

Tooth size and skin thickness in mature sockeye salmon: evidence for habitat constraints and variable investment between the sexes

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Abstract – Pacific salmon develop many sexually dimorphic features at maturity, and the extent of development varies among populations. In this study, we compared a suite of traits including body length, body depth, jaw length, tooth size and skin mass in male and female sockeye salmon breeding in beach and creek habitats. Both tooth size and skin mass varied positively with body length. Within each of the breeding habitats, males had longer teeth than females, and within each sex, beach spawners had longer teeth than creek spawners. Males also had heavier skin than females in each habitat but, unlike the case with tooth size, creek spawners showed a much stronger relationship between skin mass and body length than did beach spawners. Tooth length was positively related to jaw length and skin mass among individuals within a given sex and habitat. Taken together, these results suggested that variation in tooth size parallels variation in other sexually dimorphic traits. Males and beach spawners tend to exhibit large trait values relative to females and creek spawners, and ‘well-endowed’ individuals displayed high values of all traits rather than a trade-off as might occur if investment in one trait compromised investment in others. However, the finding that creek fish tended to have thicker skin for a given body length than did beach fish suggested that factors other than merely defense against conspecifics during battle, such as abrasion and desiccation resistance in small streams, may influence the evolution of skin mass in mature sockeye salmon.

Key words: abrasion resistance; aggression; defense; desiccation; morphology; spawning habitat

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Introduction

Pacific salmon (*Oncorhynchus* species) undergo many physiological, behavioral and morphological changes associated with mate selection, competition and display when they return from the ocean to their natal sites to spawn, including changes in fat content, skin color, body depth and jaw structure (Schroder 1981; Fleming & Gross 1994; Hendry & Berg 1999). Intraspecific differences in many sexually selected

traits occur among populations of salmon (e.g. Beacham & Murray 1985; Fleming & Gross 1989). Notably, male sockeye salmon (*Oncorhynchus nerka* Walbaum) from beach spawning populations had deeper bodies than those from river spawning populations, with a strong correlation between the water depth of the spawning habitat and the body depth of the fish (Blair et al. 1993; Quinn et al. 2001a). This pattern was attributed to the population-specific balance between sexual selection and natural

selection in different spawning environments (Quinn & Foote 1994; Quinn et al. 2001b; Hamon & Foote 2005). In addition to these differences in traits among populations, populations with more arduous migrations from the ocean to the spawning grounds allocate less energy to sexually selected traits and express smaller trait values (e.g. Kinnison et al. 2003; Crossin et al. 2004).

Observations of breeding salmon reveal that in addition to jaw length and body depth, teeth become exaggerated relative to their immature size, especially in males (Vladykov 1962; Foote et al. 1997). There are many studies on tooth morphology in fishes (e.g. Clifton & Motta 1998; Motta & Wilga 1999; Wautier et al. 2001, 2002), and the cranial bones and teeth of the different salmon species were described by Vladykov (1962). Foote et al. (1997) quantified the general observation that males had larger teeth than females for a given body size in a sockeye salmon population. However, the variation in teeth size has not been quantified among populations, nor has it been explicitly linked to the expression of other sexually dimorphic traits. Specifically, it is unknown whether populations with large values for other traits such as jaw size and body depth (notably, those spawning on beaches of lakes) also have large teeth, after adjustment for overall body size, compared with salmon spawning in small creeks.

There is also evidence of sexual dimorphism in the epidermis of salmonids (Stoklosowa 1966, 1970; Pickering & Macey 1977). Males exhibit thicker skin than females in brook charr, *Salvelinus fontinalis*, Sunapee, *Salvelinus aureolus*, and Arctic charr, *Salvelinus alpinus* (Pickering 1974; Pickering & Macey 1977), and within a population of sockeye salmon (Foote et al. 1997). Positive relationships between body size and skin thickness in males were also reported for brown trout, *Salmo trutta*, Arctic charr (Pickering 1974; Noakes 1980) and sockeye salmon (Foote et al. 1997). Males tend to be larger than females and so differences in skin thickness reflect, in part, differences in overall body size.

