Freshwater habitat associations between pink (*Onchorhynchus gorbuscha*), chum (*O. keta*) and Chinook salmon (*O. tshawytscha*) in a watershed dominated by sockeye salmon (*O. nerka*) abundance

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Abstract – To understand the interplay between habitat use and contemporary anadromous Pacific salmon, *Onchorhynchus* spp., distributions we explored the habitat associations of three species, pink (*O. gorbuscha*), chum (*O. keta*) and Chinook salmon (*O. tshawytscha*) in streams of the Wood River system of Bristol Bay, Alaska, where sockeye salmon (*O. nerka*) are numerically dominant. We developed models to investigate the occurrence of nondominant salmon in relation to habitat characteristics and sockeye salmon density, using four decades of salmon presence and abundance data. The frequency of occurrence and abundance of nondominant species increased with watershed drainage area and stream depth and decreased with sockeye salmon density. The range of occurrence varied from nonexistent to perennial for the other species in sockeye-dominated streams. Increasing watershed area resulted in larger stream habitat area and deeper habitats, allowing for the sympatric occurrence and persistence of all salmon species. The relationships between habitat and the presence of these Pacific salmon help define their requirements but also remind us that the patterns of presence and absence, within the overall ranges of salmon species, have yet to be fully understood.

Key words: nondominant species; population occurrence; salmon; freshwater habitat

Introduction

The absence of a fish species from habitat within its geographical range has been assumed to result from unsuitable habitats and is usually taken to indicate that all suitable habitats have been occupied. However, in some cases, several species may be numerically dominant yet other species are occasionally seen or persist at low abundance levels. The occurrence of subdominant species can vary spatially and temporally within and across watersheds (e.g., salmonids: Scarneccchia & Roper 2000; Esin & Leman 2008). The variability of salmon occurrence regardless of numerical dominance over time is typically related to the compatibility between specific life-history adaptations and the biophysical characteristics of the new habitats (Quinn 1984; Allendorf & Waples 1996; Pess et al. 2012). Thus, it is important to understand the relative importance of abiotic (stream channel width, average flow during migration, etc.) and biotic (competition, food resources, etc.) factors on the distribution, occurrence and abundance of less abundant species (Rosenfeld 2003). In addition, understanding how these factors affect all salmon species at a particular life-history stage (juvenile rearing, spawning, etc.) also helps determine which factors control the observed patterns...
of each species’ occurrence and abundance (Rosenfeld 2003; Isaak et al. 2007; Steel et al. 2012).

The timing, location and spawning site characteristics vary between salmon species and reflect numerous abiotic and biotic variables (Fukushima & Smoker 1998; Geist et al. 2002; Quinn 2005; Beechie et al. 2008). The variation in spawning site characteristics between salmon species typically reflects body size variation; larger fish tend to spawn in deeper and faster water, and in streambed areas with larger substrate size (Crisp & Carling 1989; Beechie et al. 2008). However, gravel size, water depth and water velocity are related, making it difficult to isolate the key attribute for spawning site selection (Quinn 2005). While spawning habitat preferences result in different preferred spawning locations among salmon species, overlap in habitat use and some level of interspecific competition is common (Fukushima & Smoker 1998).

In many regions, one cannot explore the correlations between habitats and the occurrence or abundance of nondominant salmon for a particular life stage because the populations are far below habitat saturation as a result of fishing, habitat degradation, hatcheries and non-native species introductions (NRC 1996; Montgomery 2003). However, in the Bristol Bay region of Alaska, where the dominant species in the vast majority of watersheds is sockeye salmon (Oncorhynchus nerka), several other anadromous species occur including pink (O. gorbuscha), chum (O. keta), Chinook (O. tshawytscha) and coho salmon (O. kisutch), as well as resident populations of rainbow trout (O. mykiss), Arctic char (Salvelinus alpinus) and Dolly Varden (S. malma). The patterns of habitat use can be readily studied in Bristol Bay because the habitat conditions have not been altered by anthropogenic influences and the fisheries have been managed sustainably (Hilborn et al. 2003).

The objective of this study was to examine the correlations between the occurrence and abundance of different nondominant salmon species with stream habitat characteristics and density of competing, numerically dominant sockeye salmon in streams of the Wood River system, Alaska. We hypothesised that nondominant adult salmon occurrence and abundance would increase with habitat area due to increased quantity and diversity of suitable spawning habitat, and greater scope for habitat segregation among species. We also hypothesised that nondominant salmon occurrence and abundance would vary as a function of salmon species and their relative size. Thus Chinook and chum salmon, being the largest bodied, were predicted to occur in larger streams, whereas the smaller pink salmon were predicted to have a broader range of suitable habitat, including large rivers to the smallest streams.

