

Sexual dimorphism modifies habitat-associated divergence: evidence from beach and creek breeding sockeye salmon

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Abstract

Studies of parallel or convergent evolution (the repeated, independent evolution of similar traits in similar habitats) rarely explicitly quantify the extent of parallelism (i.e. variation in the direction and/or magnitude of divergence) between the sexes; instead, they often investigate both sexes together or exclude one sex. However, differences in male and female patterns of divergence could contribute to overall variation in the extent of parallelism among ecotype pairs, especially in sexually dimorphic traits. Failing to properly attribute such variation could lead to underestimates of the importance of environmental variation in shaping phenotypes. We investigate the extent of parallelism in the body shape of male and female beach and creek spawning sockeye salmon (*Oncorhynchus nerka*) from two lake systems in western Alaska that were colonized independently after the last ice age. Although both sexes showed some degree of parallelism, patterns of beach-creek body shape divergence vary between the sexes and between lake systems. Phenotypic change vector analyses revealed highly parallel aspects of divergence between males from different lake systems (males from beaches had deeper bodies than males from creeks) but weaker parallelism in females and high parallelism between the sexes in one lake system but not the other. Body shape also had population-specific components, which were mostly, but not entirely, explained by environmental variation in the form of creek depth. Our results highlight the importance of explicitly considering the extent of parallelism between the sexes and environmental variation among sites within habitat types.

Introduction

The repeated divergence of similar traits in similar habitats, referred to as parallel or convergent evolution, has played an important role in evolutionary biology because it provides evidence for a deterministic role of selection (reviewed by Bolnick *et al.*, 2018). Specifically, whereas genetic drift or other chance processes could lead to repeated divergence, such repetition would not

show consistent habitat-associated patterns (Clarke, 1975; Wake *et al.*, 2011). Parallel evolution has been described in many taxa, including spiders (De Busschere *et al.*, 2012), lizards (Losos, 1992), plants (Ostevik *et al.*, 2012) and isopods (Eroukmanoff *et al.*, 2009). However, few studies have formally quantified the extent of parallelism between sexes (Butler *et al.*, 2007; Oke *et al.*, 2017). Most studies investigating parallelism do not directly compare male and female patterns, but instead tend to combine males and females together or consider only one sex. If sexual selection creates variation among populations that is not accounted for, even strong and consistent natural selection might appear to have acted less deterministically than it really has,

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potentially leading to an underappreciation for the determinism of natural selection. Hence, accounting for variability in patterns of divergence between the sexes should improve our understanding of the processes underlying adaptive divergence, as has been demonstrated in several recent studies (Hendry *et al.*, 2006; Butler *et al.*, 2007; Langerhans, 2009a; Riesch *et al.*, 2013; Ingley *et al.*, 2014a; Dargent *et al.*, 2016).

Males and females might be expected to respond in parallel to similar ecological changes for several reasons. Parallelism is usually assessed among related populations from the same or closely related species, and individuals from these different populations might vary not only in evolutionary histories but also in the local environmental conditions to which they are exposed (Langerhans & DeWitt, 2004). In comparing the extent of parallelism between the sexes within populations, we are comparing groups of individuals with a shared evolutionary history that are even more closely related than groups of individuals from different populations. That is, males and females share a large proportion of their genome (Pennell & Morrow, 2013; Wright & Mank, 2013), and so selection on one sex should lead to correlated responses in the other (Lande, 1980; Bonduriansky & Chenoweth, 2009; Poissant *et al.*, 2010; Griffin *et al.*, 2013). Males and females in a given population are also found in the same locations (at least during breeding) and so should experience similar selection. In spite of these similarities, there are also many reasons why phenotypic responses might differ between the sexes.

As evidenced by the pervasiveness of sexual dimorphism (Darwin, 1871) and numerous observations of sex-specific selection (Cox & Calsbeek, 2009), phenotypic optima are often sex-specific (Cox & Calsbeek, 2009; Pennell & Morrow, 2013). If, during habitat-associated divergence, sex-specific phenotypic optima exist in either (or both) habitats, patterns of parallelism might vary between the sexes. This may be especially true of traits such as body size and shape which can play important roles in sexual selection, natural selection and reproductive isolation (Bonduriansky, 2011). Although there has been increasing recent interest in the role of sexual selection in local adaptation (Connallon *et al.*, 2018), parallelism between the sexes has seldom been explicitly considered (Hendry *et al.*, 2006). In one investigation of parallelism, Hendry *et al.* (2006) found that, comparing across live-bearing fishes (Poeciliidae), sex plays at least as large a role as species in explaining shape divergence across predation regimes. At least some of the differences between male and female patterns of body shape in response to predation regimes result from constraints placed on female shape by the physiological requirements of live birth (Langerhans & Makowicz, 2009; Wesner *et al.*, 2011; Ingley *et al.*, 2014a). Providing further evidence for an important role of sex in shaping parallelism, studies have also

found that the extent of sexual dimorphism in boldness differed between populations in different predation regimes in two closely related live-bearing fishes (*Brachyrhaphis roseni* and *B. terrabensis*, Ingley *et al.*, 2014b) and in guppies (*Poecilia reticulata*, Harris *et al.*, 2010). Interestingly, while the direction and especially the magnitude of phenotypic divergence differs between the sexes in some live-bearing species, in others, the sexes show predominately shared responses (Hendry *et al.*, 2006; Langerhans, 2009b; Langerhans & Makowicz, 2009; Riesch *et al.*, 2013; Ingley *et al.*, 2014a).

Natural and sexual selection can act in a similar direction, exaggerating ecological differences in one sex or the other, or they can act in opposition, resulting in muted differences between the sexes. Situations in which sexual and natural selection push phenotypes in different directions and vary in strength across an environmental gradient provide excellent opportunities to investigate whether sexual selection might drive variation in divergence across populations (Maan & Seehausen, 2011). If the relative strength or importance of one form of selection over the other varies among populations within a given habitat type, the extent of parallelism could vary. We take advantage of one such study system, sockeye salmon (*Oncorhynchus nerka*) that spawn in creeks and lake beaches, to investigate parallelism between the sexes.

Study system

Juvenile sockeye salmon rear in freshwater (typically lakes) and then migrate to the ocean to feed and grow to their final adult size (Quinn, 2018). After 1–4 years at sea, they migrate back to their natal freshwater sites, spawn and die (Dittman & Quinn, 1996; Quinn, 2018). Immature salmon at sea are indistinguishable to sex but differences develop at the onset of maturity, to a greater or lesser extent in all species (e.g. pink salmon *O. gorbuscha*, Davidson, 1935). As a result of precise homing to their natal freshwater site, each breeding population is largely isolated from other breeding populations, limiting gene flow and allowing for local adaptation to the features of the habitats that they occupy, as is characteristic of salmonid fishes (Taylor, 1991; Hendry *et al.*, 2000; Fraser *et al.*, 2011).

As a consequence of this reproductive isolation, we might expect strong parallel evolution of the sexes occupying similar environments. In shallow creek habitats, natural selection from bear predation leads to smaller body sizes in both sexes (Quinn & Kinnison, 1999; Cunningham *et al.*, 2013a,b; Lin *et al.*, 2016). In addition, in very shallow creeks, larger fish are more likely to 'strand' in shallow water and hence die (Quinn *et al.*, 2001a; Carlson & Quinn, 2007; Cunningham *et al.*, 2013a). In contrast, sockeye salmon that spawn in beach habitats are subject to relaxed natural selection on size due to the deeper water; bears do not

successfully prey upon them in deep water, and beach-spawning sockeye salmon do not need to traverse shallow water and risk stranding (Quinn *et al.*, 2001b), unless the outlet of the lake is shallow.

