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Scaling Salmonid Life History by Habitat Area: A Conceptual Approach to Estimating Estuarine Conservation Needs

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Abstract.—Methods to define the critical estuarine habitats of salmon are needed to support conservation initiatives and species recovery strategies. In this paper, we describe a conceptual approach that might be useful for this task. Growth rates and estimates of food consumption for ocean-type Chinook salmon *Oncorhnychus tshawytscha* rearing in four estuaries (Squamish River estuary, Nanaimo River estuary, Campbell River estuary, and Fraser River estuary) discharging into the Strait of Georgia, British Columbia, Canada, were compiled using literature data and a bioenergetic model. Consumption data were then scaled according the areal extent of four habitats (open water, sand flats, marsh, and riparian) often used as surrogates for fish food production. We documented between-estuary variations in the scaled consumption data, possibly related to inter-estuary differences in habitat quantity, quality, or population-specific growth. Further analysis, calibration, and verification are needed before implementation of the concept.

Introduction

Habitat managers and conservation biologists need methods to quantify the amount of estuarine habitat needed to support specific salmon populations on the Pacific coast of Canada. These methods will be especially important if the critical estuarine habitats of salmon need to be defined in species recovery plans under Canada's Species at Risk Act legislation (Randall et al. 2003). In this paper, we present the results of a brief exploration and modeling effort based on a conceptual approach that might be useful for this task. Growth rates and estimates of food consumption for Chinook salmon *Oncorhynchus tshawytscha* rearing in four estuaries discharging into the Strait of Georgia, British Columbia, Canada, were estimated using literature data and physiological models. We focused on ocean type chinook which are known to be particularly reliant on estuaries for survival

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(Levings et al. 1989) and in some estuaries have shown evidence of density-dependence (Korman et al. 1997; Beamer et al. 2003). Juvenile ocean type chinook reside in estuaries from about April to August and in some estuaries (e.g., Nanaimo River estuary, Healey 1991) can grow from about 1 g to 15 g over this five month period. Consumption was scaled by area of riparian, marsh, sandflats, and open water, habitat types that are often assigned a high value in fish habitat conservation and restoration schemes (Emmett et al. 2000). However, certain habitat types are considered more critical than others in some systems. For example in the Fraser River Estuary Management Program (FREMP 2001), there has been a concerted effort to restore marsh, often by replacing unvegetated sand flats.

Wiens (1989) recommended that habitat ecologists should begin searching for consistent patterns in scaling effects instead of asking how results vary as a function of scale. To date, researchers working on salmon habitat have only made a few contributions to this pattern-seeking task, as noted by Armstrong et al. (1998). However, there is an emerging body of knowledge on landscape approaches to estuarine ecology (e.g., Hood 2002) that is highly relevant and will no doubt be important for future conservation strategies for species such as Chinook that are estuarine-dependent. More empirical data are clearly needed to build a body of knowledge about habitat scales, especially those relevant to fish, and we hope our contribution will be a useful contribution to that database.

Methods

This work depended on harvesting data from published information in the journal and report literature. References and detailed data sets are presented in contract reports (Oceanbound 1996 for biological data and LGL 1997 for spatial data), and only summary information is presented here.

Growth Rates

Growth rate estimates were developed by analyses of temporal changes in observed weight of Chinook caught in beach seines during the estuarine rearing period. Data from estuaries of the following rivers that discharge into the Strait of Georgia were analyzed: Nanaimo (1975–1977), Campbell (1982, 1994), Squamish (1978), and Fraser (1978, 1979, 1998). Only data from wild stock were used, but in the data set of Campbell River estuary, some unmarked hatchery fish may have been included. The daily instantaneous rate of growth by weight (g/d) was computed for each of the estuaries and each of the years. When data from multiple years were available, the mean was calculated.

Estimates of Consumption

A bioenergetic model for Chinook growth in estuaries was not available so we modified the sockeye salmon *Oncorhynchus nerka* model for freshwater developed by Beauchamp et al. (1989):

$$\mathrm{CU} = \frac{G + 2R_{\mathrm{opt}}}{1 - (R_D + F + U)}$$

where CU = energy consumption (kJ/g)

G = instantaneous growth rate

$(R_D + F + U)$ = fixed energies allocated to digestion, egestion, and excretion, respectively; fraction of a unit energy of consumed food, usually 35–40% (Brett and Groves 1979).

R_{opt} = standard and active metabolism assuming optimum swimming speed.

Energy equivalents for Chinook were used from Higgs et al. (1995). We were unable to calibrate the model to account for differences in metabolism in a saline environment because of lack of information in the literature.

A key parameter for estimating R_{opt} is temperature. Seasonal temperature data for the four estuaries were found in the literature and curves of seasonal temperature change were developed using polynomial regression. The equation used for computing R_{opt} was

$R_{opt} = aW^{b} \bullet e^{\rho T} \bullet e^{\nu U_{opt}}$ where $U_{opt} = xW^{y} \bullet e^{\varepsilon T}$. Symbols and parameter values not given in the text are described in Table 1.

