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Population ecology

Marine trophic diversity in an anadromous fish is linked to its life-history variation in fresh water

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We used carbon and nitrogen stable isotopes from muscle tissues accrued in the ocean to examine whether marine foraging tactics in anadromous sockeye salmon (*Oncorhynchus nerka*) are linked to their ultimate freshwater life history as adults. Adults from large-bodied populations spawning in deep freshwater habitats had more enriched $\delta^{15}\text{N}$ than individuals from small-bodied populations from shallow streams. Within populations, earlier maturing individuals had higher $\delta^{15}\text{N}$ than older fish. These differences in $\delta^{15}\text{N}$ suggest that the fish with different life histories or spawning habitats in freshwater either fed at different trophic positions or in different habitats in the ocean. We propose that, nested within interspecific diversity in the ecological attributes of salmon, population and life-history diversity in spawning adults is associated with variation in marine foraging tactics. These results further indicate that the trophic diversity of sockeye salmon in the ocean may be linked to trade-offs in ecological and evolutionary constraints they eventually experience as adults in freshwater ecosystems.

1. Introduction

Many species have life histories that are complex, linking habitats across life-stages. As an individual proceeds through a complex life cycle, ecological roles and evolutionary constraints in each life-stage can influence the subsequent and preceding life-stages [1,2]. For example, the quality of juvenile rearing habitat may dictate eventual success and habitat use in adult reproduction. Alternatively, a reproductive strategy assumed in adulthood might require certain developmental or behavioural pathways leading up to that stage [1]. The prevalence and significance of these latter life cycle linkages are poorly understood, particularly for organisms that migrate between spatially distinct ecosystems over their lives.

Pacific salmon (*Oncorhynchus* spp.) are characterized by considerable intraspecific diversity in many life-history attributes, including age at maturity, and body size and morphology in adults [3]. Geomorphic variation in freshwater habitats generates population-specific adaptation to local habitat features that affect their ecology during critical life-stages such as upstream migration by maturing adults, spawning, and juvenile rearing [3]. The tendency of Pacific salmon to spawn in natal habitats limits gene flow among populations and maintains life-history variation. Mating systems are characterized by sexual selection favouring extreme sexual dimorphisms whereby mature males develop exaggerated traits [4]. Sexual dimorphism is countered by constraints imposed by the geomorphology of spawning habitats and size-selective predation [5]. Comparing across variation in geomorphic conditions, there is a strong association between adult body size and habitat features, with larger and later-maturing fish characterizing populations spawning in deep habitats (e.g. rivers and lake beaches), and small, early-maturing fish characteristic of shallow streams [5]. Most wild populations are also represented by a mixed age composition of individuals, increasing life-history diversity in salmon stocks.

We evaluated nitrogen and carbon stable isotopes to compare marine feeding tactics (location or prey) of sockeye salmon (*Oncorhynchus nerka*) from different populations within a river system where considerable variation in age-at-maturity and size-at-age is related to secondary sexual characteristics among populations. Although the observed adult life-history characteristics of each population appear to be adaptations to conflicting pressures of sexual and natural selection in fresh water, we hypothesize that these differences must be supported by different foraging tactics in the ocean where sockeye salmon achieve essentially all lifetime growth.

2. Material and methods

The Wood River system of Bristol Bay, Alaska (59°16' N, 158°38' W) supports sockeye salmon displaying a wide variety of life-history characteristics associated with geomorphic conditions [5], distributed across a genetically structured population complex [6]. Sockeye typically spend 1–2 years rearing in fresh water, then 1–3 years at sea prior to returning to natal sites to spawn.

Muscle tissue samples for stable isotopes analyses were taken from sockeye salmon upon their arrival in freshwater during the spawning season (2005 and 2007). Sockeye were sampled from nine sites that span the range of habitat conditions used for spawning, including small streams (A, C, Mission, Lynx and Hansen creeks), large streams or rivers (Pick Creek and Little Togiak River) and lakeshore beaches (N-4 and Anvil Bay).

Fifteen males (2005 and 2007) and 15 females (2005) from each site were euthanized with lethal doses of MS-222. Relative body depth of each fish (residuals from depth versus length regression, log-transformed) among all individuals sampled was calculated separately for each sex as a measure of relative body size. Otoliths (to determine ocean age) and muscle tissue (to determine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values) were collected from each fish. Stable isotope analysis was completed using a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer. Isotope values are expressed in standard notation relative to universal standards for carbon (Pee Dee belemnite) and nitrogen (atmospheric N_2).