### Materials and methods

#### Study area

The Wood River system has a drainage area of 3590 km² and is a series of four large lakes (lake size from 90 to ~210 km²), connected by rivers that are relatively wide (>60 m), deep (up to 4.5 m), short (3–6 km) and low-gradient (<0.50%). The lowermost lake, Aleknagik, drains into the Wood River and from there into the Nushagak River and Bristol Bay, Alaska (Fig. 1). Over 50 watersheds make up the Wood River system, ranging from 2.5 km² to 172.2 km² (average = 31.3 km²) and 15 to 1531 m elevation (average = 210 m). The hydrology of the streams in these watersheds is a mix of snowmelt (chiefly April through June) and spring-fed, and some have small lakes, spring-fed ponds or beaver ponds.

#### Approach

We approached the subject of fish occurrence and abundance at the stream (e.g., several km) and watershed (i.e., several km²) scales using long-term (40 years) presence/absence data for pink, chum and Chinook salmon. We focused on nondominant salmon occurrence and abundance because they are scarce in many of the smaller streams throughout the Wood River system, yet they have been documented in 28 streams for over 35 years by the University of Washington’s Fisheries Research Institute (FRI) programme during annual surveys for spawning sockeye salmon. Coho salmon spawn later in the fall and so are not routinely recorded but the timing of the other three species overlaps broadly with that of sockeye salmon. We tested hypotheses pertaining to the occurrence and abundance of small salmon spawning aggregates. We used either descriptive or statistical techniques to determine the correlations between fish occurrence/abundance and physical habitat characteristics and adult sockeye densities.

#### Data

Fish occurrence data were based on annual surveys of spawning sockeye salmon collected by FRI from 1968 to 2007. In addition to counts of live and dead sockeye salmon, presence or absence of pink, chum and Chinook salmon was recorded. In some cases, there were counts but in others, only the presence was noted so both occurrence and abundance data were examined. Not all 28 streams where pink, chum and Chinook salmon have been documented could be used for our analysis of stream habitat and salmon because of inconsistent annual data collection but 15 of the streams had consistent pink, chum and
Chinook salmon data collection between 1968 and 2007. Thus, we used these 15 streams for the habitat/nondominant salmon correlation analysis. The entire reach of stream used by sockeye salmon or, for larger streams, an index reach was surveyed by two or more observers on foot between one and four times from the beginning of July through the beginning of September over the entire period of record. This time period typically corresponds to the peak abundance of sockeye salmon. The streams or index reaches averaged 2.6 km long (range: 0.35–7.6 km). All streams are clear rather than tannin-stained or glacial, facilitating surveys and species identification.

It is important to note that there is direct overlap between the observed timing of sockeye and pink, chum and Chinook salmon (Pess 2009). Peak spawning for sockeye occurs during the first 2 weeks in August (varying among streams: Hilborn et al. 2003) and over 95% all pink, chum and Chinook salmon that have been seen in systems throughout Lake Aleknagik and Nerka, also occurred in August (Pess 2009). This does not include the large connecting rivers draining the lakes and the beach areas, where spawning is later and the sampling is much less thorough (Doctor et al. 2010).

We collected stream habitat data from all 28 streams that had identified pink, chum and Chinook salmon use in the Wood River system and long-term sockeye salmon abundance data. Stream measurements included bank-full and wetted width, bank-full and wetted depth, stream channel gradient, and stream bed particle size distribution using the pebble count method (Wolman 1954). We also collected information on habitat type (i.e., pool, riffle, glide), wood loading, in-channel cover type (e.g., cut-banks, wood, boulder clusters), riparian vegetation type and the amount of in-channel cover relative to wetted width. We sampled the upper, middle and lower segments of each spawner survey index reach at 10–20 channel widths per segment, which is approximately 20–30% of the total index reach length.

Analysis

We used several steps to correlate adult pink, chum and Chinook salmon occurrence and abundance with physical habitat characteristics and with sockeye salmon abundance in the Wood River system. First, we identified similarities and differences in pink, chum
and Chinook salmon frequency of occurrence over the period of the presence/absence data (1968–2007) among the 15 streams using simple summary plots. We also plotted abundance of these species among the 15 streams from 2004 to 2007 because focused counts for the nondominant species were obtained in these later years.

