

## Research

### Matching habitat choice: it's not for everyone

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#### Oikos

129: 689–699, 2020

doi: 10.1111/oik.06932

Subject Editor and  
Editor-in-Chief: Dries Bonte  
Accepted 2 January 2020

Matching habitat choice is a habitat preference mechanism based on self-assessment of local performance, such that individuals settle in the habitats that are best suited to their phenotypes, promoting local adaptation. Despite the important evolutionary implications of matching habitat choice, examples from natural populations are rare. One possible reason for this apparent rarity is that phenotype-matching habitat choice might be manifest only in those population segments for which the cost of a phenotype–environment mismatch is high, although this hypothesis remains to be tested. Here, we test for matching habitat choice in a breeding population of sockeye salmon *Oncorhynchus nerka* where the strength of performance tradeoffs across environments, and therefore the costs of mischoosing, can be evaluated in meaningful discrete groups (e.g. male versus females, and ocean-age 2 versus ocean-age 3). Consistent with matching habitat choice, salmon of similar ocean-age and size tended to cluster together in sites of similar water depth. However, matching habitat choice was only favored (longer life span) in 3-ocean females – the segment of the population most vulnerable to bear predation. Our findings support the hypothesis that matching habitat choice is more likely to be evident in those segments of a population that suffer a major cost of mischoosing, leading to ‘partial matching habitat choice’.

Keywords: habitat selection, local adaptation, matching habitat choice, natural selection, phenotype–environment covariance, population structure, predator–prey interactions, salmon

#### Introduction

Habitat choice can strongly influence individual survival and reproductive success, and thus can have profound consequences for many ecological and evolutionary processes (Fretwell and Lucas 1969, Cody 1984, Morris 2003, Berner and Thibert-Plante 2015). Habitat choice is not expected to be random, but rather influenced by habitat preference alleles (Jaenike and Holt 1991), natal experience (Davis and Stamps 2004) and self-assessment of the phenotype–environment match, a process known as ‘matching habitat choice’ (Edelaar et al. 2008, Holt and Barfield 2008). Matching habitat choice is defined as a habitat preference mechanism by which individuals assess performance tradeoffs across environments and then settle in the habitats that are best suited to their

phenotypes, thus increasing individual performance beyond that expected under phenotype-independent habitat choice (Edelaar et al. 2008).

Matching habitat choice is assumed to produce results in the spatial clustering of similar phenotypes and eventually produces patterns of phenotype–environment covariance independently of other processes that might also generate these patterns, including the selective mortality of maladapted individuals (natural selection), and phenotypic plasticity once a given habitat is occupied (Edelaar et al. 2008, Nicolaus and Edelaar 2018). Thus, conclusively demonstrating matching habitat choice requires three conditions. First, correlations should exist among individuals between particular phenotypes and particular habitat characteristics. For instance, darker-colored individuals might choose darker habitats that better match their color, thereby improving their camouflage and reducing predation risk from visually-oriented predators (Merilaita and Stevens 2011, Edelaar et al. 2019). Second, those phenotype–habitat associations should improve the performance of those individuals over that expected from random habitat associations. For instance, the survival and breeding success of darker individuals (relative to lighter individuals) should be higher in darker than lighter habitats (Karpestam et al. 2012). Third, the above effects should be the result of habitat choice based on flexible assessment of performance tradeoffs across alternative environments, as opposed to differential mortality of phenotypic plasticity (Edelaar et al. 2008, Nicolaus and Edelaar 2018, but see Lowe and Addis 2019).

Matching habitat choice can have important evolutionary implications, as it may influence the degree and rate of local adaptation, determine individual performance, facilitate the maintenance of genetic variation and population persistence, and even lead to speciation (Edelaar et al. 2008, Berner and Thibert-Plante 2015). Nevertheless, matching habitat choice has only recently received much attention, with the available evidence mostly coming from individual-based simulations (Bolnick and Otto 2013, Nicolaus and Edelaar 2018, Mortier et al. 2019, Pellerin et al. 2019) or laboratory organisms in experimental microcosms (Karpestam et al. 2012, Wennersten et al. 2012, Jacob et al. 2017, 2018, Jacobson et al. 2017). By contrast, field tests for natural populations are limited to a handful of studies, mostly on birds (Dreiss et al. 2012, Camacho et al. 2015, Benkman 2017, Holtmann et al. 2017, but see Bolnick et al. 2009, Edelaar et al. 2019, Lowe and Addis 2019), with their infrequency due in part to logistical and inferential challenges. For instance, robust data are required for relevant phenotypes, settlement decisions and performance for many individuals – ideally replicated across populations or years. Furthermore, novel research approaches potentially including experimental manipulation of phenotypes and the use of carefully selected model systems can be required, because the effect of phenotype on habitat selection decisions needs to be decoupled from that of habitat preference alleles and natal experience (Akcali and Porter 2017). Without all of this information,

matching habitat choice is difficult to distinguish from other processes that can lead to phenotype–environment correlations (Edelaar et al. 2008, Nicolaus and Edelaar 2018, Edelaar et al. 2019, Lowe and Addis 2019).