At the same time, however, males and females differ in many ways that might alter how selection promotes divergence between habitats. Mature sockeye salmon are sexually dimorphic and males generally have larger, deeper bodies with longer upper jaws and teeth than females at a given age (Quinn & Foote, 1994; Johnson *et al.*, 2006; Quinn, 2018). This sexual dimorphism is partly due to sexual selection acting on males (primarily male–male competition) that favours larger body size during breeding (Quinn & Foote, 1994; Quinn *et al.*, 2001a; Hamon & Foote, 2005). Females do not seem to be subject to sexual selection for larger body size, but are instead subject to natural selection for larger body size because larger females are more fecund (Beacham & Murray, 1993), have larger eggs (Quinn *et al.*, 1995; Cunningham *et al.*, 2013a) and dig deeper nests that should be better protected from nest disturbance or scour (removal by ice or debris; Steen & Quinn, 1999).

The concurrent and opposing influences of natural and sexual selection in this system likely interact in ways that could vary across the gradient of water depth to produce variation in the extent of sexual dimorphism and parallelism among populations. Spawners in both habitats are subject to selection for larger body sizes that increase reproductive fitness, but water depth negatively correlates with the strength of natural selection for smaller body size (Quinn & Kinnison, 1999; Carlson & Quinn, 2007). In creeks, males are generally more susceptible to bear predation (Quinn & Kinnison, 1999; Ruggerone *et al.*, 2000; Quinn & Buck, 2001) and stranding (Quinn *et al.*, 2001a; Carlson & Quinn, 2007; Cunningham *et al.*, 2013a) because they are deeper bodied than females, but bear predation and stranding are not observed in beach habitats. Body shape seems to reflect these selective pressures. In creeks, the extent of sexual size dimorphism increases with increasing water depth and average population body size (Johnson *et al.*, 2006; Kendall & Quinn, 2013), whereas both males and females are larger and deeper bodied in beach habitats (Blair *et al.*, 1993; Quinn *et al.*, 2001b). To date, body shape parallelism between the sexes has not been explicitly considered in creek and beach-spawning sockeye salmon.

Here, we characterize body shape using geometric morphometrics, a powerful method of detecting fine-scale shape changes that may not be captured by previous methods used for these populations. Our study had five main objectives. First, we determined (separately for each sex) the extent of parallelism and nonparallelism in body shape divergence between beach and creek spawning sockeye salmon from two large lake systems in different drainage basins in south-western

Alaska. Second, we tested whether a key environmental variable, water depth, helps to explain variation in the extent of beach-creek divergence. Third, to determine the extent to which the sexes have diverged in parallel between beach and creek spawning habitats, we formally assessed parallelism between the sexes by including both sexes in the same model and partitioning the variance. Fourth, comparing between lake systems, we used recently developed phenotypic change vector analyses (PCVA) to formally quantify the extent of nonparallelism due to differences in the direction and magnitude of divergence between (i) the sexes within each lake system and (ii) lake systems within each sex. Fifth, we used exchangeability analyses to determine whether shape varies across populations within a habitat type, which would suggest local adaptation of body shape to environmental differences across populations within a lake system.

Materials and methods

Study system

We consider the body shape of adult sockeye salmon from populations in two well-studied large lake systems (Iliamna and Wood River) that drain into Bristol Bay, Alaska. These populations are entirely wild, with no artificial production from hatcheries or aquaculture that might otherwise modify selection regimes. The Iliamna Lake system is dominated by Iliamna Lake, which has an area of 2600 km² and drains into the Kvichak River (Fig. 1a), yet there are other smaller lakes as well. In the Iliamna Lake system, sockeye salmon spawn on both mainland and island beaches, as well as in creeks and larger rivers (Demory *et al.*, 1964; Quinn *et al.*, 2001b). The Wood River system consists of several large lakes that drain in series into the Nushagak River via the Wood River (Fig. 1b). In this system, sockeye salmon spawn on mainland beaches (but not island beaches) and riverine habitats that range greatly in depth and width (Marriott, 1964; Quinn *et al.*, 2001b). Our Wood River study sites included beach and creek sites from Lake Aleknagik and Little Togiak Lake. Although both lake systems contain a range of riverine habitats, the creeks we sampled were on average deeper in the Iliamna Lake system (0.30 m ± 0.14 m standard deviation) than in the Wood River system (0.20 m ± 0.10 m). Within both the Iliamna and Wood River systems, the sockeye salmon spawning in different locations show local adaptation to their specific habitats (Quinn *et al.*, 1995; Carlson *et al.*, 2007, 2009; Peterson *et al.*, 2014; Larson *et al.*, 2017). As is required of studies of parallel evolution, the divergence of beach and creek spawning forms occurred independently in each lake system, following post-glacial reinvasion (Habicht *et al.*, 2007). Thus, beach-spawning sockeye in Iliamna are more closely related to creek spawners

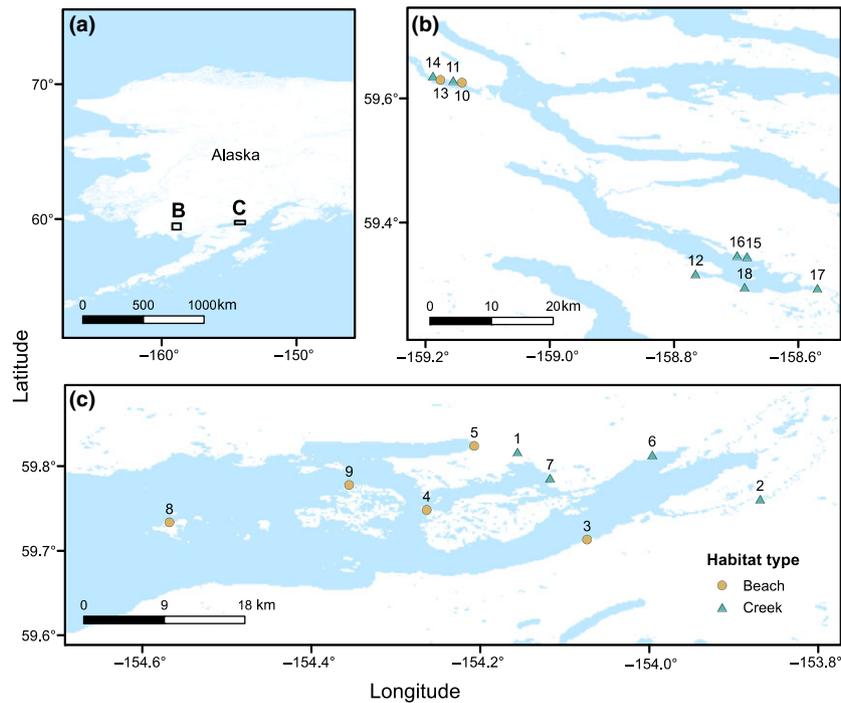


Fig. 1 Maps of sampling sites and map of Alaska (a) showing location of Wood River (b) and Iliamna Lake (c) systems. Close up maps show beach (brown circles) and creek (green triangles) sampling sites in (b) Wood River and (c) Iliamna Lake. Site names and sample sizes for males (M) and females (F) are as follows: 1. Pedro Ponds (33 M, 31 F), 2. Chinkelyes Creek (32 M, 32 F), 3. Finger Bay Beach (32 M, 35 F), 4. Fuel Dump Island (32 M, 21 F), 5. Knutson Bay Beach (34 M, 31 F), 6. Lonesome Bay Creek (32 M, 33 F), 7. Russian Creek (32 M, 32 F), 8. Triangle Island (31 M, 36 F), 9. Woody Island (33 M, 34 F), 10. A Beach (10 M, 12 F), 11. A Creek (31 M, 54 F), 12. Bear Creek (40 M, 32 F), 13. C Beach (2 M, 3 F), 14. C Creek (18 M, 30 F), 15. Hansen Creek (50 M, 33 F), 16. Happy Creek (33 M, 35 F), 17. Mission Creek (34 M, 34 F) and 18. Yako Creek (33 M, 35 F). Maps created using ArcGIS version 10.2.1 (Esri, Redlands, CA, USA).

in that system than they are to Wood River beach spawners. Previous work has emphasized beach-creek differences in body length, body depth, egg size and other features (Blair *et al.*, 1993; Quinn *et al.*, 1995, 2001b; Johnson *et al.*, 2006), whereas we here focus on body shape.