The ecological basis for differences in skin thickness between sexes and populations are unclear, as thick skin can serve several roles. Salmon engage in combat, attacking other salmon by biting them on the body, caudal peduncle or jousting with jaws (Kerns & Donaldson 1968; Schroder 1981). Among females, these attacks express competition for breeding sites whereas male aggression reflects competition for access to reproductively active females (Schroder 1981; Fleming & Gross 1994). Males have larger jaws and teeth than females (Foote et al. 1997) though both sexes display comparable levels of aggression (Quinn 1999). Presumably, larger teeth confer an

advantage during these attacks, and skin thickness may have evolved as protection. In this case, males might need thicker skin than females, and fish in populations with large teeth should also have thick skin.

Skin thickness might also have evolved as protection against abrasion and desiccation in both sexes and for protection against damage during redd excavation in females (Stoklosowa 1966; Richards & Pickering 1978; Noakes 1980). Females spend a considerable amount of time moving gravel as they prepare their nests, so they might have thicker, more abrasion-resistant skin than males. We have observed females whose skin and muscle have been so abraded from digging that the caudal fin rays and hypural bone are fully exposed. On the other hand, desiccation resistance may be more important to males, as their deep bodies protrude out of the water, exposing them to sun and wind more than females. Shallow streams are harsh abiotic environments for adult salmon where exposure to the air can lead to desiccation, causing evaporative water loss and thermal stress, and close contact with the streambed can lead to substantial abrasion on the ventral surfaces of the fish. Physical trauma and exposure to ultraviolet (UV) radiation affect skin structure, which can lead to infection and osmoregulatory failure in fish (Nowak 1999). Amphibious fishes exhibit morphological adaptations in the integument to resist desiccation because of prolonged contact with the air (reviewed in Sayer 2005). Therefore, if skin thickness has evolved in response to a harsh abiotic environment, we would expect salmon spawning in shallow creeks to display thicker skin than those breeding in deeper water such as lake beaches. On the other hand, if skin thickness has evolved in concert with other sexually selected traits, we would expect populations with deep bodies, large jaws and large teeth to also have thicker skin.

The objectives of this study were to compare tooth size and skin mass (our proxy for skin thickness) of sockeye salmon breeding in different habitats (beaches vs. creeks), between sexes, and to determine whether variation in these traits was positively correlated with two indices of overall body size (body length, body depth). Specifically, we tested the following hypotheses: (i) fish spawning along beaches will have longer teeth and heavier skin than populations spawning in creeks, paralleling the observed variation between these habitats in other traits; (ii) males will display larger trait values than females, paralleling the observed variation in other traits that differ between the sexes; (iii) average tooth length will be positively correlated with jaw length and skin mass.

Materials and methods

Study sites

Adult sockeye salmon were sampled from eight populations in Bristol Bay, Alaska, chosen to represent different habitats, body sizes and extent of sexual dimorphism (Blair et al. 1993; Quinn et al. 2001a). We sampled three creeks (Bear, Hansen and Yako) in the Wood River system entering Lake Aleknagik and one population spawning on a mainland beach (N-4, in Lake Nerka in this system). We also sampled four beach spawning populations in Iliamna Lake: two mainland populations (Finger Bay and Knutson Bay) and two island populations (Woody Island and Fuel Dump Island). A description of these study sites can be found in Quinn et al. (2001a). These systems are geographically proximate, and all the sockeye salmon returning to these systems to breed return from the ocean at the same time of the year and undergo similar migrations (both in terms of distance migrated and elevation gained; Burgner 1991). These similarities among systems minimised possible bias because of differing energetic requirements needed for migration (e.g. Crossin et al. 2004).