Matching habitat choice might be less common in nature than is theoretically expected (Edelaar et al. 2017, Nicolaus and Edelaar 2018). One reason is that, even when selection favors matching habitat choice, it might not evolve due to constraints on habitat choice (e.g. lack of suitable habitats or exclusion from preferred habitats by dominant conspecifics, Camacho et al. 2015, Edelaar et al. 2017, Jacobson et al. 2017) or on its evolution (e.g. lack of genetic variation or opposing selection across life stages or sexes; Bourret et al. 2017, Medina et al. 2017, Forsman 2018). In addition, matching habitat choice might not evolve where the costs of dispersal are high, thus precluding the evaluation of multiple environments prior to settlement (Mortier et al. 2019), or during periods of abundant resources that are accessible to a wide range of phenotypes, thus reducing the strength of performance tradeoffs between different habitats (Benkman 2017, Golcher-Benavides and Wagner 2019). We suggest that another reason why matching habitat choice might not be obvious is that it might be favored (and therefore manifest) in only part of a population: specifically the part that experiences strong performance tradeoffs between different habitats, and for which the cost of a phenotype–environment mismatch is therefore high. Stated the opposite way, matching habitat choice would not be expected for segments of a population where the cost of making a ‘mistake’ is minimal. Some hypothetical examples will serve to illustrate. 1) Habitat choice to maximize crypsis based on an individual’s color pattern should be favored only for life stages susceptible to predation. 2) Habitat choice to maximize foraging based on trophic morphology should be favored only for individuals who might suffer energy limitation. 3) Habitat choice to maximize offspring survival should be favored only for the sex that undertakes parental care. Our study will focus on these aspects of ‘partial matching habitat choice’.

### Study system

We studied a breeding population of sockeye salmon *Oncorhynchus nerka* as a model system and focused on the role of spatial variation in predation risk as a driver of habitat selection. We first examined whether individuals of different body size/age select different microhabitats for breeding, and we then assessed the effects of body size/age variation on salmon performance across environments. This system is appropriate for investigating variation in the expression of matching habitat choice among different segments of a population (‘partial matching habitat choice’) because meaningful discrete groups (e.g. males versus females, and 2-year-old versus 3-year-old fish) can be evaluated based on the traits predicted to be most relevant to habitat selection (body size and sex). Male and female salmon have different roles in nest-site selection and, therefore, sex differences in habitat selection

might be expected (Hedrick 1993). Body size (length at maturity; Quinn et al. 2001a) is a good candidate trait to guide matching habitat choice of stream fishes in general, and sockeye salmon in particular, because it commonly influences their distribution patterns and generates phenotype–environment correlations (Schlosser 1987, Quinn and Foote 1994, Quinn and Kinnison 1999, Hendry et al. 2001, Jacobson et al. 2017). Moreover, age- and length-at-maturity of salmon are (moderately) heritable traits (median  $h^2=0.21$  in both cases; Carlson and Seamons 2008) that could also mediate performance tradeoffs between microhabitats (e.g. optimal breeding sites for small salmon may not be optimal for large salmon due to the selective effects of predation; Quinn and Buck 2001, Quinn et al. 2001a, Lin et al. 2016), thus providing a basis for the evolution of matching habitat choice. Our working hypotheses are as follows:

1. Matching habitat choice should differ between the sexes – being more important for females than males. Male and female sockeye salmon have different roles in nest-site selection and parental care and hence should experience different selective pressures for matching habitat choice. Female salmon make the decision regarding the location of the nest based on the balance between the intrinsic quality of the site and the costs of predation risk and competition for that site (Tautz and Groot 1975, Hendry et al. 2001, Adkison et al. 2014). Females then remain within a meter or so of their nest for the duration of their life so as to defend it from superimposition by other females who would otherwise dig their nest in the same location (Hendry et al. 2004). Failure of a female to continue to defend their nest leads to severe loss of eggs (Essington et al. 2000), as has been shown specifically for our study population (Hendry et al. 2004). For males, however, the abundance of females and the intensity of competition for mates are more important cues than the intrinsic quality of nesting sites because males do not compete for territories but rather for access to already-settled females (Mathisen 1962, Fleming and Gross 1994, Quinn and Foote 1994, Quinn et al. 1996). Furthermore, the bond of males to a specific nest site is weaker than that of females, because males tend to defend individual females only when they are near to oviposition; otherwise they often (but not always) move around to seek other females near oviposition (Mathisen 1962, Foote 1990, Quinn et al. 1996). Thus, the fitness consequences of habitat selection should be relatively more severe for females than males due to female's particular movement restrictions imposed by parental care.
2. Matching habitat choice should depend on fish size – being more important for larger fish. In our study, bear predation is the main cause of non-senescent mortality in mature sockeye salmon (Quinn et al. 2001a, Lin et al. 2016). For instance, bears can kill up to 88–100% of the salmon breeding in some creeks (Quinn and Kinnison 1999, Carlson et al. 2007, Quinn et al. 2001b). Bears selectively kill older, larger salmon (Quinn and Kinnison

1999, Ruggerone et al. 2000, Quinn and Buck 2001, Quinn et al. 2001a, Cunningham et al. 2013), although this selectivity is manifest primarily in shallow water (Gende et al. 2004, Carlson et al. 2007). The reason is that large fish are preferred by bears; yet bears that congregate in riparian areas to feed on salmon are only able to exercise this choice in shallow water where salmon – especially large salmon – are more conspicuous and have difficulty escaping (Fig. 1a–b). One would therefore predict stronger survival tradeoffs between shallow- and deep-water habitats in larger fish than in smaller fish. In response to this tradeoff, large salmon should be more likely to seek deeper sites that reduce predation risk and increase their reproductive life span relative to shallow water. Conversely, the need of small fish to seek deep-water refuges to maximize their chances of survival until senescence should not be as great as that of large fish. Hence, the likelihood of predator-induced matching habitat choice should increase with fish size.