Next, we explored stream habitat associations using correlations and principal components analysis (PCA) of variables that were continuous, nonratio and not normalised to identify which stream habitat characteristics explained the greatest amount of habitat variation among streams in the Wood River system. The correlation and PCA reduced the number of stream habitat variables from 32 to a smaller set of ‘less correlated’ stream habitat variables for explaining relationships among streams and salmon occurrence and abundance.

We then used the reduced set of informative, ‘less correlated’ stream habitat variables to examine the correlations among pink, chum and Chinook salmon occurrence and abundance and stream habitat characteristics using a linear model selection approach. We used species frequency of occurrence over the entire time period (i.e., proportion of years in which the species was observed) or abundance per stream length as the response variable; stream habitat characteristics, and sockeye salmon density as measure of competition were the independent variables.

Lastly, we used Akaike’s Information Criterion, adjusted for small sample sizes (AICc), to determine which model best fit the data (Burnham & Anderson 2002). The difference between the AICc of a candidate model and the one with the lowest AICc provided the ranking metric ($\Delta$AICc). Generally speaking, $\Delta$AICc between 0 and 3 indicates substantial support for a model being as good as the best approximating model, $\Delta$AICc between 4 and 7 represents less support and $\Delta$AICc of >7 indicates very little support for a candidate model relative to the best model (Burnham & Anderson 2002). Akaike weights ($w_I$) were calculated, representing the strength of evidence in favour of model $i$ being the best model. The ratio of Akaike weights ($w_i/w_j$) indicates the plausibility of the best-fitting model compared with other models (Burnham & Anderson 2002). Models with an evidence ratio of 10 or less were considered plausible (Burnham & Anderson 2002). If models were not clearly the ‘best’ model based on the preceding criteria, then models within three AICc were considered competing models and results were averaged to determine the maximum likelihood estimate for the intercept and each of the independent variables that are part of the models (Burnham & Anderson 2002; Haring & Fausch 2002).

### Results

#### Stream-scale salmon occurrence patterns

All three species of nondominant salmon (pink, Chinook and chum) were seen in at least 1 year in five of the 15 streams consistently surveyed from 1968 to 2007 (Fig. 2). More streams had all three nondominant salmonids in Lake Nerka than in Lake Aleknagik streams (4 of 7 vs. 1 of 8). Similarly, five of 15 streams had both chum and pink salmon. Only two of the 15 streams had only pink salmon and both were in the Lake Aleknagik system (Fig. 2). Hansen Creek did not have any observed pink, Chinook or chum salmon from 1968 to 2007.

Pink salmon were seen in all seven streams surveyed in Lake Nerka and at least once in five of eight streams in Lake Aleknagik. The proportion of years

![Fig. 2. Pink, chum, and Chinook occurrence by stream. Stream is plotted by relative location, going from nearest to the Wood River outlet (Mission Creek) to furthest (Kema Creek). Solid black vertical line denotes streams in Lake Aleknagik to the left of the line, and Lake Nerka streams to the right of the line. It is important to note that relative location does not correspond to actual distance, which can be considerable between streams. Clear bars indicate pink salmon, black bars indicate chum salmon, and grey bars indicate Chinook salmon occurrence. Error bars represent the standard error from the mean.](image-url)
present by stream for pink salmon ranged between 0 and 65% (mean = 20%; Fig. 2). Ice and Hidden Lake creeks had pink salmon occurrence levels at or >50% from 1968 to 2007. Pink salmon occurrence in all streams also varied according to year with even-year occurrence being greater (20% ± 19%) than odd-year occurrence (7% ± 13%) in all streams with the exception of Happy (0% v. 5%) and Fenno (15% v. 19%) creeks. Chum salmon were seen at least once in 14 of 15 streams, with frequency of occurrence among years ranging from 0 to 67% (mean = 22%; Fig. 2). Ice, Pick and Fenno creeks had chum salmon occurrence levels >50% from 1968 to 2007. Chinook salmon were seen in five of 15 streams, and four of the five streams with Chinook salmon drain into Lake Nerka (Fig. 2). However, the highest proportion of years present (39%) was in Ice Creek, a tributary to Lake Aleknagik (Fig. 2). Chinook salmon were not reported in >50% of the years from 1968 to 2007 in any surveyed stream in the system.