3. Results

Sockeye salmon were differently shaped (i.e. relative body depth) in populations using different spawning habitats (ANOVA: males, $F_{7,146} = 31.7$, $p < 0.0001$; females, $F_{5,100} = 28.1$, $p < 0.0001$). Differences in body shape among populations are linked to substantial differences in body mass (table 1). Within individual ocean age groups, relative body depth and body mass increased as physical dimensions of spawning habitat increased (tables 1 and 2). Both age and site were highly significant factors for sockeye $\delta^{15}\text{N}$ (site effect: $F_{7,232} = 6.5$, $p < 0.001$), (age effect: $F_{2,232} = 24.6$, $p < 0.0001$), but sex was not (sex effect: $F_{1,232} = 0.64$, $p = 0.42$).

Stable isotope values were averaged for different ocean-aged fish from different sites, treating sexes separately. Within each sex and age group, populations with deeper-bodied fish had significantly higher $\delta^{15}\text{N}$ than fish from populations with small fish (figure 1): age-2 males ($r^2 = 0.77$; $\delta^{15}\text{N} = 4.85 \times \text{relative body depth} + 11.26$, $p = 0.021$), age-3 males ($r^2 = 0.79$; $\delta^{15}\text{N} = 5.92 \times \text{relative body depth} + 11.02$, $p = 0.018$). For females, these trends were less strong: age-2 females ($r^2 = 0.42$; $\delta^{15}\text{N} = 4.79 \times \text{relative body depth} + 11.12$, $p = 0.163$), age-3 females ($r^2 = 0.67$; $\delta^{15}\text{N} = 6.34 \times \text{relative body depth} + 11.04$, $p = 0.047$).

Table 1. Average mass (kg) for different age classes of male and female sockeye salmon by spawning habitat type.

ocean age	males			females	
	1	2	3	4	5
small streams	0.71	2.03	2.63	1.69	2.27
large streams	0.64	2.48	3.71	1.75	2.68
or rivers					
beaches	n.a.	2.46	4.31	2.04	3.09

Ocean age was a significant predictor of the average $\delta^{15}\text{N}$ within populations (ocean age effect, $p < 0.0001$), independent of whether sexes were aggregated or separate. Specifically, younger (ocean age-2) fish had higher $\delta^{15}\text{N}$ values than older (ocean age-3) fish (figure 2). Where precocious jack (ocean age-1) sockeye were sampled, they had the highest $\delta^{15}\text{N}$ (figure 2). Thus, within-population variation in body size associated with age at maturity showed the opposite association with $\delta^{15}\text{N}$ from what was observed among populations.

Carbon isotope distributions did not show the systematic differences among populations and age groups observed for nitrogen. Individuals differed in $\delta^{13}\text{C}$ among sites ($F_{7,240} = 3.9$, $p = 0.001$), ocean age ($F_{2,240} = 4.9$, $p = 0.03$) and sex ($F_{1,240} = 5.3$, $p = 0.02$). However, when data were aggregated to the population scale, neither relative body depth (for all regressions $r^2 < 0.28$, $p > 0.27$; electronic supplementary material) or sex were significant predictors of $\delta^{13}\text{C}$. Additionally, ocean age was not a significant predictor of average $\delta^{13}\text{C}$ within populations (ocean age effect, $p > 0.1$; in the electronic supplementary material).

4. Discussion

Pacific salmon species have evolved a diverse array of life histories, reproductive strategies and marine foraging tactics [7]. Here, we show that nested within this interspecific diversity, population and life-history diversity evident in the adult spawning phase is linked to considerable variation in marine foraging tactics adopted by sockeye salmon before they mature and return to fresh water to spawn. The morphology of spawning sockeye salmon is related to the geomorphology of their spawning habitat such that body depth and mass are larger in physically more expansive spawning habitats (tables 1 and 2) [5]. Such variation in body size may be linked to foraging tactics in the ocean where sockeye salmon accumulate greater than 99 per cent of their lifetime growth. Patterns of variation in $\delta^{15}\text{N}$ among age groups and among populations suggest that different adaptations for successful breeding in freshwater are supported by different foraging tactics in marine phases of their lives. The tendency for larger-bodied populations to have higher $\delta^{15}\text{N}$ supports a general expectation of trophic ecology where larger fishes generally forage at higher trophic positions than smaller individuals of the same species [8].