## Material and methods

### Data collection

Data were collected in 1995 and 1996 in Pick Creek (59°33'00"N, 159°04'18"W), a small (2nd order) creek flowing into Lake Nerka, in the Wood River Lakes system, Alaska. Sockeye salmon spawn in the lower 2 km of the creek and the total number of spawners was 4418 in 1995 (starting on 20 July) and 6189 in 1996 (starting on 21 July) (Hendry et al. 1999, 2001, Quinn et al. 2009, 2017). Data collection methods have been described in detail in previous publications (Hendry et al. 1999, 2001), and other relevant properties of the salmon population are described elsewhere (Hendry and Berg 1999, Gende et al. 2004, Hendry et al. 2004, Carlson et al. 2007, Quinn et al. 2017). We therefore here only briefly summarize key methods specifically relevant to the present analysis.

On their return from the ocean, sockeye salmon stop feeding and thereafter fuel all sexual development and spawning activity exclusively from stored energy (Hendry and Berg 1999). Before spawning, sexual development is completed over a period of days to weeks as the fish shoal in the lake (in this case Lake Nerka) immediately adjacent to their natal spawning area (in this case Pick Creek). During this shoaling period, we used seine nets to capture fish, which were then anaesthetized using tricaine (MS-222), tagged with individually-coded highly-visible Peterson disc tags (Fig. 1c), and measured for body length from the middle of the orbit of the eye to the end of the hypural plate. This measurement represents somatic length and is not biased by the extended jaws that characterize mature males (Quinn et al. 2001a). Each salmon was released back at the capture site. The present analysis is based on the 255 females (86 in 1995 and 169 in 1996) and 202 males (63 in 1995 and 139 in 1996) that underwent this procedure.

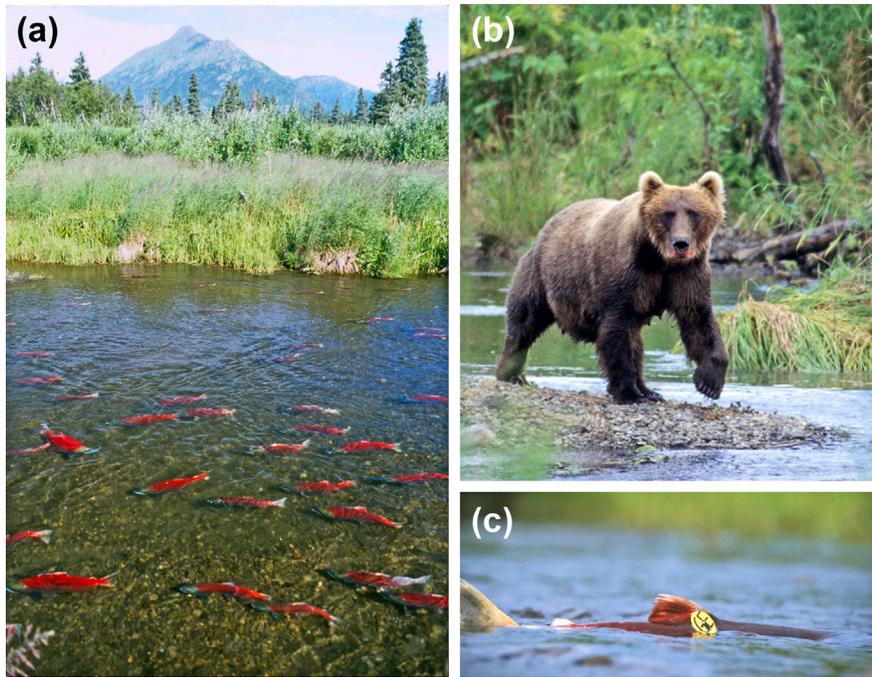


Figure 1. Photographs showing breeding sockeye salmon in Pick Creek and its main predator. (a) Breeding sockeye salmon in areas of shallow water (lower part of panel a) and deep water (central part of panel a). (b) Brown bears *Ursus arctos* congregate in riparian areas of Pick Creek to feed on spawning salmon. This individual bear killed many of the salmon in our specific dataset 1995. (c) Female salmon tagged with an individually-coded disc tag for individual identification from a distance. Photographs by A. P. Hendry.

Prior to any salmon entering Pick Creek, the 2-km long spawning area was delineated into 97 sequential 20-m long sections. The creek was then surveyed each day to determine the date that spawning commenced – the first date on which salmon entered the creek and remain thereafter. From that day onward, the entire creek was surveyed on a daily basis to determine the number of fish present in each section, which provided a daily measure of the extent of competition for nest sites and mates experienced by females and males, respectively (Mathisen 1962, McPhee and Quinn 1998). During these daily surveys, the location of each individually tagged salmon was recorded, which was possible owing to the shallow and very clear water. The monitoring of marked individuals from the moment they entered Pick Creek allowed us to discard any contribution of size-selective mortality to patterns of phenotype–environment covariance. The first day a fish was observed in the creek was defined as the onset of spawning by that fish and will hereafter be referred to as 'breeding date'. On several subsequent days, the depth and velocity of the water at each female's nest was recorded – and averaged across dates for each individual. Female sockeye salmon establish only a single nest site (called a 'redd') that is typically less than 1 m<sup>2</sup>. They then defend that nest until death, whereas the males defend females that are near to oviposition and frequently move between locations and females through the breeding season (Mathisen 1962). During the spawning period water levels are stable, as the creek is spring-fed and has a very small drainage area. Hence, the depth and

velocity measurements for a given female's nest represent several replicate fine-scale measurements of the same location.