Stream-scale salmon abundance

Relative abundance patterns from 2004 to 2007 were similar for Lake Aleknagik streams occurrence patterns; Ice Creek had the largest number of salmon other than sockeye (Table 1). Pink salmon abundance in Lake Aleknagik streams was greatest in Ice Creek, and far fewer were seen elsewhere. Chum salmon averaged in the 10s in Ice Creek, and fewer than 10 in the other streams surveyed in the Lake Aleknagik system. Chinook salmon only occurred in Ice Creek among the Lake Aleknagik streams (Table 1). Lake Nerka streams had more streams with pink salmon (Table 1). Elva Creek had 100s of pink salmon from 2004 to 2007, and Fenno, Hidden Lake and Kema creeks had 10s of pink salmon. Chum salmon averaged in the 10s in Fenno and Pick creeks but all other Lake Nerka streams had fewer (Table 1). Chinook salmon were scarce in all the Lake Nerka streams.

Table 1. Average (±SE) pink, chum, and Chinook abundance (fish per km) by stream from 2004 to 2007. Streams are in order of relative location to Wood River outlet going from nearest (Mission Creek) to furthest (Kema Creek). Hashed black horizontal line denotes streams in Lake Aleknagik above and Lake Nerka streams below. It is important to note that relative location does not correspond to actual distance, which can be considerable between streams.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Pink salmon</th>
<th>Chum salmon</th>
<th>Chinook salmon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mission</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Big Whitefish</td>
<td>2.7 (±1.4)</td>
<td>0.5 (±0.5)</td>
<td>0.0</td>
</tr>
<tr>
<td>Yakon</td>
<td>0.3 (±0.1)</td>
<td>0.6 (±0.3)</td>
<td>0.0</td>
</tr>
<tr>
<td>Eagle</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Hansen</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Bear</td>
<td>2.9 (±1.4)</td>
<td>1.4 (±0.1)</td>
<td>0.0</td>
</tr>
<tr>
<td>Happy</td>
<td>1.5 (±1.6)</td>
<td>0.6 (±0.1)</td>
<td>0.0</td>
</tr>
<tr>
<td>Ice</td>
<td>17.8 (±5.8)</td>
<td>1.4 (±0.5)</td>
<td>2.6 (±1.1)</td>
</tr>
<tr>
<td>Fenno</td>
<td>11.3 (±3.4)</td>
<td>2.1 (±0.8)</td>
<td>0.0</td>
</tr>
<tr>
<td>Stovall</td>
<td>3.8 (±1.3)</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Lynx</td>
<td>35.4 (±17.1)</td>
<td>0.4 (±0.1)</td>
<td>0.0</td>
</tr>
<tr>
<td>Pick</td>
<td>0.8 (±0.2)</td>
<td>2.1 (±0.8)</td>
<td>0.0</td>
</tr>
<tr>
<td>Elva</td>
<td>199.0 (±88.0)</td>
<td>1.0 (±1.0)</td>
<td>3.0</td>
</tr>
<tr>
<td>Hidden Lake</td>
<td>3.1 (±1.3)</td>
<td>0.3 (±0.1)</td>
<td>0.0</td>
</tr>
<tr>
<td>Kema</td>
<td>3.8 (±2.0)</td>
<td>0.3 (±0.3)</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Habitat characteristics

Many of the habitat variables in the Wood River system were correlated with each other because they are: (i) derived from one of the other variables (e.g., width to depth ratios), (ii) a per cent of a total estimate (e.g., % habitat depth) or (iii) an indicator of the overall drainage area in a watershed (e.g., width, depth, stream channel gradient and stream particle size) (Table S1). For example, several key variables were highly correlated (e.g., >0.50) with drainage area, including bank-full width, bank-full depth, wetted width, wetted depth, average depth by habitat type and the number of key pieces of wood or log-jams in a watershed (Table S1).