Fish were sampled between 25 July and 24 August, 2002 at the peak of maturation for their respective populations to avoid the shrinkage associated with senescence and death (Quinn & Blair 1992). At Hansen Creek, the fish sampled had just stranded as they tried to ascend the shallow mouth of the creek. Fish sampled in all other sites were captured by beach seine, anaesthetised and sacrificed. In Pacific salmon, the sex ratio is often somewhat male-biased at the beginning of the run and the fish tend to be larger, on average, than later arriving fish (Hendry et al. 1999; Morbey 2000; Woody et al. 2000; reviewed in Quinn 2005). Our objective was to characterise the relationship between various traits and body size, and not the relationship between these traits and arrival timing to the spawning grounds. Consequently, our sampling at all sites occurred around the midpoint of each run and covered a range of body sizes to define the relationship between each trait and body size.

Data collection

Sampled fish were measured for body length (mid-eye to hypural plate to avoid bias from variation in jaw length between sexes and among populations), body depth (dorso-ventral distance, from the anterior insertion of the dorsal fin to the belly), jaw length (mid-eye to tip of upper jaw), tooth length and skin mass. The heads and a skin sample approximately 2 cm², including the dermis and some underlying muscle tissue were removed from each fish and stored frozen until



Fig. 1. Frontal view of sockeye salmon teeth sampled in this study. Three teeth on each side of the midline of the upper and lower jaws were measured for a total of six teeth from each jaw.

the teeth and skin could be measured. The six most anterior teeth in the upper and lower jaws, identified by counting three teeth on either side of the jaw from the midline for both the upper and lower arches, were measured for length (Fig. 1). These teeth are equally sized and more exaggerated relative to the prespawning state than other teeth in the jaws, and, given their location, are the most likely teeth to be used as weapons in combat. Tooth length was measured with digital calipers to 0.01 mm as the straight-line distance from the tip of the tooth cusp to the insertion into the jaw tissue. An average tooth length was calculated for the 12 teeth measured per individual (six teeth each from the upper and lower jaws).

All skin samples were taken from the right side of the fish, centred on the lateral line below the insertion of the dorsal fin, to eliminate any variation because of location on the body (Pickering 1974). While not the location where desiccation or abrasion are most likely to occur in the fish, we sampled this area because we could assume that the tissue had not already been damaged because of either abrasion or desiccation. Thus, these skin samples provided an index of skin thickness for comparison between sexes or habitats. Underlying muscle tissue and fat were removed from the skin and a 1.8-cm diameter cork bore was used to cut skin samples to a uniform size. We measured the skin mass of this 1.8-cm core as our proxy for skin thickness (variously called 'skin thickness' or 'skin mass'). Specifically, skin samples were dried in a 60 °C drying oven to a constant mass determined by multiple weighing events. An identical mass obtained at four consecutive weighing events was an indication that no further moisture was present

Table 1. Populations, spawning habitat, sample size, and average trait values \pm standard deviation. Data are partitioned by sex.