The above daily surveys also were used to determine the date that each male and female died, as indicated by their disappearance from the spawning site. The difference between this date and the date each individual was first observed in the stream was defined as the 'reproductive life span' (RLS) – the fitness component we analyze here. Although other factors certainly contribute to reproductive fitness, RLS is critically important for both females and males because it determines, respectively, the duration of nest (egg) defense from superimposition by other females and the duration of male defense of their females against intruders (Hendry et al. 2004, Lin et al. 2016). Moreover, RLS is a primary candidate for direct influences of habitat choice, especially in females, since they are more strongly tethered to a particular nest site and would therefore be more vulnerable to bear predation when nesting in risky habitats.

In nearly all cases, the absence of a tagged fish from its spawning section corresponded with its death, as revealed by the discovery of its carcass or by its complete disappearance from the creek. Otoliths were removed from each carcass to determine the number of years the fish had spent at sea – an 'ocean age' of either two or three (Quinn and Kinnison 1999). The association between body length and ocean age was very strong for those fish whose carcasses were recovered (females:  $r^2=0.83$ ,  $F_{1,183}=908.5$ , males:  $r^2=0.71$ ,  $F_{1,90}=221.3$ , both  $p < 0.001$ ), and so we estimated ocean age for the fish whose

carcasses were not recovered (39% of all individuals) by reference to their length at tagging.

### Statistical analyses

All statistical analyses were performed using R ver. 3.5.1 (<www.r-project.org>). To test for differential habitat use according to salmon size, we examined the relationship between body length and water depth through linear regression analyses using all fish ( $n = 457$ ) captured in 1995 and 1996 (LM, year  $\times$  body length:  $p = 0.535$ ). Even though exploratory analyses showed no significant differences between sexes or age classes in the size–depth relationship (LM, sex  $\times$  body length:  $p = 0.288$ , age  $\times$  body length:  $p = 0.578$ ), the pool of fish was classified in a hierarchical manner into six smaller subgroups to look more closely at the association between body size and water depth in different segments of the population, including males ( $n = 202$ ), females ( $n = 255$ ), 2-ocean males ( $n = 123$ ), 3-ocean males ( $n = 79$ ), 2-ocean females ( $n = 135$ ) and 3-ocean females ( $n = 120$ ).

To assess the adaptive value of size-dependent habitat choice, we tested for correlational selection stemming from the covariance between body length and habitat use (water depth) using methods of Lande and Arnold (1983). RLS was used as the fitness metric, as justified above. Obviously, the selective basis for matching habitat choice and the pattern of it are interrelated and may be viewed as a single natural process, but in the context of this work they will be treated separately for analytical reasons. By combining the linear regression analyses and the analysis of selection on the interaction between body length and water depth we can explicitly test for matching habitat choice, because the latter would indicate whether the strength of performance tradeoffs between habitats in terms of life expectancy differs between small and large phenotypes (i.e. the selective basis for the evolution of matching habitat choice), while the former would indicate whether individuals select optimal breeding environments given their body size (i.e. the expression of matching habitat choice; Karpestam et al. 2012, Camacho et al. 2015).

Our selection analysis was based on a linear model with normal error distribution and an identity link function. In addition, as suggested by Morrissey and Sakrejda (2013), we ran a tensor product smoother-based generalized additive model (GAM), using the default settings in the function `gam()` in the R-package MGCV (Wood 2006). However, as expected when phenotype is multivariate normal (Morrissey and Sakrejda 2013), the results obtained with this complementary approach were virtually identical to those of the classical least squares regression. For simplicity, only the latter are presented in this work.

Prior to analysis, each individual's RLS was divided by the mean life span of all individuals in a given year to calculate relative fitness. In addition, all the predictor covariates (body length, water depth, breeding date and competition level) were standardized to a mean of zero and a standard deviation of one. Body length, its quadratic term, water depth, sex and their pairwise interactions were included as the key predictor

variables in the full model. Models for each population segment had the same structure as the full model, except for sex. The effect of ocean age could not be explicitly modeled due to collinearity problems resulting from ontogenetic variation in body length and, therefore, age-class differences in selection on matching habitat choice were inferred from body lengths, provided the little overlap in size between 2-ocean and 3-ocean fish (Fig. 1). Breeding date (onset of breeding) was included as a covariate to control for its effects on energy allocation and therefore life span (McPhee and Quinn 1998, Hendry et al. 1999, 2004). Competition intensity, estimated as the lifetime average number of other females in the stream section of each focal female (McPhee and Quinn 1998), was also included as a covariate to control for the potential effect of energy expenditure in nest defense on the duration of life span (Hendry and Berg 1999, Hendry et al. 2004).

Model selection was carried out using both forward and backward selection, which produced the same results. To avoid misleading conclusions based on statistical artifacts, we systematically performed diagnostic statistics (e.g. inspection of residuals plotted against predicted values and examination of influential data points and interrelations between predictor variables). None of these showed obvious deviation from the assumptions of normality and homogeneity of residuals, confirming model stability (diagnostic plots for the models can be found in Supplementary material Appendix 1).

## Results

### The pattern of matching habitat choice

Body length influenced the distribution of male and female salmon within Pick Creek, with larger fish occupying deeper-water habitats than did smaller fish (Table 1, Fig. 2). This size–depth based distribution actually resulted from the spatial segregation of 2-ocean and 3-ocean fish, as age is the primary determinant of body length in salmon (Table 1, Fig. 2). The degree of overlap in body length between 2-ocean and 3-ocean fish shown in Fig. 2 remained the same when only fish of exactly known age were considered ( $n = 277$  individuals, data not shown). Most 3-ocean fish spawned at depths greater than 40 cm (males: 69%, females: 59%), whereas 2-ocean fish did so more rarely (males: 37%, females 24%; Fig. 2).

Table 1. Linear regression models examining the relationship between body length and water depth in different segments of the sockeye salmon population of Pick Creek.