A PCA of the habitat variables revealed that several stream habitat categories were important in differentiating streams in Lake Aleknagik and Lake Nerka (Fig. 3). Only the first two axes of the ordinations of sample sites were interpreted because they explained the greatest amount of the variability in the data. The first axis described an increasing trajectory from streams with small drainage areas (and, consequently, shallow, narrow and steeper channels) to streams with larger drainage areas (i.e., deeper, wider and lower slope) (Fig. 3). The second axis described an increasing trajectory between sites with small streambed particles, a larger proportion of the area in pools and more in-stream channel cover than streams with larger streambed particles, less pool area and less stream cover. These two axes explained 61% of the variance, suggesting strong linear relationships among the habitat variables. Several general categories of habitat variables were identified with the correlation and PCA analysis including stream habitat area and associated stream widths and depths (drainage area, bank-full depth, bank-full width, riffle depth and residual pool depth), in-stream cover (average bank cover width, pool area and logs per channel width), stream channel gradient and streambed particle size (15th, 50th and 85th percentile diameter size of the streambed particle distribution).

Correlating salmon occurrence and abundance with habitat characteristics

Drainage area (km²) was an important, positive factor in the development of suitable habitat for
species besides sockeye salmon (Table 2a,c). Drainage area was in all of the candidate models for pink and Chinook salmon occurrence and 40% of the candidate models for chum salmon occurrence (Table 2a). The highest AICc ranked chum and Chinook models included glide depth as a positive effect (Table 2a). To understand which aspects of streams with larger drainage areas are driving higher occurrence and abundance we examined models without drainage area, leaving other correlated variables such as width and depth (Table 2b). After eliminating drainage area, pink salmon occurrence was best explained by models including wetted width, a variable highly and positively correlated with drainage area. Glide depth associated models were the best for chum salmon (Table 2b). Chinook salmon occurrence had at least one depth or width variable associated with each candidate model (Table 2b). However, $R^2$ and AICc ranking were lower in almost all cases in models without drainage area. This suggests that drainage area may provide a useful summary of the different specific characteristic that drive occurrence.

Candidate models relating pink, chum and Chinook salmon abundance in the recent years to habitat attributes were similar to occurrence models using the longer time series of data (Table 2c). The highest AICc ranked models of pink salmon abundance included positive coefficients for drainage area and streambed particle size (D50) (Table 2c). The best AICc scored chum salmon abundance models all included a positive coefficient for drainage area (Table 2c). Chinook salmon abundance models had considerably lower $R^2$ (0.406 and 0.372), and the lack of difference in the evidence ratios ($w_I / w_0$) between the candidate models and the null model suggests that none of the models explained Chinook salmon abundance adequately.
The relationship between sockeye salmon and other salmon species

Sockeye salmon density was a significant variable in only one of the best pink salmon occurrence models and two of the best Chinook salmon occurrence candidate models (Table 2a,c). Sockeye salmon density was negatively correlated with pink salmon occurrence but positively correlated with Chinook salmon occurrence and abundance (Tables 2a,c). Stream specific average pink and chum salmon occurrence typically decreased in Wood River streams as stream specific average sockeye salmon density increased (Fig. 4). Occurrence levels were <25% where average sockeye densities were >0.40 m⁻², and went to 0 where densities were >0.60 m⁻². Sockeye salmon density did not strongly affect occurrence and abundance of pink, chum and Chinook salmon because the effects of other variables, notably drainage area, were so prominent (Fig. 4). For example, pink, chum or Chinook salmon did not occur in two watersheds in the Wood River system with drainage areas <8 km² and occurrence ranged from 10% to 51% for watersheds with drainage areas between 8 and 50 km². Occurrence of pink, chum or Chinook salmon exceeded 50% in the two watersheds >50 km².

Predicting pink, chum and Chinook salmon occurrence and abundance

Model based predictions of occurrence and abundance differed by species (Tables 2a,c). The best models for occurrence, including drainage area,
estimated that the probability of occurrence for pink salmon was 2–5 times greater than for both chum and Chinook salmon for a given watershed area (Tables 2a through c). Pink salmon were estimated to still occur at a higher proportion than chum and Chinook salmon with an increase in stream channel width and depth, but the estimates levels of occurrence were less than when drainage area was incorporated into the models. Lastly, abundance estimates suggested that pink salmon can number in the 100s in larger drainage areas with relatively large substrate (Fig. 5). However, over 75% of the watersheds in the Wood River system are <50 km² and have a D50 of 35 mm or less, and these features result in estimates of 100 or fewer fish (Fig. 5). Both chum and Chinook salmon abundance estimates are considerably lower than pink salmon abundance estimates, ranging in the 10s even in the largest watersheds with the largest stream channel widths and depths.