Although we predicted that body size alone would dictate the marine foraging tactic of sockeye, within populations we also found linkages between ocean age at maturity and marine foraging. In contrast to the variation in marine trophic position observed among populations, earlier maturing, thus

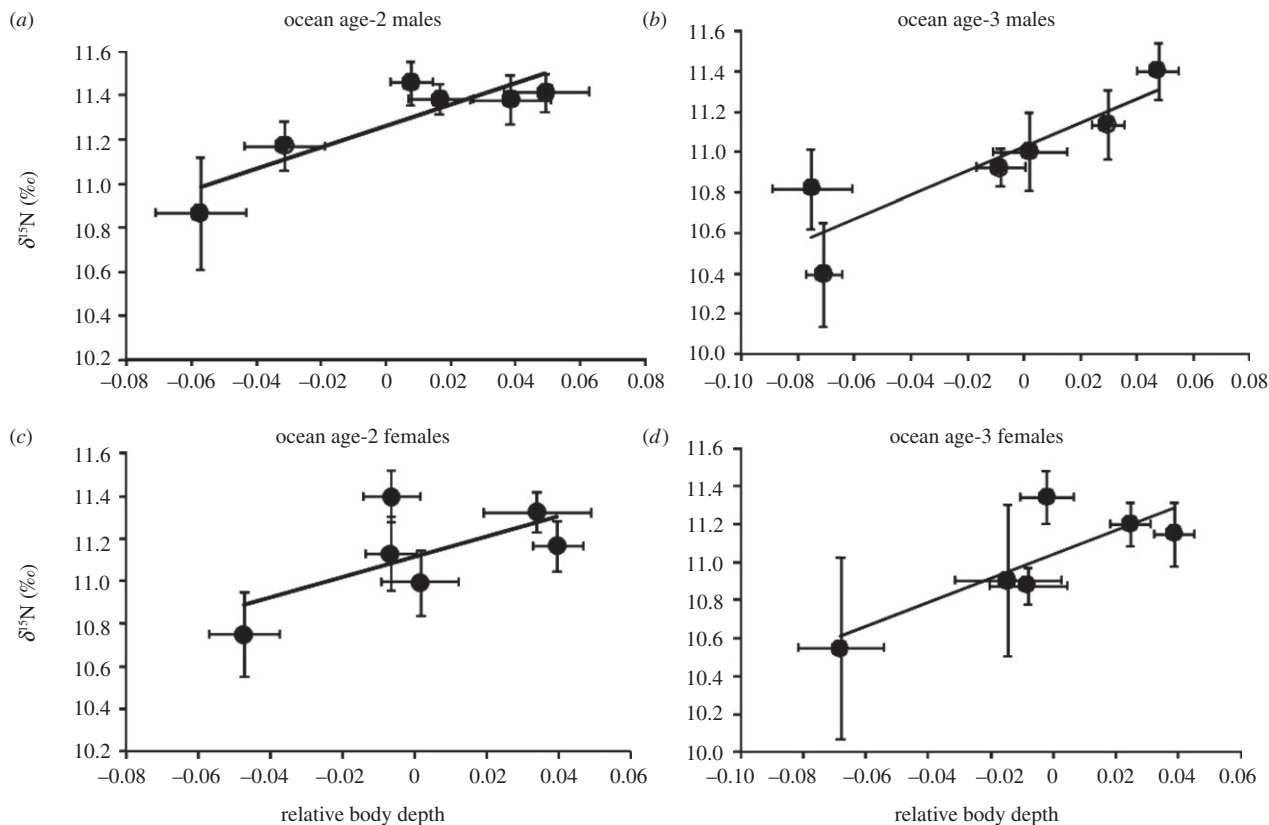


Figure 1. $\delta^{15}\text{N}$ versus relative depth of male and female sockeye salmon separated by age class among six populations. Each point is an average for an individual population. Error bars are standard errors.