Geometric morphometrics

Adult sockeye salmon were photographed in 2013 at the end of their return migration to fresh water to breed at their natal spawning grounds. We included only those fish that were fully sexual mature, as judged by colouration (deep red body and green head, as opposed to chrome or silver) and development of secondary sexual characteristics (hooked upper jaw and teeth in both sexes, and a pronounced dorsal hump in males). We likewise excluded sockeye salmon that showed signs of having already spawned, such as frayed fins and gaunt shape, body scars, skin dried from exposure to the air and advanced stages of infection or decay (Quinn & Blair, 1992; Hendry & Berg, 1999). Small males that had returned after 1 year at sea (jacks) also were excluded because too few were

sampled to allow us to consider them separately from other males, and no females of comparable length and age were captured.

All sockeye salmon were sampled using either a beach seine deployed from a boat or a tangle net, both of which minimize selection on size or shape (Kendall & Quinn, 2012). For beach habitats, sockeye salmon were sampled directly from the spawning area after at least a few fish had begun to settle on redds (nests). The shallowness of the creeks prevented the use of beach seines directly on the spawning site, and so fish were instead sampled from the mouths of the creeks where they congregated prior to upstream movement. These methods cannot completely preclude the possibility that some fish were sampled while *en route* to other sampling sites, but long-term tagging studies from one of our study sites, Hansen Creek, have shown that very few fish collected using these methods subsequently move to other sites (Hamon & Foote, 2005; Cunningham *et al.*, 2013a). Similarly, studies have shown that very few fish leave their tagging site for another site among the beaches (Blair & Quinn, 1991; Hendry *et al.*, 1995) and creeks (Quinn, unpublished data).

Each fish was photographed with an Olympus Stylus waterproof digital camera (Olympus, Tokyo, Japan) on a tripod at a standardized height (about one metre). A metre stick was included in all photographs for scale. Live sockeye salmon were lightly anesthetized with AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand) and placed left side up on a flat board under the tripod. After sampling, all fish had their adipose fin clipped (to prevent re-sampling) and released. Photographs were landmarked in the program tpsDIG2 (life.bio.sunysb.edu/morph/) in random order and blind to sampling site. In total, 20 fixed landmarks and 36 sliding semi-landmarks making up two separate curves were placed on photographs of the left side of 1095 individual fish (Fig. 2). Using the *geomorph* package (Adams & Otárola-Castillo, 2013) in R (R Core Development Team 2012), we aligned coordinates via generalized Procrustes analysis and calculated consensus shape, centroid size and relative warps (Rohlf & Slice, 1990; Adams & Otárola-Castillo, 2013; Collyer *et al.*, 2014).

Statistical analyses

Statistical testing was based on a nonparametric multivariate analysis of covariance (MANCOVA) procedure based on a randomized residual permutation procedure (RRPP) developed by Collyer *et al.* (2014) for high-dimensional morphometric data and extended by Levis *et al.* (2016) to allow the inclusion of random effects. To perform these analyses, we used the function *procD.lm* from the *geomorph* package (Adams & Otárola-Castillo, 2013; Collyer *et al.*, 2014). We first constructed models for each sex separately. Because total body shape was our phenotype(s) of interest, all relative warps (RWs) were included as the response variables. The logarithm of centroid size was included as a covariate to account for the potential allometric influence of body size on shape. Spawning habitat (beach or creek), lake system (Iliamna or Wood River) and their interaction were included as fixed factors. To determine whether population of origin influenced shape within a habitat type, we used log-likelihood ratio tests to compare models with and without a random variable of

sampling site (Levis *et al.*, 2016). Following Levis *et al.* (2016), when testing the importance of the random site effect, we included only the RWs that together accounted for roughly the first 95% of shape variation (RW1-RW10), which avoided difficulties with model convergence. Models without the random site effect included all 112 RWs as response variables. All permutation tests were iterated 1000 times.

Log-likelihood ratio tests revealed no significant difference in fit between the model that included a random site effect and that that did not ($P = 1$ for models on both males and females). Given this result, and the statistical challenges associated with mixed MANCOVA (e.g. see supplemental information for Levis *et al.*, 2016), we excluded the random effect of site. Thus, we analysed a model that included only fixed factors (habitat, lake system and their interaction) and the centroid size covariate. As a measure of effect size, we calculated the partial η^2 ($\frac{SS_{\text{effect}}}{SS_{\text{effect}} + SS_{\text{error}}}$) from models with the exact same structure as those described, but using instead a standard parametric MANCOVA. In no cases did interpretations differ between the parametric and nonparametric MANCOVAs. Parametric MANCOVAs were performed with the *car* package (Fox & Weisberg, 2011), and partial η^2 estimates were calculated using the package *heplots* (Fox *et al.*, 2007).

Next, to test whether water depth influenced the extent of beach-creek divergence, we constructed a set of models to consider the role of water depth in the body shape of creek fish of each sex. These models included the fixed effect lake system and covariates for creek depth and the logarithm of centroid size. Wetted creek depth was obtained from previous surveys of the habitat upstream of our sampling sites (Quinn *et al.*, 2001b; Pess, 2009; Ching *et al.*, 2014).

In addition, we repeated the mixed MANCOVAs described above but included both sexes in the same model. This new model had the same structure as above, but also included sex as a fixed factor. The fixed factors included in this model were sex, habitat, lake system, and all two- and three-way interactions. Once again, we compared models with and without a random site effect and found no significant differences

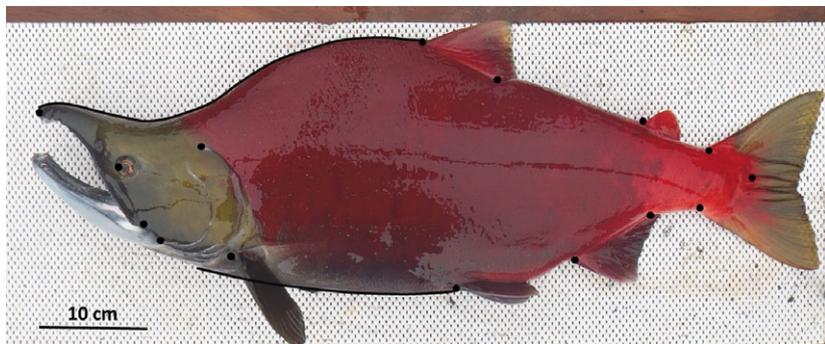


Fig. 2 Landmarks (black circles) and curves (black lines along body) placed on each sockeye salmon photograph for geometric morphometrics. Shown here is a male from Finger Bay Beach, Iliamna Lake.

between the models ($P = 1$): thus, we excluded site from our final models.