Discussion

The vast majority of streams in the Wood River system are used for spawning by sockeye salmon but only a fraction of them are used regularly, if at all, by chum, pink and Chinook salmon (Hilborn et al. 2003; Pess 2009). Thus despite generally suitable habitat conditions (e.g., water depth, gravel size, and temperature), the other species are notably scarce, although present. Chinook salmon are much more large-bodied than sockeye salmon and differ in juvenile habitat requirements (i.e., juveniles rear in streams rather than in lakes as in the case of sockeye salmon: Healey 1991; Burgner 1991), thus their absence from small streams with very simple channel morphology is understandable. However, pink and chum salmon are more similar in size to sockeye salmon and, like sockeye salmon, migrate immediately from the streams as juveniles. Pink and chum salmon

![Graph](image-url)

**Fig. 4.** Pink, chum, or Chinook salmon occurrence between 1968 and 2007 v. average spawning sockeye density (fish per meter²) between 1968 and 2007. Solid, black diamonds indicate average pink salmon occurrence for drainage areas <8 km², while clear rectangles indicate average pink salmon occurrence for drainage areas >8 and <50 km². Grayed triangles denote drainage areas >50 km².

![Graph](image-url)

**Fig. 5.** The most plausible candidate model for predicting the abundance of pink salmon from stream habitat attributes in the Wood River system. The solid white area denotes estimated pink salmon abundance between 0 and 100 individuals. The solid black area denotes estimated pink salmon abundance between 100 and 200 individuals. The solid grey area denotes estimated pink salmon abundance between 200 and 300 individuals. The clear, speckled area denotes estimated pink salmon abundance between 300 and 400 individuals, and the clear vertically hashed area denotes estimated pink salmon abundance between 400 and 500 individuals.
Correlating salmon occurrence and abundance with habitat characteristics

Occurrence and abundance of all three nondominant species increased with drainage area, consistent with the hypothesis that increased quantity and diversity of suitable spawning habitat would provide greater scope for habitat segregation among species. Stream depth, width, the amount of in-channel cover and streamed particle size were also related to the distribution of pink, chum and Chinook salmon. Numerous aquatic and terrestrial studies (Thomas et al. 1992; Rieman & McIntyre 1995; Magnuson et al. 1998; Dunham & Rieman 1999; Haring & Fausch 2002) have supported the species–area relationship: the probability of a species being present in a habitat increases with area (MacArthur & Wilson 1963).

The species–area relationship begs the question, what is the significance of habitat area? The positive relationship between species richness and area is, in part, an ‘epiphenomenon associated with sampling effort’, meaning that larger areas contain more individuals, and thus sample the species pool more effectively (Connor & McCoy 1979; Angermeier & Schlosser 1989). However, fish-habitat associations that include drainage area and other factors such as stream depth, width and habitat complexity are well documented, and patterns of species abundance and distribution result from a combination of metapopulation dynamics, habitat diversity and sampling (Connor & McCoy 1979; Rieman & Dunham 2000; Haring & Fausch 2002; Pess et al. 2002). In addition, an increase in habitat area also increases the carrying capacity of a watershed, which affects the genetic diversity and differentiation (e.g., Atlantic salmon: Ozerov et al. 2012). Nonetheless, mechanistic interpretations are limited because it is difficult to interpret the slope of the species–area regression with respect to physical conditions and biological processes associated with occurrence and abundance such as habitat availability, habitat selection, immigration and extinction (Magnuson et al. 1998).

Several features correlated with and determined by drainage area were important for understanding the physical habitat conditions that allow for nondominant salmon occurrence and abundance in the Wood River system. Larger watersheds provided a greater amount of habitat area which could be used by salmon species, and watershed area can be a useful predictor of salmonid occurrence and abundance (Haring & Fausch 2002). The increase in area may result in a greater diversity of habitat types, promoting the survival at each life stage of enough individuals to sustain populations (Haring & Fausch 2002). Area has also been hypothesised to allow existing populations to be less vulnerable to natural and anthropogenic disturbance and reduce the potential for extinction (Lande 1993). An increase in habitat area alone, without changes to habitat types or increased resilience to disturbance, can also result in an increase in the occurrence and abundance of animals (Steffan-Dewenter 2003). This was the case in the Wood River system for pink, chum and Chinook salmon, but not for sockeye salmon; they are found in very small streams, often at the highest densities.

