C and D in 2007 were not conducted because too few spawning events were observed.
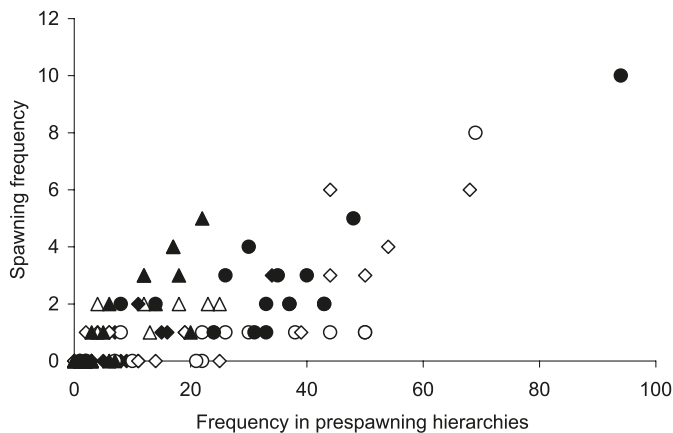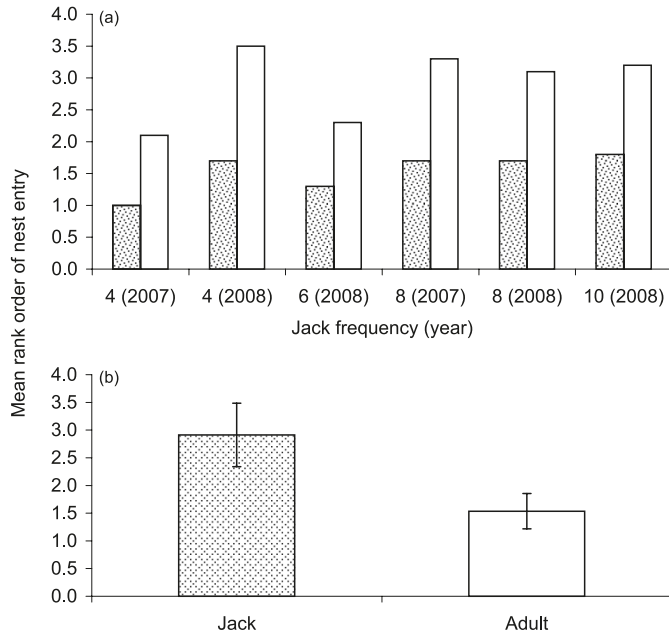

Fig. 2. The average proportion (±95% confidence interval, CI) of observed spawning events in which adults (open bars) and jacks (stippled bars) participated. The number of jacks in each of the independent breeding groups is shown on the *x* axis with the year in parentheses. The asterisk next to the 4 jack group in 2008 indicates that all jacks had died prior to 80% of the observed spawning events, so all subsequent participations were limited to adult males.
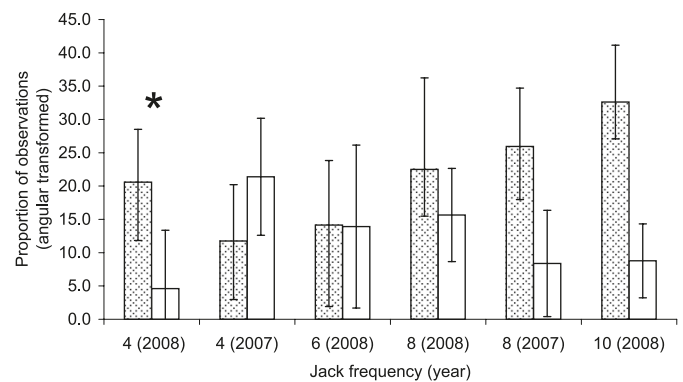
male to enter the nest during spawning in either year (Table 2). There were significant phenotype by jack frequency interactions for the participation as the second male to enter the nest in 2007 and third to enter in 2008 (Table 2). In both cases, jack and adult male success in spawning from a satellite position was inversely related to their frequency

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Fig. 3. (*a*) Average rank order of nest entry for jack (stippled bars) and adult (open bars) males. Lower ranks entered the nest sooner than higher ranks (i.e., the first male to enter the nest at the time of spawning was given a rank of 1, second to enter had a rank of 2, and so on). Panel (*b*) shows averages and 95% confidence intervals for the combined data.
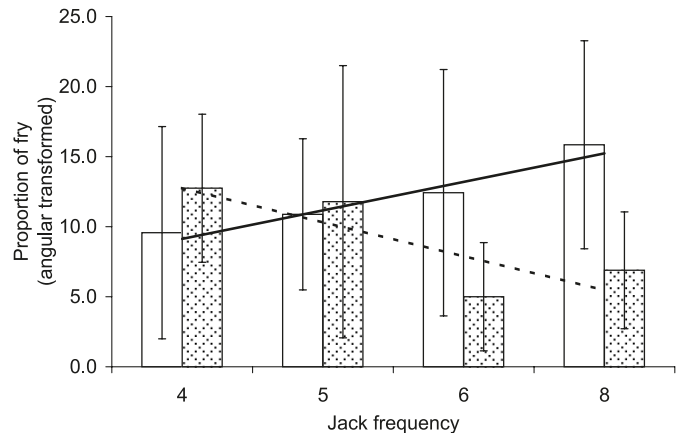