Population segment	$r^2$	F	df	p
All fish	0.143	75.60	1,455	<0.001
Males only	0.101	22.36	1,200	<0.001
Females only	0.174	53.35	1,253	<0.001
2-ocean males	0.004	0.46	1,121	0.499
3-ocean males	0.024	1.92	1,77	0.170
2-ocean females	0.001	0.10	1,132	0.753
3-ocean females	0.015	1.79	1,117	0.184

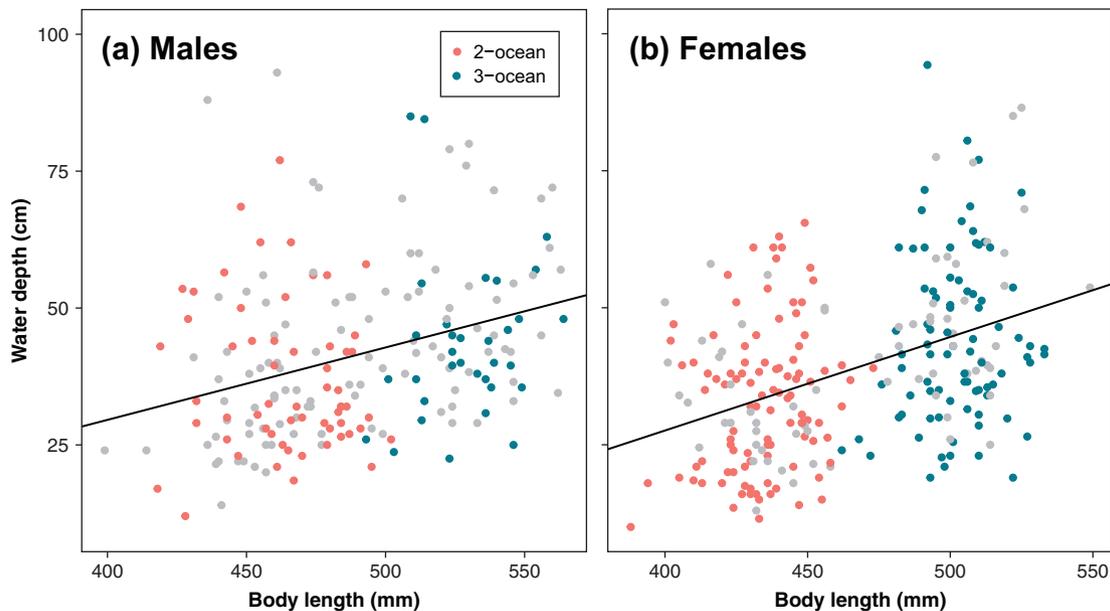


Figure 2. Relationship between body length and the depth of the spawning sites of male and female sockeye salmon breeding in Pick Creek in 1995 and 1996. Grey dots denote fish aged by reference to their length at tagging.

However, a closer look at this correlation for each ocean-age separately revealed that, regardless of sex and body length, individuals of the same age distributed at random along the water depth gradient (Table 1).

### Selection on matching habitat choice

RLS ranged from 1 to 23 days in males (median: 15, interquartile range [IQR]: 11 to 28) and from 2 to 33 days in females (median: 19, IQR: 13 to 22). RLS was jointly influenced by body length and water depth, although this effect differed between males and females, as shown by the three-way interaction (Table 2a). Further analyses of the data ignoring the effect of sex revealed that, across all fish, RLS increased linearly with body length ( $p=0.003$ ), but was not influenced by water depth, neither as a main effect ( $p=0.769$ ) nor through an interaction with body length, neither in its linear nor quadratic forms ( $p=0.797$  and  $0.427$ , respectively). For the population as a whole, then, selection appears to act on body length independently of habitat use and would therefore not favor matching habitat choice.

Looking at each sex separately, we found evidence of selection for matching habitat in females, but not in males, after controlling for the effect of competition (Table 2a–c, Fig. 2). Larger females had longer life expectancies than small females, and particularly so in deep waters. Conversely, the RLS of the smallest females in the population did not change substantially along the water depth gradient (Fig. 3). Female RLS decreased in shallow-water habitats, although this effect was most pronounced for those fish in the upper and the lower limits of the body size range, resulting in a significant non-linear effect (Table 2c, Fig. 3). Even though this effect was not very strong in absolute terms (Table 2c), the performance tradeoff with respect to water depth and the relative

costs of mischoosing were much more severe for the largest females of the population. For instance, a 10 cm decrease in spawning depth (median = 43 cm, range: 19–94) would reduce RLS by 7% for those females at the upper limit of the body size range, but only 0.5% for the smallest females (Fig. 3). Overall, then selection appears to (weakly) favor matching habitat choice in the largest females, but not in other segments of the population.

### Discussion

Breeding sockeye salmon of similar ocean age and size tend to cluster together in stream sites of similar depth, producing a phenotype–environment association consistent with matching habitat choice. However, analysis of the effect of body size variation on individual performance (reproductive life span) in discrete segments of the population revealed group-specific differences in the strength of performance tradeoffs between habitats (Table 3). Overall, these findings support the hypothesis that matching habitat choice is not equally important for all individuals in a population, but only for those that suffer a major cost of mischoosing – leading to ‘partial matching habitat choice’.