Further, to determine the extent of creek-beach parallelism between the sexes and lake systems, we performed explicit tests of the extent of variation in the magnitude and direction of divergence using phenotypic change vector analyses (PCVA; Adams & Collyer, 2007). PCVA was used to project populations into multivariate trait space and calculate change vectors between beach and creek population means in a given lake system. By comparing the length and angle of divergence across vectors, the extent of nonparallelism in the magnitude and direction of divergence can be determined (Adams & Collyer, 2007; Oke *et al.*, 2017). The randomized residual permutation procedure was used to determine whether vectors differed significantly in their direction or magnitude (Adams & Collyer, 2007; Collyer & Adams, 2007; Adams *et al.*, 2009; Collyer *et al.*, 2014). In our case, we wished to compare male and female phenotypic change vectors within each lake system and across lake systems. Thus, four change vectors were created, one for each sex in each lake system. All shape coordinates were included as traits, thereby creating a 112-dimensional trait space. PCVA was conducted using the *trajjectory.analysis* function in the *geomorph* package (Adams & Otarola-Castillo, 2013).

We considered parallelism across sampling sites within lake systems; however, no method has been developed to perform PCVA on populations without paired structures. That is, although we sampled several beaches and several creeks from Iliamna, these populations cannot easily be organized into beach-creek pairs based on either geographical proximity or evolutionary relationships. Thus, instead of PCVA, we performed exchangeability analyses (Hendry *et al.*, 2013) at the population level to compare the similarity of phenotypes across sampling sites. Because males and females had very different body shapes and because we wanted to explicitly test the exchangeability between the sexes, males and females from the same site were considered to be different groups for the purpose of these analyses. Exchangeability analyses take advantage of the full distribution of phenotypes available and use the likelihood of assigning each individual to each population based on their phenotype to determine the extent to which individuals are exchangeable across groups (Hendry *et al.*, 2013). Exchangeability then provides a measure of phenotypic similarity among groups or populations. For our purposes, populations for which exchangeability is high are more similar morphologically, so high exchangeability between populations from the same habitat type indicates high parallelism.

Following previous exchangeability analyses, we used the *dapc* function from the *adegenet* package to perform discriminate analyses on principal components (Jombart, 2008; Jombart *et al.*, 2010; Jombart & Ahmed,

2011; Hendry *et al.*, 2013; Oke *et al.*, 2016). We included the lowest number of principal components that captured at least 90% (4 PCs) of variation and all discriminate functions that accounted for at least 2% of variation (3 DFs). To determine whether individuals were more likely to be assigned to the habitat type and sex of their home group, we first conducted a 'misclassification' analysis in which individuals can be assigned to either their home group or to another group. Here, we summed the number of individuals assigned to all groups within five categories: the home group, groups from the same sex and same habitat type, groups from the same sex but a different habitat, groups from the other sex but the same habitat and groups from the other sex and habitat. To account for random expectations, we divided the total number of individuals assigned to each category by the number of sites within that category. Next, we supplemented the misclassification analysis with a 'cross-classification' analysis that assigns individuals to a group other than their home group and repeated the steps above. As cross-classification analyses are expected to be more informative (Hendry *et al.*, 2013), we focus on cross-classification when reporting results.

All analyses were performed in R (Team, R.D.C., 2012) using the packages *lme4* for mixed models (Bates *et al.*, 2014) and *geomorph* for morphometrics (Adams & Otarola-Castillo, 2013).

Results

Body shape

Geometric morphometrics showed that sockeye salmon shape differed between beach and creek habitats in both lake systems and in both sexes (Table 1, Figs 3–5). Sexual dimorphism is well documented in sockeye salmon, and, as expected, body shape was predominantly determined by sex, but beach-creek shape differences and an influence of body size were also observed

Table 1 Results from nonparametric MANCOVAs conducted using randomized residual permutation that included both sexes and effect sizes from parametric MANCOVAs on models of the same structure (see Materials and methods section, in no case did the interpretations from parametric and nonparametric models differ).

Model term	Partial η^2	F	P -value
Log Centroid size	0.366	$F_{1,1086} = 815$	0.0001
Sex	0.822	$F_{1,1086} = 1131$	0.0001
Habitat	0.065	$F_{1,1086} = 160$	0.0001
Lake system	0.061	$F_{1,1086} = 45.8$	0.0001
Sex-by-habitat	0.036	$F_{1,1086} = 41.0$	0.0001
Sex-by-lake system	0.015	$F_{1,1086} = 12.1$	0.0001
Habitat-by-lake system	0.118	$F_{1,1086} = 29.4$	0.0001
Sex-by-habitat-by-lake system	0.055	$F_{1,1086} = 9.64$	0.0001

(a) Knutson Beach



(b) Hansen Creek



(c) Finger Bay beach male



(d) Finger Bay beach female



(e) Hansen Creek male



(f) Hansen Creek female



Fig. 3 Example photographs of beach (a, Knutson Beach) and creek (b, Hansen Creek) habitats, and example photographs of beach (c & d) and creek (e & f) males (c & e) and females (d & f) that show the shape differences between these groups that are clearly distinguishable by eye.

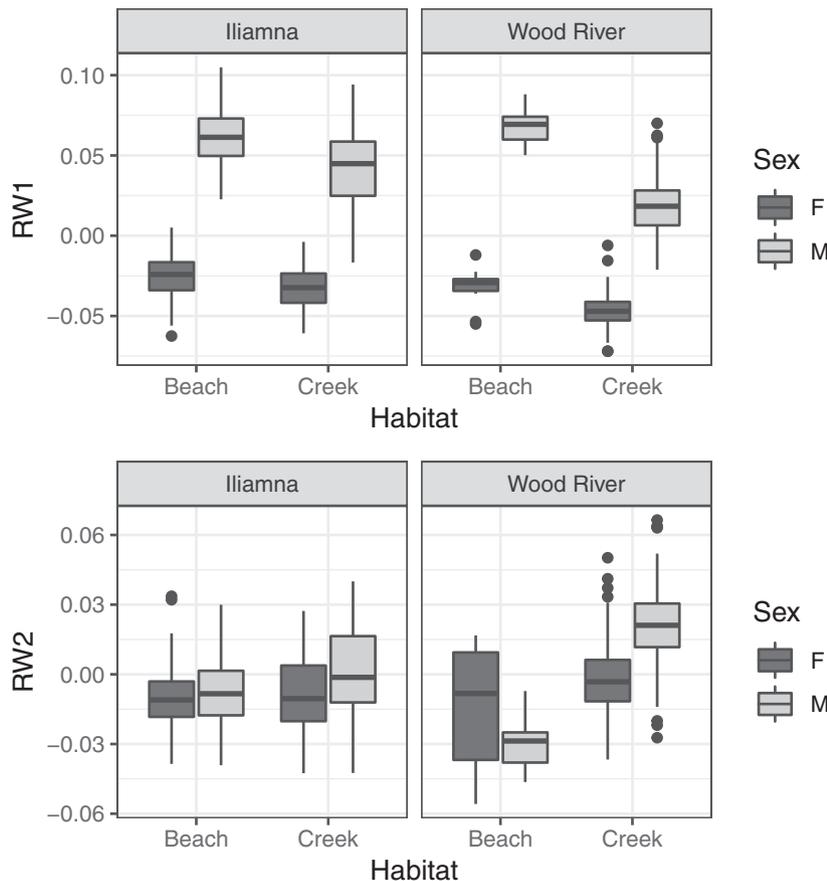


Fig. 4 Males (light grey) and females (dark grey) are separated along the first relative warp from geometric morphometrics (top, higher values indicate deeper bodies and longer upper jaws). Males are deeper bodied, with longer upper jaws. Within each sex, beach fish are also deeper bodied with longer jaws than creek fish in both lake systems. Only males from Wood River show large divergence in the second relative warp (bottom), with beach males having deeper, more protruding bellies and creek males having sleeker bellies.