Fig. 4. Average (±95% confidence interval, CI) proportion (angular transformed) of offspring produced within each breeding group for jack (stippled bars) and adult males (open bars). The lines reflect least squares regression analysis testing for linear relationships between jack frequency and mean reproductive success values ($N = 4$ breeding groups) for jack (dashed line, $r^2 = 0.56$, $P = 0.26$) and adult males (solid line, $r^2 = 0.93$, $P = 0.03$).

in a breeding group. Overall, adult males had a significantly lower rank order of nest entry (i.e., entered the nest earlier, $t = 11.316$, $P < 0.01$), and the difference was fairly consistent across the range of jack frequencies (Fig. 3).

We assigned parentage to 1877 offspring from the four breeding groups in 2007. Nine offspring were dropped from the analyses because they could not be genotyped for at least four loci. All parentage assignments met the 95% confidence level. All of the females, except for the two that died prior to spawning, produced offspring in the 10% subsamples of the four fry populations, so the male reproductive success results reflect matings that occurred in two breeding groups with five females each ($n = 5$ jacks and $n = 6$ jacks) and two breeding groups with six females ($n = 4$ jacks and $n = 8$ jacks).

The interaction between phenotype and jack frequency on adult-to-fry reproductive success was nonsignificant ($F_{[3,56]}$, $P = 0.345$; Fig. 4). The regression analysis did indicate that average adult male reproductive success increased significantly with increasing jack frequency (and decreasing adult frequency, $n = 4$ breeding groups, $r^2 = 0.93$, $P = 0.031$; Fig. 4). The average jack reproductive success declined with increasing jack frequency, but the correlation was not significant ($n = 4$, $r^2 = 0.56$, $P = 0.23$; Fig. 4). The relationships between frequency and reproductive success had a stabilizing effect on the total proportion of fry sired by the two male phenotypes in each breeding group. In the breeding group with the fewest jacks, 21% of all fry (i.e., fry per jack × the number of jacks) were sired by jacks, which was very close to their proportion in the breeding group (25%). Jacks collectively sired 33%, 9%, and 19% of the fry frequencies of five, six, and eight jacks per breeding group, re-

spectively. The combined average jack contribution across all four breeding groups in 2007 was 20.3% and did not differ significantly from the total adult contribution (79.7%, $F_{[1,56]} = 1.23$, $P = 0.27$). Jack and adult males mated with a similar number of females across all breeding groups (2.0 mates per adult male and 2.1 mates per jack), but the number of offspring produced per mating was significantly less for jacks (10.2 per mate) than for adult males (23.6 per mate, $t = 2.64$, $P = 0.011$).

Discussion

As expected, adult males competed for courting opportunities, in many cases monopolizing access to females, and spawned as the lone male participant in over one-third of the observed spawning events. The finding that the much larger adult males dominated access to females is not surprising given the large body of literature indicating that larger salmonid males tend to have a breeding advantage over smaller males (reviewed by Esteve 2005). Jacks participated almost exclusively by sneaking into the nest from satellite positions and sired 20.3% of all progeny that were genotyped.

Sperm quality, ejaculate volume, and precedence (timing of contact with the egg) could all potentially affect fertilization success. It is unclear from this study whether the later timing of nest entry of jacks participating in multiple-male spawning events impaired their fertilization success, because we could not differentiate between offspring that were produced from single pair matings and those produced during multiple-male spawning events. In rainbow trout, sperm volume did not affect fertilization rate and males did not adjust milt volume based on male competitor presence (Fitzpatrick and Liley 2008). In Chinook salmon, jack and adult males were equally capable of fertilizing eggs during natural spawning when each phenotype was paired as the lone consort with an individual female (Berejikian and Tezak 2005).

In the present study, the finding that jacks entered the nest later and had lower reproductive success and significantly fewer offspring per mate is consistent with the hypothesis that sperm precedence influenced fertilization success in multiple-male spawning events. Sperm precedence effects have been inferred in other studies on chum salmon (*Oncorhynchus keta*: Schroder 1981), sockeye salmon (Chebanov et al. 1983), and iteroparous Atlantic salmon (Mjølnerød et al. 1998) and brook trout (*Salvelinus fontinalis*: Blanchfield et al. 2003).