### The pattern of matching habitat choice

Our results confirm the findings from earlier regression-based analyses of the same data in showing a correlation between salmon size and spawning site depth (Hendry et al. 2001). Importantly, however, stratified analyses by sex and age revealed that this pattern was not repeatable across all individuals. In particular, no evidence for size–depth correlations was found within either the younger (2-ocean) or older

Table 2. Linear models testing for correlational selection acting on morphology (body length) and breeding habitat use (water depth) of male and female salmon, as estimated using methods of Lande and Arnold (1983). Reproductive life span (RLS) was used as the fitness metric. Breeding date and competition intensity were included as covariates in all models to control for their impact on RLS. Note that we do not report a formal selection coefficient for the interaction term, as it represents the fitness consequences of the covariance between a phenotypic trait and a physical variable, as opposed to the covariance between two traits. Statistics and p-values of non-significant terms are those obtained by adding them individually to the final models, in which only significant predictors (main effects and interactions) were retained. p-values <0.05 were considered statistically significant.

	Estimate	SE	t	p
(a) All fish				
Sex	-0.211	0.033	-6.39	<0.001
Breeding date	-0.175	0.013	-13.37	<0.001
Competition intensity	0.011	0.013	0.86	0.388
Body length	0.052	0.022	2.40	0.017
Body length <sup>2</sup>	0.005	0.018	0.29	0.776
Water depth	-0.003	0.020	-0.17	0.866
Body length × Water depth	0.005	0.022	0.24	0.808
Body length <sup>2</sup> × Water depth	0.017	0.014	1.25	0.211
Body length × Sex	-0.016	0.032	-0.51	0.611
Body length <sup>2</sup> × Sex	-0.009	0.025	-0.37	0.710
Water depth × Sex	0.007	0.033	0.22	0.823
Body length × Water depth × Sex	0.012	0.029	0.43	0.670
Body length <sup>2</sup> × Water depth × Sex	-0.038	0.019	-1.98	0.049
(b) Males only				
Breeding date	-0.128	0.023	-5.67	<0.001
Competition intensity	0.063	0.024	2.63	0.009
Body length	-0.024	0.024	-1.00	0.321
Body length <sup>2</sup>	0.002	0.022	0.10	0.921
Water depth	-0.015	0.023	-0.65	0.518
Body length × Water depth	0.010	0.022	0.46	0.648
Body length <sup>2</sup> × Water depth	-0.024	0.019	-1.24	0.217
(c) Females only				
Breeding date	-0.206	0.014	-14.53	<0.001
Competition intensity	-0.037	0.014	-2.72	0.007
Body length	0.017	0.015	1.16	0.246
Body length <sup>2</sup>	0.017	0.010	1.76	0.080
Water depth	-0.016	0.016	-1.04	0.302
Body length × Water depth	-0.010	0.014	-0.72	0.474
Body length <sup>2</sup> × Water depth	0.018	0.008	2.13	0.034

(3-ocean) segments of the population, which indicates that the size-based segregation seen at the population level reflects an age-dependent shift in habitat preferences – probably owing to the large size difference (13% on average) between 2-ocean and 3-ocean fish.

Experimental manipulation of phenotypes is often required to distinguish matching habitat choice from direct genetic habitat choice and imprinting, because these processes all might operate simultaneously, either synergistically

or antagonistically (Akcali and Porter 2017). Although we did not perform such a manipulation, we are confident that these other processes do not explain the fine-scale phenotype–habitat associations that we observed. Imprinting: salmon juveniles move away from the nest soon after emergence and, although olfactory imprinting guides their return to the natal site as adults (Dittman and Quinn 1996), the possibility that emerging juveniles acquire cues to guide breeding habitat choice at such small spatial scales seems very unlikely. Direct genetic habitat choice: although a few studies suggested a possible genetic component to large-scale (different stream reaches) habitat choice (Quinn 2018), no study has even suggested that such a genetic basis could apply to fine-scale variation in nest site choice within salmon populations. Moreover, for direct genetic habitat choice to explain the observed habitat segregation of size (age) classes, some sort of ontogenetic mechanism would have had to control the expression of potential habitat preference genes. Differences in habitat selection behavior have been reported for distinct life history stages of clonal invertebrates (Leibold et al. 1994). However, such variation among life history stages would be unlikely to confound matching habitat choice of salmon because, from a functional point of view, all breeding individuals can be considered as being in the same life history stage, regardless of whether they have spent two or three years at sea (Carlson and Seamons 2008).

Competition intensity is often considered a major confounding factor in studies of breeding habitat selection, because some individuals might be constrained to settle in suboptimal sites in the presence of superior competitors (Berner and Thibert-Plante 2015, Camacho et al. 2015). Competitive exclusion of small subordinate salmon by larger ones might occur in our study system because, even though there are plenty of both shallow and deep spots to choose, not all deep-water sites are necessarily optimal, and the optimal deep-water sites (e.g. more water flow) might be occupied and defended by large dominant individuals. However, this is unlikely to be a major issue in this study because, even if competition excludes subordinate individuals from some deep spots, there are still plenty of unoccupied deep-water sites to choose, so a small fish would ultimately have to make a choice between suboptimal (e.g. less water flow) deep sites and optimal (e.g. more water flow) shallow sites. Moreover, it is important to note that, although competition-dependent habitat choice has traditionally been considered an alternative mechanism to matching habitat choice (Edelaar et al. 2008, Berner and Thibert-Plante 2015), more recent literature suggests that competition-dependent habitat choice is one of the multiple ways in which matching habitat choice can proceed. Competition is indeed an additional feature of the environment that could generate performance tradeoffs and could therefore be used by inferior and superior competitors to make settlement decisions (see Akcali and Porter 2017 for a more detailed discussion on this idea).