Streams with large drainage areas tended to be wider and deeper than streams in smaller basins. These attributes, in turn, were associated with higher levels of occurrence and abundance of pink, chum and Chinook salmon. Similar positive relationships between presence and abundance and stream width and depth have been found in previous studies (Angermeier & Schlosser 1989; Nelson et al. 1992; Dunham & Rieman 1999; Haring & Fausch 2002). Angermeier & Schlosser (1989) found that habitat volume predicted species richness more precisely than habitat area, thereby suggesting that the area and depth of streams influence the distribution of fishes.

More mechanistically oriented studies have also identified the importance of stream depth to adult pink, chum and Chinook salmon. Migratory behaviour of both pink and chum salmon was monitored in the Shibetsu River, Japan, where the preferred swimming depth for chum salmon was between 0.2 and 0.4 m, and 0.6 and 0.8 m for pink salmon (Akita et al. 2007). Both species migrated at these depths along defined riverbanks and near the bottom of the streamed (Akita et al. 2007). Pink salmon typically require a minimal depth of 0.15–0.2 m for spawning (Raleigh & Nelson 1985; Bjornn & Reiser 1991). Likewise, chum salmon commonly spawn at widths, depths and velocities similar to many of the streams in this area (Salo 1991). Chinook salmon, the largest bodied of all salmon, typically spawn in deeper (>0.3 m) locations (Healey 1991).

All the streams in the Wood River system where pink, chum and Chinook salmon were never observed between 1968 and 2007 had average wetted depths <0.15 m, identified as a minimal spawning depth for pink salmon (Bjornn & Reiser 1991). In addition, many of the same streams do not have well defined, deep riverbanks at the mouth of the streams where they drain into the lakes (Quinn et al. 2001; G. Pess, personal observation, 2004 & 2005). The combination of shallow water and an ill-defined stream channel mouth could inhibit pink salmon from entering these smaller streams. However, sockeye salmon enter these streams in large numbers, despite some-
times severe mortality from stranding before they can reach spawning habitats (Quinn & Buck 2001), and the sockeye salmon are larger-bodied than pink salmon.

Average cover width (m), predominantly undercut banks in these streams, was negatively correlated with pink salmon occurrence and abundance but positively correlated with Chinook salmon occurrence and abundance. It is not clear why there was a negative effect of cover on pink salmon but the positive effect of cover on Chinook salmon abundance is consistent with published reports on other salmon species. The distribution of over-summering steelhead in the New River, California, was more strongly controlled by physical characteristics of pools, including cover, than by the availability of thermal refuges (Nakamoto 1994). Pool spacing, a larger-scale metric of holding water and cover, was a dominant correlate of adult Chinook and coho salmon in the Puget Sound region of Washington State (Montgomery et al. 1999). Similarly, the amount of cover in a given holding location was an important component of preferred holding habitat for adult masu salmon in the Masuhoro River, Japan (Edo & Suzuki 2003). An increase in channel cover, whether it be in the form of undercut banks, depth or structure such as wood provides visual isolation that can reduce predation from bears in the Wood River system (Quinn & Buck 2001; Quinn et al. 2011).

Streambed particle size (D50) was also an important component of several of the best candidate models for pink and chum salmon occurrence and abundance. However, the correlation varied positively and negatively by species and metric (occurrence or abundance), making it difficult to interpret. Median particle size at the redd site has been positively correlated with the average length of female salmonids (Kondolf & Wolman 1993). Larger females thus can typically spawn in larger substrates (Quinn 2005). Pink salmon, the smallest species (Quinn 2005), would thus have a negative relationship with streambed particle size. However, this is only the case for occurrence and not abundance.

Habitat area and segregation between sockeye and pink salmon

The occurrence of pink salmon was positively related to watershed drainage area and stream size but negatively related to sockeye salmon density. Conversely, sockeye salmon densities decreased with watershed area and stream depth. Unfortunately, the data do not allow us to determine whether this inverse relationship reflects competition or independent habitat segregation. Habitat segregation between spawning sockeye and pink salmon was also evident at the

reach scale in Ice Creek (Pess 2009), where pink salmon tended to occupy habitats lower within the drainage network than sockeye salmon, even though their spawning timing was similar.

Observations in southeast Alaska also showed pink salmon concentrated in the lower portions of a river system and sockeye salmon predominately upstream (Fukushima & Smoker 1998). Differences in depth, velocity and stream channel gradient were also observed in the nest sites used by these species (Fukushima & Smoker 1998). Sympatric salmonid populations typically exhibit spawning habitat segregation (Witzel & MacCrimmon 1983; Bagliniere et al. 1994; Fukushima & Smoker 1998) and this may reflect both interspecific aggression (Quinn 1999) and habitat choice.