(Table 1). Males and females were clearly distinguished along the first relative warp (RW1; Figs 4 and 5), which explained 65.92% of shape variation and was due mostly to body depth and jaw length: males had deeper bodies and longer jaws than females. Beach and creek fish also differed along RW1, because beach fish of each sex had deeper bodies than creek fish of the same sex. Interestingly, overlap was evident along RW1 for creek males and beach females, although these groups were separated along RW2. Wood River males from different habitats were especially well separated along RW2 (13.93% of shape variation), which described variation in ventral streamlining, with more ventrally extended bellies in beach males in contrast to slender and streamlined bellies in creek males. Females from different habitats showed little separation on this axis. Some variation in head morphology also was explained by RW2, with longer upper jaws in creek fish. RW3 (5.35% of shape variation) was due in part to bending during placement of the fish's bodies for photographs, but also to some variation in head morphology. RW4 (3.69%) was more difficult to interpret, but also appeared to account for some facial morphology variation and streamlining differences. All other RWs each explained < 3% of shape variation.

Parallelism between lake systems

Results from the models analysed separately for males and females consistently showed evidence for parallelism of body shape, although they also indicated that parallelism was far from perfect (Table 2). In sex-specific models, body size had the strongest effect on body shape, but beach-creek differences were also clearly detectable (Table 2). In both sexes, beach fish had deeper bodies and longer jaws than creek fish (habitat term: males: partial $\eta^2 = 0.17$, females: partial $\eta^2 = 0.15$), but patterns of beach-creek divergence differed between the Wood River and Iliamna Lake systems (habitat-by-lake system interaction: males: partial $\eta^2 = 0.16$, females: partial $\eta^2 = 0.22$; Table 2). These lake-specific responses to habitat were reflected in the first two relative warps, especially RW2 (Fig. 4). In RW1, it was primarily the magnitude of divergence that differed between lake systems; habitat-associated differences in body depth and jaw length were more pronounced in Wood River fish. A large response to habitat along RW2 in Wood River males was not shared by Wood River females or Iliamna males (Fig. 4): Wood River system creek males had slender, streamlined bellies, whereas beach males had more rounded bellies.

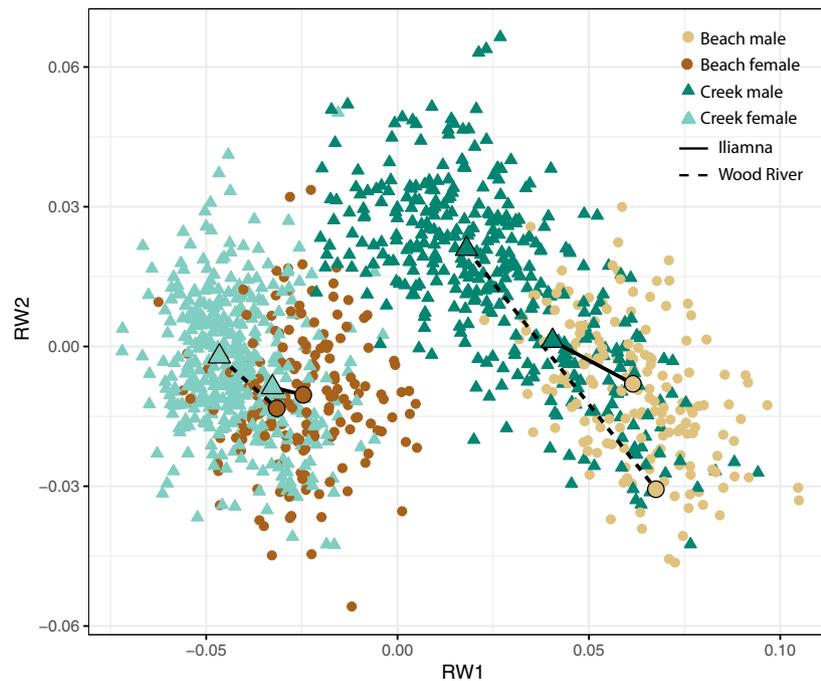


Fig. 5 Both parallel and nonparallel aspects of divergence between sexes and between lake systems are detected in phenotypic change vector analysis (PCVA). Males from different lake systems diverge in a parallel direction between habitats, but vary in their extent of divergence. Females from different lake systems differ in both their direction and magnitude of divergence. Within a lake system, males and females from Wood River are parallel in direction but vary in their extent of divergence, whereas in Iliamna, males and females differ in both direction and magnitude of divergence. Shown are the first two principal coordinates of the shape coordinates included in PCVA for the ease of visualizing the 112-dimensional trait space (equivalent to the first two relative warps). Dashed lines connect beach and creek populations from the same sex in the Wood River system, and solid lines connect Iliamna populations. Population means are shown in large symbols with black outlines, and small symbols (without outlines) are individuals.

Table 2 Results from nonparametric MANCOVAs conducted using randomized residual permutation conducted on each sex separately and effect sizes from parametric MANCOVAs on models of the same structure (see Materials and methods section, in no case did the interpretations from parametric and nonparametric models differ).

Model term	Sex	Partial η^2	F	P -value
Log centroid size	Males	0.375	$F_{1,537} = 172$	0.0001
	Females	0.340	$F_{1,539} = 56.5$	0.0001
Habitat	Males	0.165	$F_{1,537} = 131$	0.0001
	Females	0.152	$F_{1,539} = 40.3$	0.0001
Lake system	Males	0.114	$F_{1,537} = 35.7$	0.0001
	Females	0.113	$F_{1,539} = 18.5$	0.0001
Habitat-by-lake system	Males	0.164	$F_{1,537} = 27.2$	0.0001
	Females	0.215	$F_{1,539} = 8.96$	0.0001

PCVA revealed several interesting patterns (Fig. 5, Table 3). The *magnitude* (length of the vector in multidimensional shape space) of beach-creek divergence was greater in Wood River than in Iliamna Lake for both sexes. Females also differed between lake systems in the *direction* (angle of the vector in multidimensional

Table 3 Results from phenotypic change vector analyses, with P -values in the upper diagonal, and in the lower diagonal, pairwise differences between vectors in the angle (A) and distance (B).

	Females		Males	
	Iliamna	Wood River	Iliamna	Wood River
(A)				
Females				
Iliamna		0.01	0.01	0.02
Wood River	63.5		0.01	0.13
Males				
Iliamna	32.9	52.1		0.17
Wood River	50.8	39.5	29.4	
(B)				
Females				
Iliamna		0.02	0.01	0.01
Wood River	0.015		0.63	0.01
Males				
Iliamna	0.013	0.002		0.01
Wood River	0.062	0.047	0.049	

Significant P -values indicate a significant difference in either the angle or distance between vectors from two groups (i.e. nonparallelism). Highlighted in grey are those pairwise comparisons that are parallel (i.e. do not differ significantly).