Population	Habitat	Sex	N	Length (mm)	Depth (mm)	Jaw (mm)	Skin mass (g)	Tooth length (mm)
Bear	Creek	female	9	446.22 \pm 43.96	125.89 \pm 16.03	58.89 \pm 10.56	0.084 \pm 0.014	3.34 \pm 0.70
Hansen	Creek	female	20	442.80 \pm 35.54	116.85 \pm 10.20	57.05 \pm 9.25	0.086 \pm 0.014	3.45 \pm 0.38
Yako	Creek	female	14	436.14 \pm 36.39	118.5 \pm 11.20	52.64 \pm 7.53	0.083 \pm 0.017	3.25 \pm 0.56
Finger bay	Beach	female	3	490.67 \pm 30.29	144.33 \pm 10.79	74.33 \pm 10.02	0.091 \pm 0.013	4.46 \pm 0.35
Fuel dump	Beach	female	6	414.50 \pm 10.01	106.33 \pm 4.27	46.33 \pm 5.82	0.079 \pm 0.009	3.37 \pm 0.21
N-4	Beach	female	5	462.60 \pm 29.19	130.2 \pm 12.05	60.00 \pm 3.94	0.073 \pm 0.013	3.44 \pm 0.40
Woody Island	Beach	female	6	415.50 \pm 15.74	111.5 \pm 6.53	52.50 \pm 2.66	0.078 \pm 0.005	3.64 \pm 0.47
Bear	Creek	male	10	477.20 \pm 50.15	161.9 \pm 27.82	98.60 \pm 14.98	0.097 \pm 0.018	5.60 \pm 0.89
Hansen	Creek	male	21	466.71 \pm 51.54	141.76 \pm 17.44	91.10 \pm 14.64	0.095 \pm 0.012	5.34 \pm 0.89
Yako	Creek	male	15	455.13 \pm 43.05	148.27 \pm 20.98	91.80 \pm 16.11	0.094 \pm 0.014	4.95 \pm 0.91
Finger bay	Beach	male	6	518.00 \pm 36.74	211.67 \pm 16.88	103.83 \pm 14.97	0.089 \pm 0.011	6.49 \pm 0.58
Fuel dump	Beach	male	12	441.50 \pm 27.98	169.17 \pm 15.51	84.67 \pm 8.86	0.083 \pm 0.006	5.43 \pm 0.59
Knutsen bay	Beach	male	6	484.33 \pm 29.62	196.33 \pm 20.30	95.83 \pm 6.18	0.089 \pm 0.009	6.41 \pm 0.60
N-4	Beach	male	7	496.57 \pm 38.23	194.43 \pm 30.32	95.29 \pm 17.13	0.089 \pm 0.013	5.87 \pm 0.63
Woody Island	Beach	male	13	450.46 \pm 14.99	170.77 \pm 6.50	80.23 \pm 5.78	0.078 \pm 0.007	5.37 \pm 0.70

in the sample. The skin mass we present therefore represents the mass of solids (all water removed) in the skin tissue. In total, 63 females and 90 males were sampled for all traits (Table 1).

Statistical analyses

To compare traits among populations that differ markedly in body size, we employed analysis of covariance (ANCOVA). We measured two traits to characterise overall body size: body length and body depth. Because these two traits are positively correlated, we ran parallel analyses using each of these two measures of body size as the covariate. Specifically, analyses were run with either tooth length or skin mass as the response variable, sex (male/female coded 0/1) and breeding habitat (beach/creek coded 0/1) as categorical predictors and either body length or body depth as the covariate. This resulted in a total of four ANCOVAs. In all cases, a complete model with all main effects and interaction terms was run initially. Interaction terms were dropped when nonsignificant ($\alpha = 0.10$) and the model was re-run until all remaining interaction terms in the model were statistically significant. Sex and habitat were included in the final model as main effects terms if: (i) they were statistically significant ($\alpha = 0.05$), or (ii) they were not statistically significant but they appeared in a significant interaction term.

To assess whether tooth length was positively related to skin mass or to jaw size and whether these relationships differed by sex or habitat, we again employed analysis of covariance. These analyses proceeded as before except that tooth size was the response variable in both cases, combined with either jaw length or skin mass as the covariate. This yielded two additional ANCOVAs and allowed us to assess whether these traits co-varied positively and whether

any differences emerged between males and females or between fish utilising different breeding habitats.

Results

Tooth size: comparisons between habitats, sexes and body sizes

Tooth size was positively related to body length (Fig. 2a) and varied between sexes within a habitat and between habitats for a given sex. In particular, within a sex, the slope relating tooth length and body length was the same for beach and creek fish facilitating a comparison of intercepts. This revealed that beach fish had longer teeth than creek fish even after removing the effect of length (Fig. 2a). Within a breeding habitat type, the slope relating tooth size to body length differed for males and females, precluding a direct comparison of intercepts. However, for a given breeding habitat, the regression line representing males fell entirely above the line representing females, demonstrating that males had longer teeth than females for a given body length (Fig. 2a).