An estimate of the mean CUs required to support observed growth over the rearing period was obtained by summing the units and then dividing by the number of estimates available, which ranged from two (Nanaimo River estuary, inner estuary only) to seven (Campbell River estuary) (Oceanbound 1996).

Areas of Estuaries

Estimates of the areal extent of open-water, mud/sand flat, marsh, and riparian habitat on the Nanaimo, Campbell, and Squamish River estuaries were obtained fromEnvironmental Research Associates (LGL) (1997). Data for the Fraser River estuary are from Fraser River Estuary Management Program (FREMP) (2004). The proportions of the estuaries that have been anthropogenically altered were also obtained from LGL (1997) for the Nanaimo, Campbell, and Squamish River estuaries and from Pacific Fisheries Resource Conservation Council (PFRCC) (1999) for the Fraser River estuary. Estimates were obtained for the closest year to the time period when growth rates were calculated. Energy consumption estimates for each estuary were then scaled by the areas of the four key habitat types to derive habitat-scaled consumption units (HSCU).

The scaling procedure we used involved at least three key assumptions: 1) that food supply for the fish would be proportional to area, 2) that food supply limited growth and survival (i.e., growth was density-dependent), and 3) that density or biomass of Chinook was relatively similar in the four estuaries. At the time the data were obtained, there was some support for the latter assumption as juvenile Chinook density based on beach seine data varied between 0.1 and 0.9 fish/m^2 in 10 out of 16 estuaries in British Columbia (Levings 1984). As the density data were obtained from before major chinook hatchery development in British Columbia, they are likely mainly for wild fish.

Results

Mean instantaneous growth rates during the rearing period (estimated day of the year 120 to day 220) ranged from 0.023 g/d at the Fraser River estuary to 0.446 g/d at the Squamish River estuary. Water temperature ranged from 8°C to 12°C at the Squamish River estuary, 11–16°C at the Nanaimo and Campbell River estuaries, and 13–18°C at the Fraser River estuary. Mean CU over the rearing period ranged from 2,825 at the Fraser River estuary to 13,460 at the Squamish River estuary (Table 2).

Areal data for the estuaries and four habitat types (riparian, marsh, sand flats, and open water) are given in Table 3. Area of marsh ranged from 25 ha at the Campbell River estuary to 2,274 ha at the Fraser River estuary. The total area of the Nanaimo River estuary, the Campbell River estuary, the Squamish River estuary, and the Fraser River estuary was 1,758, 286, 1,505, and 21,371 ha, respectively. Percent of habitat that was

Table 1. Symbols and parameter values used in bioenergetic equations.

Symbol	Description	Nominal value
a	Intercept of the power function for the weight dependence of R_{opt}	0.00143
W	Body weight (g)	–
b	Coefficient of the power function for weight dependence of R_{opt}	–0.209
p	Exponential coefficient for respiration *vs* temperature($1 \cdot °C^{-1}$)	0.086
T	°C	–
v	Exponential coefficient for respiration *vs* swimming speed ($cm \cdot s^{-1}$)	0.0234
U_{opt}	Optimal swimming speed ($cm \cdot s^{-1}$)	–
x	Intercept of the power function for the weight dependence of swimming speed ($cm \cdot s^{-1}$)	9.9
y	Coefficient of the power function for weight dependence of swimming speed ($cm \cdot s^{-1}$)	0.13
z	Temperature-dependence coefficient of optimal swimming speed ($1 \cdot °C^{-1}$)	0.0405

Table 2. Mean instantaneous growth rates for chinook salmon during the estuarine rearing period, temperature ranges, and mean consumption units at four estuaries in the Strait of Georgia, B.C. Dates in parentheses for growth rates indicate years when growth rate data were obtained.

Parameter	Nanaimo River estuary	Campbell River estuary	Squamish River estuary	Fraser River estuary
Temperature range (°C)	11–16	11–16	8–12	13–18
Mean growth rate (g*d)	0.071 (1991)	0.122 (1986)	0.446 (1978)	0.023 (1978)
Consumption units	3,500	4,357	13,460	2,825

anthropogenically altered (log storage, docks, and industrial development) ranged from 16% at the Nanaimo River estuary to an estimated 70% at the Fraser River estuary.

The distribution of HSCU data among the four estuaries suggested that if Chinook were distributed and feeding uniformly over all habitat types, they would need to consume about 0.1 units/ha at the Fraser River estuary to grow at the observed rate, compared to about 2, 9, and 15 units/ha for the Nanaimo River, Squamish River, and Campbell River estuaries respectively (Table 4). If the fish were feeding only on marsh habitat, they would need about one uni/ha at the Fraser River estuary, 23 units/ha at the Nanaimo River estuary, 103 units/ha at the Squamish River estuary, and 174 units/ha at the Campbell River estuary. The ranked importance of marsh relative to the other three habitats varied both between and within estuaries. If the fish were uniformly distributed in each of the four habitat types at a particular estuary, marsh ranked first at the Fraser, Nanaimo, and Campbell River estuaries, whereas sandflats were more

Table 3. Habitat areas for the Fraser River, Nanaimo River, Campbell River, and Squamish River estuaries in the Strait of Georgia, B.C. The percent of disrupted habitat ("anthropogenic") for each estuary is given in parenthesis in row five. n.a. = data not available.