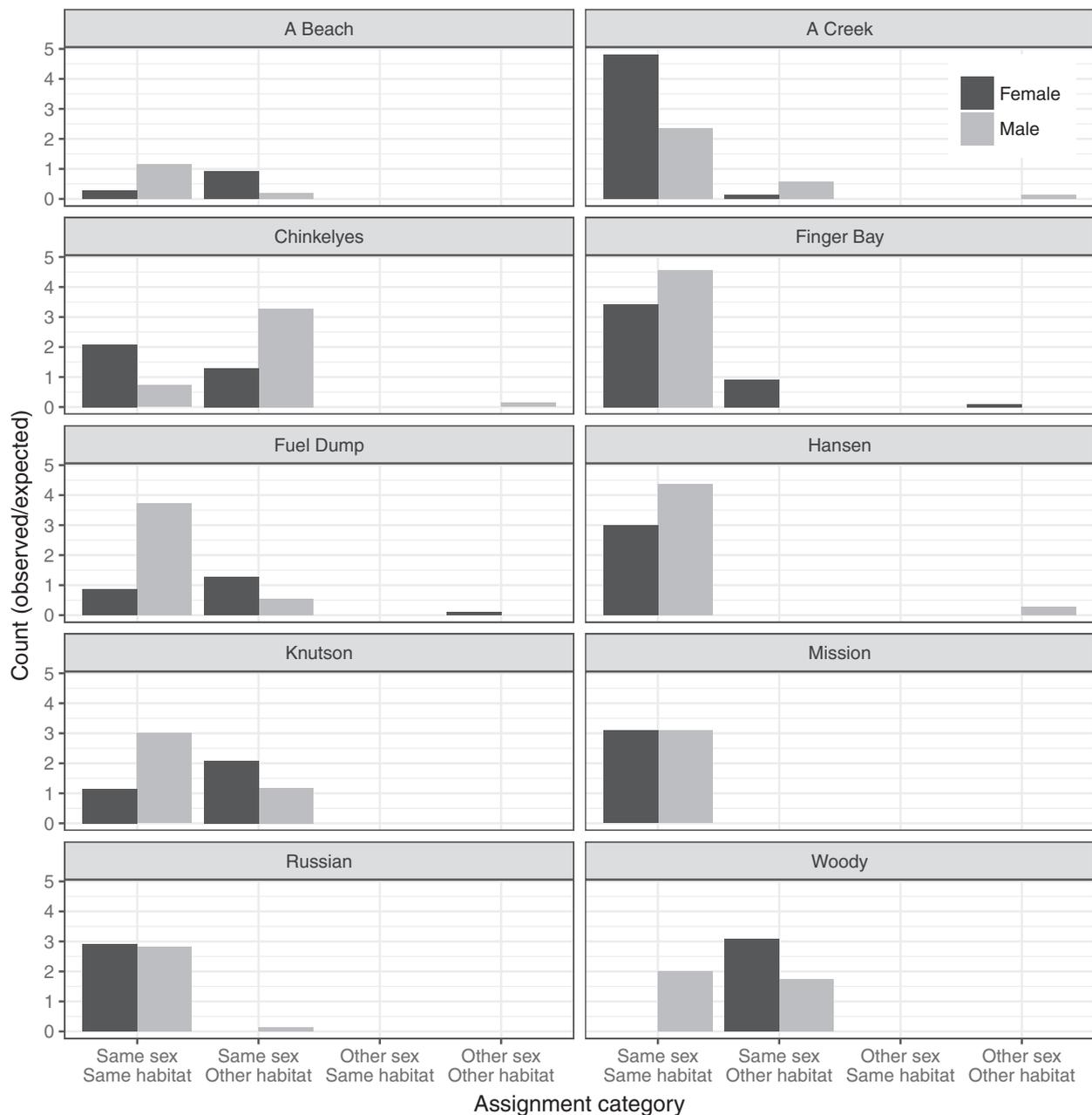


Fig. 6 Cross-classification results for several representative sites. Cross-classification analyses assigned most individuals to groups of the same sex, assignment to the other sex was very rare, suggesting that sex is the strongest driver of body shape. Within each sex, support for both parallelism and nonparallelism was evident. In some sites, assignment was most likely to groups from the same habitat types, suggestive of parallelism. In others, especially sites from Iliamna, nonparallelism was suggested because many fish were assigned to groups of the other habitat type. Sometimes, such as in Woody Island males, assignment was even overwhelmingly most likely to males of the creek form. Thus, the extent to which individuals from within a habitat type resemble other individuals from populations from the same habitat types varies between lake systems. Here, counts are presented as observed/expected or the number actually assigned to each group divided by the number of sites with each group (1 for home, 7 for beach habitats and 11 for creek habitats).

shape space) of beach-creek divergence vectors, whereas males from the two lake systems had highly parallel beach-creek divergence vectors. Thus, only

males showed high beach-creek parallelism between systems, and they varied in the *magnitude* of beach-creek divergence.

Environmental variation partly explains nonparallelism

Within each lake system, the patterns of habitat-associated body shape change varied among individual sites. In misclassification analyses, the relatively high assignment probability to the home category for certain groups, such as Hansen Creek males, Russian Creek females, A Creek females and Finger Bay Beach males and females, indicated some population-specific aspects of shape (Fig. S1). Cross-classification analyses showed evidence for parallelism of beach-creek divergence, but not all sites showed high parallelism (Fig. 6). For some sites, individuals were most likely to be assigned to groups from the same habitat type as their home group, indicating that body shape was most similar within habitats and highly parallel. For other sites, especially those in Iliamna, site-specific body shape was more apparent, and individuals were more likely to be assigned to groups from the other habitat type. This latter result is consistent with PCVA results which showed more drastic shape change in Wood River than in Iliamna.

Some of the variation in body shape among sites can be explained by environmental variation, in particular, water depth. Considering creek sockeye salmon separately, depth strongly influenced body shape of both males (partial $\eta^2 = 0.29$, $F_{1,363} = 57.2$, $P = 0.0001$) and females (partial $\eta^2 = 0.31$, $F_{1,376} = 36.1$, $P = 0.0001$). In short, shallower bodied fish spawn in shallower creeks. However, creek depth could not fully account for shape differences among watersheds. Even after accounting for creek depth, body shape differed between lake systems (males: partial $\eta^2 = 0.14$, $F_{1,363} = 25.2$, $P = 0.0001$; females: partial $\eta^2 = 0.13$, $F_{1,376} = 18.3$, $P = 0.0001$). Importantly, the extent of shape change in response to creek depth differed between lake system (lake system-by-creek depth interaction, males: partial $\eta^2 = 0.18$, $F_{1,363} = 15.6$, $P = 0.0001$; females: partial $\eta^2 = 0.14$, $F_{1,376} = 5.87$, $P = 0.0001$). Thus, although differences between lake systems in the depth of the creeks we sampled partially explained nonparallelism, each lake system also had unique aspects of shape change that were not fully explained by creek depth.

Parallelism between sexes

When considering both sexes together, body shape was influenced by sex, body size, habitat, lake system and all interactions between these effects (Table 1). However, comparing effect sizes (Table 1) shows that sex had by far the largest influence on body shape (partial $\eta^2 = 0.82$). The importance of sex was also reflected in the grouping of individuals in principal component space (Fig. 5), which showed that individuals of the same sex were generally more similar in shape than individuals from opposite sexes, especially in terms of

RW1 (which explained 65.9% of shape variation). In exchangeability analyses, both males and females were overwhelmingly assigned to their correct sex in both analyses, with very few exceptions (Figs S1 and Fig. 6).