Limitation of the study

There are several limitations to this study. First, the occurrence and abundance data depended on visual foot surveys that are subject to various sources of observation and process error including, but are not limited to, observer experience, weather conditions, fish behaviour and stream characteristics such as turbidity, water level and habitat type (Korman & Higgins 1997; Jones et al. 1998; Korman et al. 2002). The Wood River system streams are amenable to visual surveys because water clarity during the spawning season is excellent and the four salmon species are readily distinguishable by their size, shape and colour, so misidentification is unlikely. Accuracy of counts may also decrease as fish density increases (Jones et al. 1998) and a few nonsockeye salmon might be missed under high sockeye salmon densities. Because sockeye salmon are so much more abundant, it is more likely that the other species were present but not noticed rather than incorrectly reported as present. Salmon may also have been absent on the survey day but present on other days in that season, resulting in underestimation of the rarer species. However, the other salmon species tend to be observed with similar general temporal distributions to the sockeye salmon so we assumed this was not a large source of bias. Despite these limitations, patterns and trends emerged over space and time suggesting that salmon other than sockeye were more common in larger systems than smaller systems. Nonsockeye salmon are more easily noticed in small, shallow streams, thus the lack of occurrence in such habitats is particularly striking.

Do pink, chum and Chinook salmon exist as self-sustaining populations in the Wood River system?

The lack of consistent pink, chum and Chinook salmon occurrence and low abundance levels suggest
that most of the study streams are likely not small, persistent populations but rather the salmon are strays from larger ‘source’ populations elsewhere. This is corroborated for Chinook salmon and chum salmon by recent genetic information that suggests the Wood River likely receives substantial immigration from neighbouring watersheds, such as the Nushagak River system (Lin et al. 2011). However, Ice and Lynx creeks had pink salmon occurrence and abundance levels that might indicate small, self-sustaining populations. Both streams had occurrence levels in even years near or >0.50 and abundance levels at or >100 individuals, and the habitat necessary for segregation from sockeye salmon. Perhaps more interestingly, there is an upward trend in abundance of pink and chum salmon in the Wood River system streams (Pess 2009). This might indicate merely high survival rates at sea during the recent years, or perhaps the early stages of population establishment, or a combination of both (Pess 2009).

There are two main potential sources of pink, chum and Chinook salmon strays into the study streams – the ‘trunk’ rivers connecting each of the four lakes in the Wood River system, and the nearby Nushagak River (Lin et al. 2011). Pink salmon strays are likely to come from the Agulukpak River, flowing from Lake Beverly into Lake Nerka, the Agulowak River, flowing from Lake Nerka to Lake Aleknagik, or the Nushagak River, into which the Wood River flows (Rogers & Burgner 1967; Baker et al. 2006). The Nushagak River had an average estimated pink salmon escapement between 1968 and 2007 of 1.3 million pink salmon (Baker et al. 2006). However, the pink salmon spawning in the small streams that we surveyed are significantly smaller-bodied than the later-spawning pink salmon that spawn in the larger rivers of the system (T. P. Quinn, unpublished data), so it is not clear that the former are merely strays from larger rivers. There are no major source populations of chum and Chinook salmon within the Wood River system, and they probably come from the Nushagak River (average annual escapement of 256,000 chum salmon and 173,000 Chinook salmon: Baker et al. 2006). Regardless of the fact that the salmon seen in these streams are probably strays, their consistent use of some streams rather than others indicates strong habitat association.

Summary

This study demonstrates the utility of evaluating the role of habitat conditions on salmon occurrence and abundance. Presence/absence, abundance and descriptive models at a hierarchy of scales provided hypotheses for linking habitat variables and fish presence or abundance. While the relationships developed from our study cannot determine the absolute habitat requirements needed for nondominant salmonid populations to persist and sustain themselves in the Wood River system, they advance our mechanistic understanding of the relationship between salmonids and their habitats. Future monitoring and research efforts associated with the enumeration of adult salmonid populations should consider nondominant species in their study designs and incorporate presence/absence metrics to document long-term changes in species composition.

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References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Pearson’s correlation coefficient among habitat variables in the Wood River system, Alaska.