Table 2. The relative size (average residual values from regression of body depth on length) of sockeye salmon by spawning habitat type. (Sites are listed in order of increasing size. Data are an average for a given population, age class and sex. Standard error (s.e.) is 0.01 in all cases except for females of ocean age-2 in N4 beach and ocean age-3 in Hansen creek where s.e. is 0.02.)

ocean age	males			females	
	1	2	3	2	3
A and C creeks	n.a.	-0.048	-0.061	-0.047	-0.068
Hansen creek	-0.005	-0.034	-0.068	0.007	-0.015
Mission creek	-0.008	-0.078	n.a.	n.a.	n.a.
Lynx creek	-0.062	0.004	n.a.	n.a.	n.a.
Pick creek	n.a.	0.025	0.003	0.002	0.003
Little Togiak River	n.a.	0.056	0.041	-0.007	-0.009
N4 beach	n.a.	0.016	0.015	0.034	0.024
Anvil bay beach	n.a.	0.047	0.059	0.040	0.038

smaller, fish within populations had enriched muscle tissue $\delta^{15}\text{N}$ relative to those fish spending a longer time at sea (figure 2). While this pattern could be produced by differences in prey selection among fish of different ages, we suspect that increased $\delta^{15}\text{N}$ in young fish reflects their more coastal marine distribution, as suggested from tagging studies [9], compared with older fish that tend to occupy more offshore waters with a more depleted (lower $\delta^{15}\text{N}$) food web [10].

Numerous factors contribute to life-history diversity in Pacific salmon. Stocks (i.e. aggregates of populations) of sockeye salmon are often characterized by considerable genetic structure among component populations, including those in this study [6]. Geomorphic conditions in spawning habitats

impose constraints on body size and shape. Our results suggest that this expression of life-history diversity relevant to sockeye ecology as spawning adults in freshwater ecosystems is linked to their marine trophic ecology. Not only do sockeye salmon from different populations differ in duration of marine residence, length at age and weight at length, as shown previously [5], but they apparently feed in different areas, on different prey or a combination of these factors at sea.

To discern the ultimate cause of $\delta^{15}\text{N}$ differences among salmon, it is necessary to distinguish the isotope values of primary producers at the base of the food web where salmon feed. Because source isotopes vary in space and time, isotopic baselines are difficult to acquire for highly migratory animals spending multiple years foraging in the

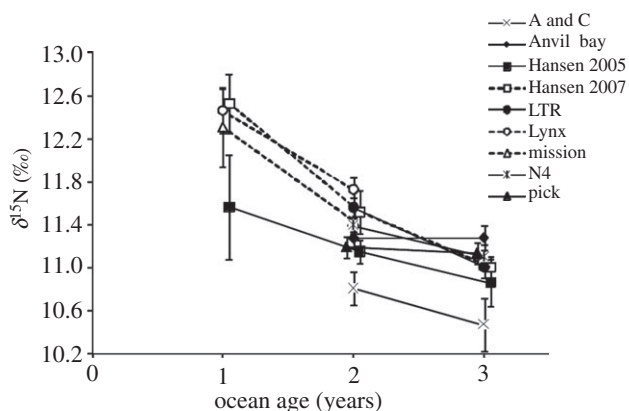


Figure 2. $\delta^{15}\text{N}$ for each age class of sockeye salmon in a sample population. Data points are averages for sockeye sampled (male and female) of that age class in a population. Populations with open symbols (Lynx, open circle; Mission, open triangle; Hansen, open square) were sampled in 2007, and all others were sampled in 2005. Error bars are standard errors. Data points are jittered on the x -axis for clarity where overlap occurs.

ocean. Recent developments of compound-specific stable isotope analyses [11] may clarify the mechanisms for isotopic diversity we observed in sockeye salmon associated with their eventual life-history fate in fresh water.

Stable isotopes, providing a coarse-scale glimpse at marine feeding tactics, suggest that habitat heterogeneity in

fresh water and its associated diversity in life-history strategies of sockeye salmon are linked to a diversity of marine foraging tactics. There is increasing appreciation that the diversity of geographical and life-history strategies of sockeye salmon stocks is critical to maintaining stock productivity. For example, locally adapted salmon populations exhibit distinctly asynchronous population dynamics even for populations spawning in different tributaries of the same river watershed [12]. Our results show that the ecological variation observed for spawning salmon in freshwater ecosystems is linked to their trophic diversity in the ocean. How such heterogeneity and linkages between ecosystems in sockeye salmon stocks, or any exploited species, contribute to their responses to changes in marine productivity and food web structure, and ultimately their own resilience and productivity remains essentially unexplored.

This study complies with all ethics and permitting requirements of the University of Washington, and the State of Alaska under the UW IACUC (International Animal Care and Use Committee). The protocol number is 3142-01 and the research was specifically covered under the protocol.

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