The significant positive correlation between jack frequency and average adult male reproductive success, the significant interactions between male phenotype and jack frequency for total spawning participations in 2007, and the sneak spawning opportunities (second and third to enter the nest during spawning) indicate support for the FDS model. Although a significant interaction for total spawning participations was not detected in the 2008 data, the patterns were similar to those in 2007 except for the breeding group containing the fewest number of jacks (four) for the reasons mentioned in the Results. The present study is the first to our knowledge to experimentally test the hypothesis of FDS in salmonids. Gross (1985) found that intermediate-sized coho salmon males maintained distances further from nesting females than did larger adult males and smaller jacks, suggesting disruptive selection on male size. In Atlantic salmon, the average proportion of eggs fertilized by mature male parr, which are an order of magnitude smaller than anadromous males, decreased with their increasing frequency in the population (Hutchings and Myers 1988). However, parr frequency increased with total male density, so density dependence could not be separated from frequency dependence. Evidence for FDS, controlling for density dependence, has been clearly demonstrated in lizards (Sinervo and Lively 1996; Bleay et al. 2007), where it functions to maintain genetic color polymorphisms that have a high heritability (96%).

Is frequency-dependent mating in salmon a result of intrasexual male competition or female choice? Male phenotypic diversity in other fishes may evolve and persist through male competition (Dijkstra et al. 2008) or as a mechanism to circumvent female choice (Hurtado-Gonzales and Uy 2009). Evidence for female choice comes from females delaying nest construction in the presence of smaller (putatively less preferred) males (Foote 1989; Berejikian et al. 2000; but see Allen et al. 2007). However, male competition for access to females is very intense, appears to constrain female choice, and strongly influences mating patterns in salmonids. We hypothesize that the evidence for FDS in the present study resulted from male competition within life history phenotypes. That is, when jacks were abundant they competed for fewer satellite and sneak spawning opportunities per individual jack, and when adult males were abundant there were fewer courting opportunities per individual. Furthermore, we observed some evidence of jacks mimicking female coloration patterns. Female Chinook produce a thick lateral band as spawning nears, which becomes continuous just prior to spawning, then dissipates and reappears just prior to each subsequent spawning event. Jacks in our study, and some satellite adult males, mimicked female spawning coloration by producing and maintaining a dark,

thick band along the lateral line, which we suspect functions to reduce competitive pressure (attacks) from the dominant male.

In Atlantic salmon, alternative male life history phenotypes are presumed to be maintained by FDS, for which there is some support (Hutchings and Myers 1988). Atlantic salmon age-at-maturity is best modeled as a threshold trait rather than purely status-dependent, because it is heritable and differs among populations and among individuals within a population (Piché et al. 2008). Growth rate and attainment of a threshold body size determines whether an individual will mature. Evidence for strong heritability for age-at-maturity (Heath et al. 2002), similar growth and body size triggers for early male maturation (Larsen et al. 2004; Shearer et al. 2006), and the evidence of FDS provided in the present study suggest that alternative male phenotypes in Chinook salmon may be most accurately modeled in a manner similar to that for Atlantic salmon.

To the extent that age-at-maturity of Chinook salmon populations fits the threshold trait model, it may be strongly influenced by anthropogenic forces. Most notably, the majority of Chinook salmon along the west coast of the USA and Canada are now produced from hatcheries (Naish et al. 2008). During the artificial spawning process, hatchery operators may exert intentional and unintentional bias regarding the inclusion of jack gametes that may reduce jack contributions in coho salmon (Van Doornik et al. 2002). Even random mating schemes in hatchery programs may significantly alter age-at-maturity of the offspring in Chinook salmon (Hankin et al. 2009). Currently, Pacific salmon hatchery operations in the USA follow no explicit scientifically based guidance regarding the appropriate level of jack inclusion during artificial spawning. However, Hankin et al. (2009) have proposed a model where matings would be restricted pairings in which male length exceeds female length to avoid reducing age-at-maturity. Data from the present study might suggest that hatchery broodstock management should be sensitive to changes in the relative abundance of jack and adult males where mimicking natural life history patterns and selection processes is a management objective. Generally, our data suggest that a greater per capita contribution should come from adult males when they are relatively rare in the population, and a lower per capita contribution from a greater number of individuals may be more appropriate in years when the adult to jack ratio is high. In many river systems, weirs are deployed to count, sample, and in some cases control the abundance of hatchery and natural spawners. Our data suggest that jacks not be excluded intentionally because contribution will be stabilized to some degree by FDS. However, other anthropogenic forces such as size-selective harvest (Hankin and Healey 1986; Hankin et al. 2009) and hatchery rearing methods that promote high juvenile growth rates and early male maturation (e.g., Knudsen et al. 2006) should be considered as well.

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