No fish became stranded (falling over and dying in shallow water) during this study. Indeed, in Pick Creek the probability of stranding is unlikely (Quinn et al. 2001a), so

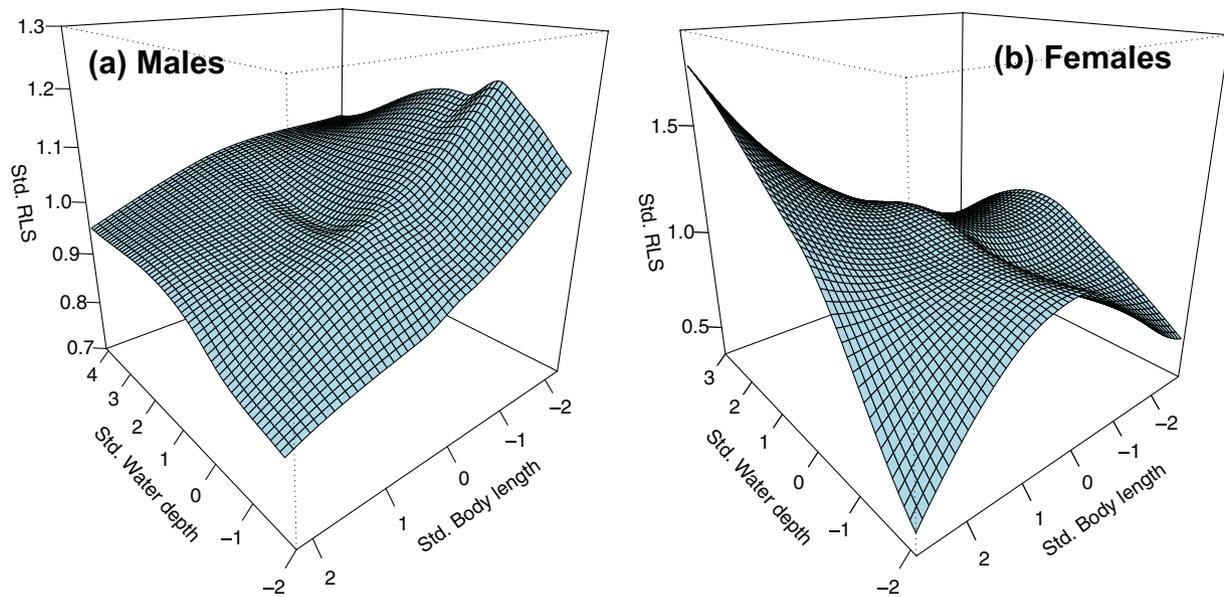


Figure 3. Correlational selection, estimated using methods of Lande and Arnold (1983), acting on salmon morphology (body length) and breeding habitat use (water depth), each standardized to mean zero and unit variance. Reproductive life span (RLS, divided by the mean life span of all individuals in a given year and adjusted for breeding date) was used as the fitness metric. For RLS, smaller values indicate a shorter life. Body sizes below and above zero roughly correspond to 2-ocean and 3-ocean fish, respectively.

passive sorting of large and small fish due to physical barriers to movement can also be excluded as a cause of phenotype–environment correlations. In addition, salmon density and water depth are not correlated in this creek ( $r=0.1$ ,  $p=0.28$ ), so these factors are unlikely to act additively and confound matching habitat choice. For all these reasons, it seems unlikely that salmon entering Pick Creek are constrained by either physical (minimum depth) or social (competitive exclusion) factors to assess all alternative habitats in search of the places that offer the best fitness prospects given their body size (Tautz and Groot 1975, Hendry et al. 2001, 2004, Adkison et al. 2014).

### Selection on matching habitat choice

Matching habitat choice by breeding salmon did not seem to be favored in the population as a whole. Yet, consistent with our predictions, a closer look at discrete population segments

revealed age- and sex-specific differences in selection resulting from variation in the strength of performance tradeoffs between habitats. Natural selection did not favor matching habitat choice in the smaller 2-ocean females nor in males of either size, for which the benefits of seeking particular habitats (in this case, deep-water refuges that provide more escape opportunity from bear attacks) are not as obvious as for the larger 3-ocean females (Quinn and Kinnison 1999, Gende et al. 2004). Non-random settlement in 3-ocean females, however, had the potential to improve individual performance (i.e. reproductive life span) over that expected from random settlement, providing the means and the opportunity for matching habitat choice in this group.

Taken together, the results of this study indicate that phenotype–environment matching can occur even in the absence of obvious selection for it. Male and female salmon of similar size clustered together in the same microhabitats, despite matching habitat choice being favored in large 3-ocean females only. Of course, in complex natural environments, additional performance tradeoffs might be generated by factors other than predation risk (e.g. oxygen concentration, substrate structure) that might ultimately influence other aspects of performance (e.g. fecundity). Nonetheless, it is unclear whether estimates of the strength of performance tradeoffs would change if performance components other than reproductive life span, or habitat selection cues other than predation risk, were considered. For instance, male salmon might rely more strongly on access to females as a cue for habitat selection (Quinn et al. 1996). This tendency might be especially advantageous when performance tradeoffs between natural and sexual selection are very weak or absent (i.e. the male preferred by the female is not more likely to be killed by the

Table 3. Summary of the results regarding the first (spatial outcome) and second (selective basis) components of matching habitat choice.

Population segment	Components of matching habitat choice	
	Phenotype–environment correlation	Detectable selection on matching habitat choice
All fish	+	no
Males	+	no
Females	+	yes
2-ocean males	n.s.	no
3-ocean males	n.s.	no
2-ocean females	n.s.	no
3-ocean females	n.s.	yes

predator; de Lira et al. 2018), such that the spatial segregation of males might be influenced to a greater extent by mating opportunities than by predation risk (Porter and Akcali 2018). For small 2-ocean females, however, phenotype–environment matching might not provide an immediate survival benefit as in large 3-ocean females; instead, the preference of 2-ocean females for shallow-water habitats might improve their overall fitness through enhanced fecundity. Nests in shallow waters might increase embryo survival due to e.g. reduced disturbance by large females (Fleming and Gross 1994, Steen and Quinn 1999) and/or more benign developmental conditions (e.g. cool, oxygenated water through the nest gravel; Jensen et al. 2009). However, no data on the emergence and subsequent fate of fry are available and, therefore, the potential fitness benefits of habitat selection for 2-ocean females remain unclear.