Continuing to consider both sexes in the same model, the strong habitat term (partial $\eta^2 = 0.07$) indicated some parallel evolution when considering both sexes together, but the significant habitat-by-lake system (partial $\eta^2 = 0.12$) and sex-by-habitat-by-lake system (partial $\eta^2 = 0.06$) interactions indicated that the extent of parallelism differed between lake systems and sexes within lake systems. Importantly, the sex-by-habitat interaction (partial $\eta^2 = 0.04$) indicated that the sexes differed in their patterns of habitat-associated shape divergence. PCVA also revealed that the similarity of male vs. female beach-creek divergence patterns depended on their lake system of origin. In Iliamna, males and females differed in both the *magnitude* and *direction* of body shape change between beach and creek habitats. In contrast, Wood River males and females did not differ in the direction of their divergence, but beach-creek shape differences were much more pronounced in males than in females. Overall, though, nonparallelism between lake systems was stronger than that between the sexes.

Discussion

Patterns of beach-creek body shape parallelism in sockeye salmon were complex and sex-specific. Body shape was overwhelmingly determined by sex: body depth (RW1) accounted for 65.9% of shape variation by capturing dramatic sexual dimorphism in shape that is easily observed by eye. Male sockeye salmon had deeper bodies and longer upper jaws than female sockeye, consistent with previous work (e.g. Blair *et al.*, 1993; Quinn *et al.*, 2001b; Quinn, 2018). Both sexes have also diverged between beach and creek habitats, including body depth (RW1). Consistent with previous studies, both males and females had deeper bodies and longer upper jaws in beach habitats than in creeks (Figs 3 and 4), although this difference was much more dramatic for males than females. The difference between beach and creek body shape was much more dramatic in the Wood River system than in Iliamna Lake. Taken together, our analyses confirmed that, in both lake systems, sockeye salmon of both sexes had deeper bodies and longer jaws in beach habitats than creek habitats, but significant interactions between habitat and the main effects of lake system and sex indicated that in order to fully characterize beach-creek divergence, lake system-specific and sex-specific components must be considered. Thus, although beach-creek shape divergence in sockeye salmon can be generally be considered as an instance of phenotypic parallelism, beach-creek patterns are nuanced and dependent on both sex and lake system.

Parallelism between lake systems

What contributes to the variation in the extent of parallelism between sockeye of the same sex from Wood River and Iliamna Lake? It appears that much, but not all, of the difference between lake systems can be explained by differences in water depth. In males, beach-creek divergence was parallel in direction but showed considerable variation in the magnitude of divergence (Table 3). These results appear to be driven by the dramatic differences in shape between beach and creek males in Wood River, which included some of the most extreme shape divergence observed for both habitat types. The mean water depth of sampled creeks in Wood River ($0.20 \text{ m} \pm 0.10 \text{ m}$ standard deviation) is lower than in Iliamna Lake ($0.30 \text{ m} \pm 0.14 \text{ m}$), and extremely shallow water where stranding occurs is more common in some Wood River creeks (Quinn *et al.*, 2001b). Specifically, sockeye salmon returning to shallow creeks like Hansen Creek in the Wood River system must navigate very shallow water ($\leq 4 \text{ cm}$) to reach the spawning habitat whereas none of the Iliamna Lake populations that we sampled have such difficult access, nor such shallow water as sockeye salmon experience in Hansen, A and C creeks in the Wood River system (Quinn *et al.*, 2001b). In these shallow creek mouths, strong natural selection from both bear predation and stranding (Quinn & Buck, 2001; Carlson & Quinn, 2007) was reflected in the very slender shape of shallow creek populations in Wood River and also their generally young age at maturity and small length at a given age (Quinn *et al.*, 2001b). Within the creek habitat category, water depth strongly influenced body shape, with more extreme shallow bodies found in more extreme shallow creeks. There are deeper riverine habitats in the Wood River system (Marriott, 1964), but we did not sample them. However, creek depth cannot explain all of the variation between lake systems, given the significant effects of lake system (males: partial $\eta^2 = 0.14$, females: partial $\eta^2 = 0.13$) and the creek depth-by-lake system interaction (males: partial $\eta^2 = 0.18$, females: partial $\eta^2 = 0.14$). Thus, it appears that although the fact that we sampled deeper creeks in Iliamna Lake than in Wood River partly contributed to the observed differences between lake systems, it does not tell the whole story, and some lake system-specific aspects of shape change remain even after accounting for creek depth.

Wood River beach males also had more extreme shapes than Iliamna Lake beach males. This difference could arise from the fact that the Wood River system does not include any island beach spawners, which, in Iliamna, are generally younger and shorter for their age than mainland beach spawners (Blair *et al.*, 1993; Quinn *et al.*, 2001b). In Iliamna, mainland and island beach spawners are genetically distinct (Gomez-Uchida

et al., 2011). Island beaches have large spawning and incubation gravel, and females from island beaches lay large eggs, even though the females themselves are smaller than mainland females (Quinn *et al.*, 1995). The drivers of this nonparallelism between island and mainland beach spawning in Iliamna males remain unclear, but could be related to differences in gravel size (Blair *et al.*, 1993) especially if male shape is somehow genetically correlated with changes in female shape driven by gravel size.

More generally, exchangeability analyses make clear that body shape also showed population-specific components, likely due to local adaptation among populations. Assignment probability to home groups was high, especially for groups from particularly shallow creeks. Hamon & Foote (2005) suggested, based on selection estimates for sockeye salmon in Hansen Creek, that selection might favour different body depths at water depths within and among habitats, leading to different optimal shapes across populations and even years. It seems likely that beach and creek habitats are not well-distinguished, binary categories, and instead reflect a gradient of body shapes formed along selective gradients due to predation and stranding risk. In addition, manoeuvrability in deep, fast water may also play a role. Specifically, sockeye salmon in large rivers are not susceptible to stranding, nor to predation, yet they are not as deep-bodied as those in beaches (Quinn *et al.*, 2001b), so an intermediate body shape might be most efficient. Finally, we have no estimate of the 'construction cost' of the sexually dimorphic features. As capital breeders, the salmon are not feeding during the time when the dramatic changes in shape are taking place, and there is presumably some energetic cost to this, as indicated by experiments (Kinnison *et al.*, 2003). Our study design also does not allow for us to consider the roles of evolutionary history or plasticity, which may also affect population-specific variation in body shape.

A potential weakness of our study arises from the unbalanced nature of sampling sites between lake systems (Fig. 1). This difference across lake systems reflects in part the variation in the availability of habitat in each lake system. In Lake Aleknagik in the Wood River system, relatively few sockeye salmon spawn on beach habitats (although lakes farther up in the system have more beach spawners), and some creeks are often only accessible via stretches of very shallow water at the mouths of the creeks (Quinn *et al.*, 2001b). No island beach-spawning populations are found in the Wood River system (Quinn *et al.*, 2001b). The Iliamna Lake system, in contrast, consists of many beach and island beach-spawning populations, but relatively few small creek habitats or creeks with very shallow mouths (Quinn *et al.*, 2001b). However, these are large lake systems with many spawning populations, and the generality of our results to other populations remains unknown.