Habitat area (ha)	Nanaimo River estuary	Campbell River estuary	Squamish River estuary	Fraser River estuary
Riparian	310	132	560	4,144
Marsh	155	25	131	2,274
Mud/Sand flats	511	29	15	7,796
Open water	495	31	516	7,157
Anthropogenically altered	287 (16)	69 (24)	283 (19)	n.a. (70)
Total	1,758	286	1,505	21,371

Table 4. Habitat scaled consumption units for total habitat and four habitat types at four estuaries in the Strait of Georgia. 1–4 rank of habitats within an estuary; A–D rank of a particular habitat across estuaries.

Habitat	Nanaimo River estuary	Campbell River estuary	Squamish River estuary	Fraser River estuary
Consumption units/ ha: total estuary	1.9	15.2	8.9	0.1
Riparian	$11.3^{2,C}$	$33.0^{4,A}$	$24.0^{4,B}$	$0.6^{2,D}$
Marsh	$22.5^{1,C}$	$174.2^{1,A}$	$102.7^{2,B}$	$1.2^{1,D}$
Sand flats	$6.8^{4,C}$	$150.2^{2,B}$	$897.3^{1,A}$	$0.3^{4,D}$
Open water	$7.1^{3,C}$	$140.5^{3,A}$	$26.1^{3,B}$	$0.4^{3,D}$

important at the Squamish River estuary. If the estuaries were dominated by only one habitat type and fish were distributed uniformly within it, there was variation between estuaries, with riparian, marsh, and open water ranking first for the Campbell River estuary and sandflats first for the Squamish River estuary (Table 4).

Discussion

Use of Results in Conservation and Management

Scaling consumption by habitat area is a gross estimate of the trophic requirements of juvenile Chinook in estuaries and requires a number of critical assumptions (listed in Methods, above) that need to be tested for particular estuaries. For this reason, we recommend further analyses to test our proposed conceptual approach before implementation. Alternate data may also be available for scaling. For an understanding of ecosystem dynamics, the change in biomass method (Healey 1982) is a more rigorous technique. Juvenile Chinook are opportunistic feeders and likely obtain food from a variety of habitats, and this needs to be taken into account in future initiatives. For example, at low tide, the fish might obtain zooplankton in open-water habitat, at mid-tide harpacticoid copepods from sandflats, and insects from marsh habitats at high tide. In a comparative sense, the scaling method might provide an insight into the relative support provided by various habitats between estuaries. The estuary with the smallest marsh (Campbell River estuary) showed the highest HSCU, implying that, relative to the other estuaries, this habitat type was more important for Chinook growth. If marsh area is therefore in fact a limiting factor, this implies that a very strict marsh conservation and restoration program would be required to maintain Chinook production in this river system. Habitat-scaled consumption units for other habitat types (e.g., eelgrass, salt marshes) could also be compared. However in most BC estuaries, monitoring programs to document and track the area of specific habitat types are not in place. Estuary-specific biological and habitat information should be obtained to foster a landscape approach to fish habitat management and restoration (Gray et al. 2002). Fish density and growth rates on specific habitat types is perhaps the most critical and most difficult to obtain information that is missing from databases used in estuary management plans in the region.

Factors Influencing Interestuary Differences in Growth and Consumption

Temperature, food supply, disease mediated by contaminants, and smoltifaction are factors that have been shown to influence growth rate of ocean-type Chinook in estuaries (MacFarlane and Norton 2002; Palm et al. 2003). Data for a thorough comparison are not available for the latter three parameters at the four estuaries in our analysis, and given that the temperature data were obtained in different years, there may have also been some interannual differences to account for. Although temperature is often regarded as a primary controlling factor in food demand and consumption, the cooler water temperature in the glacier fed Squamish River did not seem to result in lower growth rates for this population—in fact, the highest growth of the four estuaries was observed at this estuary. Conversely, Chinook growth at the Fraser River estuary, exhibiting the warmest temperature, was the lowest of the four estuaries. Abundant prey resources and lower metabolic costs associated with food acquisition may have improved growth efficiency in the Squamish River estuary, as discussed by MacFarlane and Norton (2002), for ocean-type Chinook in a study off coastal California. An alternate suggestion is that estuarine growth has a genetic basis as found for freshwater growth of the other life history types of Chinook salmon (Withler et al. 1987). However, our understanding of the genetic basis of adaptations to specific habitat types river estuaries and habitats within estuaries is poor (Levings 1993) and further data are required on this topic.

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