Not only predation risk, but also competition intensity, might shorten the reproductive life span of salmon and therefore play a role in matching habitat choice by generating performance tradeoffs (Schlosser 1987, Adkison et al. 2014). In fact, we found that females tended to die sooner in more densely populated sections of the stream, possibly because they have to use more of their limited energy for nest defense against other females (Hendry and Berg 1999). Competition, however, had a positive effect on male life span, but this is probably due to the female-centric nature of our measure of competition, namely the density of other females in a given section (McPhee and Quinn 1998). From the male perspective, the number of competing females influences the availability of potentially receptive mates, that is, operational sex ratio (Mathisen 1962). Thus, the positive effect of local female abundance on male life span is likely explained by the fact that males should allocate less energy to mate defense when more females were available and, as a result, the intensity of male–male competition decreased (Quinn et al. 1996). Nevertheless, in Pick Creek, predation risk should impose stronger selection for matching habitat choice than the number of conspecifics, regardless of the direction of the latter effect. This is because, on the one hand, salmon density is relatively low compared to other streams in the region (Quinn et al. 2017) and, on the other hand, size-selectivity by bears increases considerably under low-density conditions (Carlson et al. 2007, Cunningham et al. 2013). One might argue that correlational selection on female size and micro-habitat use was not very strong. Nevertheless, the fact that the amount of variance explained by the covariance between quadratic size and water depth ( $r^2 = 0.0023$ ) is greater (64th percentile) than the average values reported in the literature for nonlinear selection gradients (Fig. 2.5 in Hendry 2017) supports its ecological relevance.

### Differential costs of mischoosing: evidence and implications

Matching habitat choice, in contrast to other forms of habitat choice (e.g. due to imprinting or habitat preference alleles; Akcali and Porter 2017), is based on self-assessment

of local performance and, therefore, a good knowledge about the strength of performance tradeoffs between alternative environments is essential (Camacho et al. 2015, Benkman 2017). However, as illustrated by this salmon population, the strength of performance tradeoffs and, therefore, the costs of mischoosing, are not expected to be uniform across the entire range of phenotypic variation. Matching habitat choice might thus be more likely to be expressed in a subset of individuals, particularly those that experience strong performance variation between different environments.

Examples of matching habitat choice in natural populations are still very scarce, though half of the field studies conducted to date have found inconsistencies in the relationship between the spatial distribution of phenotypes and the predicted optimal distribution. These inconsistencies are usually attributed to constraints on the expression of matching habitat choice, such as the exclusion from preferred habitats by dominant conspecifics (Camacho et al. 2015, Jacobson et al. 2017) or the lack of alternative habitats (Edelaar et al. 2017, Mortier et al. 2019). However, to our knowledge, the potential role of group-specific costs of mischoosing as a constraint on the expression (and detection) of matching habitat choice has not been previously considered in the literature. Based on the results of this study, it seems plausible that matching habitat choice has gone undetected in past population-level analyses due to the unequal relevance of this mechanism to different population segments. This may potentially explain the apparent rarity of matching habitat choice in nature, but further studies combining individual-based simulation models and field data are required to confirm this hypothesis.

### Alternative viewpoints

‘The authors confound speculation with evidence [...] whether the exact mechanisms fall into matching habitat choice, genetic preference or imprinting is unclear’, one reviewer stated. Experimental demonstration of matching habitat choice in nature ideally requires some degree of phenotype or genotype manipulation, but this may be seldom possible under field conditions. Consequently, in the middle of what can be called ‘the age of matching habitat choice’, the available evidence is limited to simulation studies and controlled experiments using microcosms. One could thus argue that what is written so neatly in a body of theoretical and highly controlled empirical work might not bear any resemblance to reality. Then, at this point, a decision must be made: should research efforts continue to rely on microcosm and a petri-dish settings, even though conclusions based on simplified ecosystems might not apply to more realistic scenarios, or should they rather be directed to understand the actual relevance of matching habitat choice in nature using probably imperfect model systems, but in which the effect of alternative mechanisms can be reasonably excluded based on natural history knowledge? Or, stated another way, is making the best of a bad job justified when some might argue that we are putting the cart before the horse? To us, the answer

is definitely yes: we need more work on matching habitat choice in nature - even when manipulations are not possible.

### Data accessibility statement

The data supporting the results of this study are available at <<https://digital.csic.es/handle/10261/193938>> (Camacho and Hendry 2020).

*Acknowledgements* – CC thanks Jesús Martínez-Padilla for advice on the selection analysis. APH thanks Prof. Thomas Quinn for guidance during fieldwork, and for recent input. Pim Edelaar kindly contributed some ideas for the interpretation and discussion of the results.

*Funding* – CC received financial support from the Spanish MINECO through the grants SVP-2013-067686 and EEBB-I-16-11000.

*Conflict of interest* – The authors declare that they have no conflict of interest.

*Author contributions* – CC and APH conceived the study. APH collected the data and CC analyzed them. CC wrote the manuscript upon which APH improved.

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Supplementary material (available online as Appendix oik-06932 at <[www.oikosjournal.org/appendix/oik-06932](http://www.oikosjournal.org/appendix/oik-06932)>). Appendix 1.