Parallelism between sexes

Male and female sockeye salmon demonstrated sex-specific beach-creek changes, as well as differences in their overall extent of parallelism. For example, characterizing body shape using geometric morphometrics revealed an unexpected difference in beach-creek divergence patterns for Wood River males compared to all other groups. Specifically, Wood River beach and creek males were very divergent along RW2, whereas females and Iliamna Lake males were not (Fig. 3). RW2 appears to explain variation in the ventral streamlining of males, with larger, more rounded bellies in beach males and slender, streamlined bellies in creek males. A previous study comparing selection on Wood River males from different creeks found similar trends for males with streamlined bodies and relatively long jaws in Hansen Creek, a very shallow creek and one of our study sites (Carlson *et al.*, 2009). This response to very shallow water in males of some Wood River populations helps explain both some of the variation in the extent of parallelism between both lake systems and sexes.

Although females from both lake systems had deeper bodies in beach habitats, females were much less parallel between lake systems than males, given that female beach-creek divergence vectors differed significantly in both magnitude and direction. Again, this result could be due in part to the presence of shallower creek habitats that were sampled in the Wood River, which could contribute to differences in the magnitude of beach-creek change. Still, females seemed to show truly lake system-specific shape differences, since the *direction* of female beach-creek divergence differed between lake systems. Whether these differences between females from different lake systems could be explained by other environmental variables or evolutionary histories remains unclear.

What drives variation in the extent of beach-creek parallelism between male and female sockeye? Differences in beach-creek divergence were more apparent between lake systems than sexes, but variation in the extent of parallelism between the sexes nonetheless represented an important aspect of sockeye body shape in this system. Within each lake system, habitat-associated shape change was far less dramatic in females than in males, but in general, shape change occurred in a similar direction along RW1 (Fig. 4). Interestingly, the extent of sexual dimorphism differed between the two lake systems (Figs 3 and 4). PCVA revealed that the differences between male and female shapes were much greater in Wood River than in Iliamna Lake (Table 3). Moreover, the extent of divergence in Wood River males was significantly greater than the extent of divergence in any other group, likely because males from shallow Wood River creeks are subject to the strongest selection for shallow bodies. Males are more

likely to strand in shallow water, likely due to their deeper bodies (Carlson & Quinn, 2007), and stranding risk is much higher in some Wood River creeks than those at Iliamna Lake (Quinn *et al.*, 2001b; Carlson & Quinn, 2007). Studies conducted on some of the same populations as those included in this study often find that males are more likely to be eaten by bears (Quinn & Kinnison, 1999; Ruggerone *et al.*, 2000; Quinn & Buck, 2001), although not always (Lin *et al.*, 2016). It appears that differences in the strength of natural selection due to habitat accessibility and bear predation, which is felt more acutely by males, might explain variation in the extent of parallelism between not only lake systems but also sexes.

Parallelism between the sexes is rarely considered, but Hendry *et al.* (2006) investigated parallelism between the sexes in guppies in response to different predation regimes, and variation in the extent of parallelism driven in part by stronger natural selection from predation on males than on females. The authors suggested several alternative explanations that could explain variation in the extent of parallelism between the sexes, other than differences in predation pressure between males and females, including sex-specific plasticity, dispersal and niche partitioning. The life history characteristics of sockeye salmon allow us to largely rule out sexual niche partitioning, because spawning sockeye salmon of both sexes are found within very close proximity and have ceased to feed (Quinn 2018). Moreover, salmon show no sexual dimorphism during marine residency and only develop the exaggerated spawning morphologies we study here during their return migration (Hendry & Berg, 1999, Quinn 2018). Despite this, males and females display very different behaviours during spawning, and it remains possible that differences in the physical environments of beaches and creeks may lead to different optimal shapes for sex-specific behaviours such as redd digging or male–male aggression. Sex-specific dispersal also seems unlikely to explain nonparallelism between sexes in sockeye because nearly all sockeye return to their natal rivers to spawn (Dittman & Quinn, 1996; Quinn, 2018). Our study design does not allow us to rule out the possibility of sex-specific plasticity.

Our study populations are also subject to size- and sex-selective commercial gill net fisheries. Males tend to return at a larger size and thus are more likely to be harvested (Kendall & Quinn, 2013). In addition, the strengths of both fishing pressure and directional selection vary across populations, with more fish removed from larger bodied populations by the fishery but stronger directional selection on body size in smaller bodied populations (Kendall & Quinn, 2009). It is possible that certain body shape phenotypes might also be more likely to be removed by the fishery. The spawning body shapes that we investigated become fully developed only after freshwater entry, after sockeye have made it safely

through the fishery. However, the early stages of these transitions may nonetheless make certain shapes more catchable, as appears to be the case with males in general (Kendall & Quinn, 2013). In Little Togiak Lake, part of the Wood River system, Hamon *et al.* (2000) found that body girth shortly after entering the lake was highly predictive of eventual body depth at maturity, and they estimated that deep-bodied beach fish were being removed by the fishery at a greater rate than small-bodied creek fish. Thus, the extent of shape divergence between beach and creek populations might be even more extreme in the absence of fishing pressure.

One important aspect of our results is that we would not have reached the same conclusions if we had only considered one sex. Sexual dimorphism complicates studies of parallel evolution, and many studies deal with this complication by considering only one sex (Butler *et al.*, 2007). If we were to compare our PCVA results across lake systems in only males or only females, we would have come to different conclusions. Specifically, males from different lake systems showed high parallelism in the direction of their beach-creek divergence, whereas females did not. This difference in interpretation has important implications for studies of parallelism in sexually dimorphic species. Wherever possible, parallelism in both sexes should be considered, because ignoring one sex could fail to capture the full story (Butler & Losos, 2002), as would have been the case for our results. Furthermore, divergent sexual selection might play an important or even dominant role in driving adaptive divergence and speciation in some systems (Svensson *et al.*, 2006; Bonduriansky, 2011; Maan & Seehausen, 2011). Just as studies at the interface of local adaptation and sexual dimorphism are fostering advances in each discipline (Connallon *et al.*, 2018), the extensive literature on the evolution of sexual dimorphism could also inform our understanding of parallelism and provide opportunities to test new hypotheses. For example, studies on the evolution of sexual dimorphism in different habitats or along environmental gradients (e.g. De Lisle *et al.*, 2018a,b; Svensson *et al.*, 2018) likely also represent opportunities to consider parallel evolution between the sexes. In contrast, failing to consider and compare parallelism in both sexes could lead us to miss important drivers of phenotypic variation.

Conclusions

Here, we have shown that, in sockeye salmon, the interplay between contrasting sexual and natural selection leads to variation in the extent and direction of beach-creek body shape divergence both between lake systems and sexes. Variation in the extent of parallelism between the sexes has also been shown in other species. For example, variation in the extent of parallelism

between the sexes has been previously detected in guppies (Hendry *et al.*, 2006; Dargent *et al.*, 2016; Jacquin *et al.*, 2016) and other live-bearing fishes (Langerhans & Makowicz, 2009; Wesner *et al.*, 2011; Ingley *et al.*, 2014a), although these inferences are complicated by the different ecological and physiological roles played by the sexes. Consistent with previous work in live-bearing fishes, our results show that although there are often parallel aspects of divergence between the sexes during habitat-associated divergence, important differences in male and female patterns contribute to overall variation in the extent of parallelism. Together, these results reveal the importance of explicit consideration and quantification of variation in the extent of parallelism between the sexes. Studies that fail to consider the potential for sexual dimorphism and sexual selection to induce variation across evolutionary replicates could miss important dynamics that shape divergence and the extent of parallelism.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 As shown for several representative sites, misclassification analyses assigned most individuals to their home group (same sex, same sampling site), indicating site-specific aspects of shape are common.

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