When considering our second measure of body size, body depth, the results differed slightly from those detailed above. Tooth length was again positively related to the body size covariate. However, within a sex, the slope relating tooth length and body depth differed for beach and creek spawners, precluding a direct comparison of tooth length at a common body depth. Furthermore, the overlap in the regression lines suggested no clear pattern with respect to breeding habitat type (Fig. 2b). Within a habitat type, however, the slope relating tooth length to body depth did not differ between males and females allowing a comparison of intercepts. This again revealed that males had longer teeth than females breeding in the same habitat type (Fig. 2b).

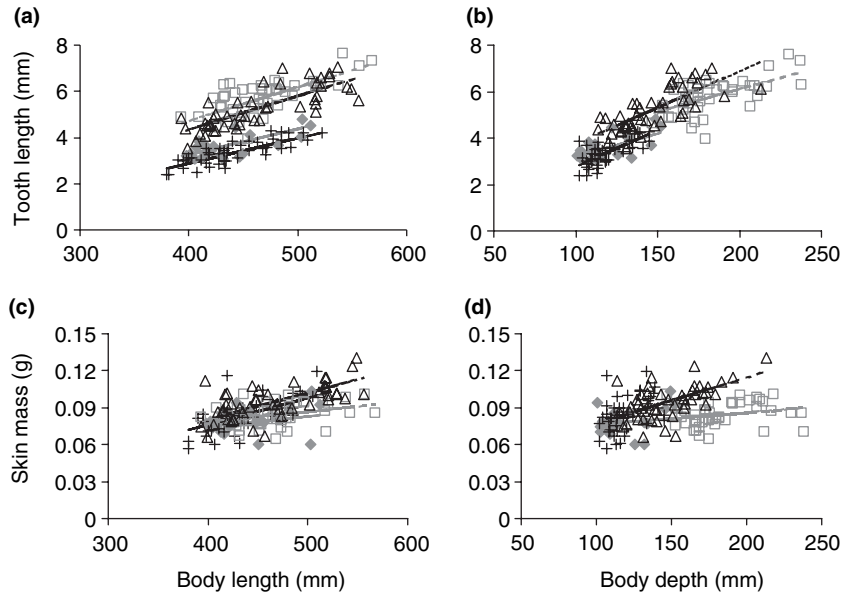


Fig. 2. Tooth length versus body length (a) and body depth (b) as well as skin mass versus body length (c) and body depth (d). Regression lines represent each combination of sex and breeding habitat: male beach spawners (open grey squares, dashed grey line), male creek spawners (open black triangles, dashed black line), female beach spawners (closed grey diamonds, grey line) and female creek spawners (black cross symbols, black line).

Skin mass: comparisons between habitats, sexes and body sizes

Including body length as the covariate, skin mass varied consistently between sexes within a habitat type but not between habitat types for a given sex. Specifically, the slope relating skin mass to body length did not differ between males and females breeding in the same habitat type, facilitating a direct comparison of the elevation of the regression lines. This revealed that males had thicker skin than females breeding in the same habitat type (Fig. 2c). A comparison of skin mass between individuals of the same sex breeding in different habitat types was precluded because of differences in the slope relating skin mass to body length for the focal groups. Interestingly, for both males and females, the relationship between skin mass and body length was stronger for creek spawners than beach spawners (Fig. 2c).

When including body depth as the covariate instead of body length, the results again differed slightly from

those reported above. Notably, no difference between sexes within a habitat type were evident (i.e. same intercept and slope, Fig. 2d). As with the body length analysis, the slope relating skin mass and body depth differed between creek and beach spawners. However, inspection of the plots revealed that, for all but the least deep-bodied individuals, creek fish had thicker skin for a given body depth. Furthermore, the slope relating skin mass to body depth was again stronger for creek spawning individuals than for their beach spawning counterparts (Fig. 2d).

Comparisons between traits

ANCOVA indicated that tooth length was positively related to jaw length (Fig. 3a). Consistent with our previous results, within a breeding habitat, males had longer teeth than females (same slope, different intercept; Fig. 3a) and within a sex, beach spawners had longer teeth than creek spawners (same slope, different intercept; Fig. 3a).

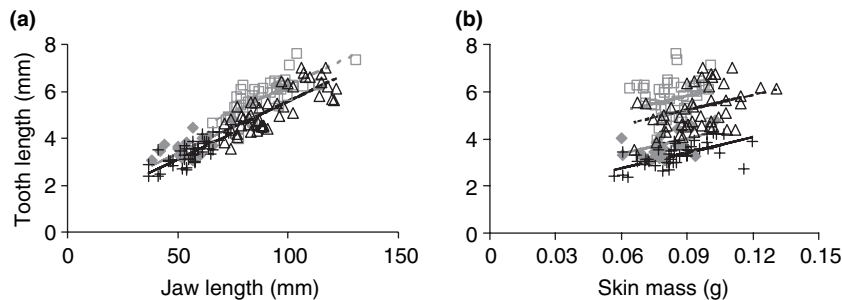


Fig. 3. Average tooth length versus jaw length (a) and skin mass (b). Regression lines represent each combination of sex and breeding habitat: male beach spawners (open grey squares, dashed grey line), male creek spawners (open black triangles, dashed black line), female beach spawners (closed grey diamonds, grey line) and female creek spawners (black cross symbols, black line).

We found that tooth length was also positively related to skin mass (Fig. 3b) for all combinations of sex and breeding habitat. Moreover, clear differences between the sexes and between habitat types are evident. Within a sex, beach fish had longer teeth than creek fish, relative to their skin thickness (Fig. 3b) and within a breeding habitat, males had longer teeth than females, relative to their skin thickness (Fig. 3b).

Discussion

Our analysis of secondary sexual characteristics of male and female sockeye salmon from different spawning habitats yielded the following general conclusions. First, beach spawning sockeye had longer teeth than their creek spawning counterparts when body length was used as a covariate in analyses but no differences emerged when body depth was instead used as the covariate. Second, within a breeding habitat, males had longer teeth than females, relative to both their body length and depth. Third, the slope of the relationship between skin mass and body size differed between creek and beach spawning fish, precluding a direct comparison of traits. However, creek spawners showed a stronger positive relationship between skin mass and body size (both length and depth) than beach spawners. Fourth, males had thicker skin than females relative to their body length, but when their greater body depth was used as the covariate there was no difference between the sexes. Fifth, fish with large teeth tended to also have large jaws and thick skin. Sixth, males had longer teeth for a given jaw length and for a given skin thickness than females. Finally, beach spawners had longer teeth for a given jaw length and for a given skin thickness than creek spawners.

Overall body size considerations

Because our focal traits (tooth length, skin thickness) varied positively with body size, we needed to consider this important source of variation in our analyses. The choice of which metric of body size to include, however, was not trivial. In breeding salmonids, obvious possibilities include body length, body depth and/or body weight – all of which are highly correlated. However, the relationships between these traits vary significantly among populations and between males and females. Our data set included information on both body length and body depth and so we performed parallel analyses using each of these as a covariate. Our results differed slightly depending on which covariate was included, largely because males are deeper-bodied than females for a given length, and because beach spawning sockeye salmon are deeper-bodied for their length than creek spawners

(Quinn et al. 2001a). Use of weight as a covariate rather than body depth would have resulted in the same problem because deeper-bodied fish are not merely shaped differently; they are heavier for their length than less deep-bodied fish within a given population (Quinn & Foote 1994) and among populations (Quinn, unpublished data). Moreover, males tend to be heavier than females for a given length. We focus our discussion on interpretation of the body length analyses, but also present the results relative to body depth results to illustrate the ways in which interpretations might vary.

Comparisons between habitats

Bishop (1990) and Blair et al. (1993) showed that, in general, beach spawning sockeye salmon displayed more exaggerated secondary sexual characteristics (especially body depth) relative to their body length than creek spawners. Our study revealed that this pattern is also true for tooth length (Fig. 2a). Furthermore, male sockeye salmon had longer teeth than females within a breeding habitat (Fig. 2a,b) consistent with studies examining other traits apparently subject to sexual selection in sockeye salmon (Blair et al. 1993; Foote et al. 1997) and other salmon species. Males generally expend more energy in secondary sexual characteristics than females to increase success in competition for mates (e.g. Andersson 1994; Hendry & Berg 1999). Female salmon, conversely invest energy in egg production and characteristics that aid in redd construction and defense (Bishop 1990; Hendry & Berg 1999). This is consistent with our results; the teeth of males are larger than those of females in the same breeding habitat type. This result does not reflect a lack of aggression among females. Indeed, the frequency of attacks by females is similar to that by males (Quinn 1999). Moreover, within a sex, the largest individuals also had the longest teeth. Therefore, within a population, where absolute tooth size will matter in terms of aggression, it is the largest males that are most prepared for battle. Thus, tooth size should be considered among the suite of salmon secondary sexual characteristics.

For a given body length, males had thicker skin than females spawning in the same habitat type (Fig. 2c), but the variation in skin thickness between fish breeding in different habitats did not parallel the patterns in other secondary sexual traits (e.g. body depth and tooth size). The relationship between skin mass and body size was stronger for creek spawning individuals than for beach spawners (Fig. 2c,d). This suggests that this trait is not simply evolving in parallel with a suite of sexually dimorphic traits in sockeye salmon but it may be under selection, at least in part, from other factors. One possibility is that

thicker skin is an adaptation to abrasion and desiccation that creek spawning individuals experience. Salmon spawning in shallow creeks spend a significant amount of time in contact with the substrate and are therefore subject to skin abrasion on their ventral surfaces when swimming over rough gravel in these shallow streams. Creek spawning sockeye salmon typically display roughened skin along both the dorsal and ventral surfaces after several days of reproductive activity, and so may develop thicker skin to resist abrasion and desiccation. Beach spawning salmon are not exposed to the air along their dorsal surfaces and also do not rub their ventral surfaces along the substrate to the same extent as creek fish because they are spawning in water that is deeper than their bodies.

Interestingly, males had thicker skin than females of the same body length in both breeding habitats (Fig. 2c); perhaps, reflecting the role that skin also plays in defense against attacks. Males have larger teeth than females and males almost exclusively attack each other rather than attacking females (Quinn 1999), so to some extent this is a case of 'arms and armor', notwithstanding the other functions that thick skin may serve. However, when body depth was instead included as the covariate in analyses, no difference between the sexes was apparent. This simply reflects the fact that males have deeper bodies than females, so any analysis comparing body depth will minimise differences between the sexes.

Comparisons among traits

In general, individuals with long teeth tended to also have long jaws and thick skin (Fig. 3b), revealing that some individuals are 'well endowed' in all these traits rather than a pattern of trade-offs in which emphasis on one trait comes at a cost for another trait. Moreover, clear differences between fish spawning in the two habitats and between the sexes emerged with regard to these traits. In particular, for a given jaw length and skin thickness, males had longer teeth than females consistent with Foote et al. (1997), and beach spawners had longer teeth than creek spawners (Fig. 3a). These results further support our hypothesis that tooth size parallels variation in other sexually dimorphic traits and therefore should be considered among the suite of sexually selected traits.

Conclusion

The size of teeth in mature sockeye salmon is sexually dimorphic and is part of a suite of traits that differ consistently between breeding habitats. These traits (e.g. body depth and tooth size) are more exaggerated in sockeye salmon spawning in beaches compared

with creek habitats, and males are more modified from their immature form than are females. However, skin thickness may not be evolving in simple association with these other traits. Rather, we hypothesise that skin thickness serves to reduce the effects of abrasion and desiccation in small streams in addition to the role that the skin may play in defense against attack. A more complete understanding of the functional significance of skin thickness would benefit from further research comparing creek spawning populations that span a range of depth and flow conditions, and differences in spawning substrate. Studies on the changes in the skin of salmon as they migrate from salt to fresh water, and undergo the complex changes in shape associated with sexual maturation would also be of interest, including comparisons with iteroparous species.

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