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Application of diversity indices to quantify early life-history diversity for Chinook salmon

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ABSTRACT

We developed an approach to quantify early life history diversity for Chinook salmon (*Oncorhynchus tshawytscha*). Early life history diversity (ELHD) is the variation in morphological and behavioral traits expressed within and among populations by individual juvenile salmon during downstream migration. A standard quantitative method does not exist for this prominent concept in salmon biology. For Chinook salmon, ELHD reflects the multitude of possible strategies undertaken during the juvenile (fry through smolt) phases of their life cycle, where a life history strategy (or pattern) describes the combination of traits exhibited by an organism throughout its life cycle. Increasing life history diversity to improve resilience and aid recovery of diminished salmon and steelhead populations is a common objective in fish population recovery efforts. In this paper, we characterized early life history traits and prioritize timing and fish size as two appropriate, measurable dimensions for an ELHD index. We studied diversity index literature, identified an indexing approach based on the effective number of time-size trait combinations, and tested several candidate indices for performance and usefulness in case studies using juvenile salmon catch data from the lower Columbia River and estuary. The recommended ELHD index is diversity expressed as the effective number of time-size trait combinations for the Shannon Index, modified to include an adjustment for missing time-size trait combinations and a sample coverage factor. This index applies to multiple life history strategies of juvenile salmonids; incorporates fish abundance, richness, and evenness; and produces readily interpretable values. The ELHD index can support comparisons across like locales and examinations of trends through time at a given locale. It has application as a high-level indicator to track trends in the status of the recovery of salmon and steelhead populations in the Columbia River basin and elsewhere where salmon recovery efforts are under way.

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1. Introduction

A remarkable characteristic of Chinook salmon (*Oncorhynchus tshawytscha*) is that these fish express multiple life history strategies among and within species and populations throughout much of their life cycles (Healey, 1991, and Groot and Margolis, 1991). A life history strategy (or pattern) describes the combination of traits exhibited by an organism throughout its life cycle (Quinn, 2005). For Chinook salmon, early life history diversity (ELHD) reflects the multitude of possible strategies undertaken during the juvenile (fry through smolt) phases of their life cycle. Formally, ELHD is the variation in morphological and behavioral traits expressed within and among populations by individual juvenile salmon during their downstream migration (modified after ISAB, 2012a). Greater diversity of life histories may strengthen population resilience (Bottom et al., 2009), i.e., the ability to persist in spite of fluctuations or changes in the environment (Holling, 1973).

Early life phases of Chinook salmon have been segregated into two general categories: "ocean-type" and "stream-type" (Healey, 1991 and Quinn, 2005). Stream-type salmon typically rear in freshwater habitats for a year or more prior to migrating to the sea. Ocean-type salmon reside in freshwater for less than one year before commencing a seaward migration. It is well-known, however, that the early life history strategies of Chinook salmon are far more complex than the aforementioned general categories (e.g., Hayes et al., 2008; Reimers and Loeffel, 1967; Rich, 1920). For example, Connor et al. (2005) described an alternative life history for juvenile Snake River fall Chinook salmon (*O. tshawytscha*) termed "reservoir-type." Juvenile Chinook salmon exhibiting this life history strategy begin migration but delay in reservoirs to spend

Abbreviations: ELHD, early life history diversity; ESA, Endangered Species Act; LCRE, lower Columbia River and estuary; NMFS, National Marine Fisheries Service.

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their first winter in freshwater, and resume seaward migration the following year to enter the ocean as yearlings. In the lower Columbia River and estuary (LCRE), Burke (2004) and Bottom et al. (2005a) reconstructed historical data of Chinook salmon life history traits (e.g., size, timing of migration, rearing characteristics) and concluded that, compared to more contemporary data sets, the diversity of these strategies has decreased due to anthropogenic-related factors.

Life history diversity of Chinook salmon has been reduced by habitat alterations, hatchery practices, and hydropower development and operations (Williams, 2006 and Ruckelshaus et al., 2002). As evidenced in the Columbia River basin, river impoundments have eliminated habitats and along with them many stocks of salmon from the upper Snake and Columbia rivers (Lichatowich et al., 1999; NMFS, 2004; Nehlsen et al., 1991; NRC, 1996, and Williams, 2006). Hatchery production, which now provides the majority of out-migrating juvenile salmon and steelhead in the basin, has diminished the diversity of life histories by suppressing volitional migration through release practices and limiting salmonid size ranges at release (NMFS, 2004). In the Pacific Northwest, the overall decline of many populations has resulted in the listing under the U.S. Endangered Species Act (ESA) of 18 salmon and steelhead populations. Recovery plans often include habitat improvement and other work to eliminate, minimize, or mitigate adverse impacts on salmon and increase ELHD (e.g., NMFS, 2011). The premise is that increased ELHD will improve salmon resilience and population size, thereby increasing the potential for recovery of endangered and threatened salmon populations (Bottom et al., 2005a and Lichatowich et al., 1995).

Given the objective of increasing ELHD in the recovery effort, the need for a method to quantify ELHD for Chinook salmon was identified in the 2008 biological opinion on operation of the Federal Columbia River Power System (NMFS, 2008), which stipulated development of a life history diversity index (Reasonable and Prudent Alternative 58.2). Accordingly, we undertook an effort to develop an index to support periodic, quantitative assessments of the ELHD of Chinook salmon. A salmon life history diversity index may serve as a high-level indicator (quantitative measure designed to communicate progress) to assess the success of ecosystem restoration efforts targeting listed salmon species in the Columbia River basin, and elsewhere. Furthermore, such an index provides an evaluative framework for assessing linkages between restoration projects and improvements in ELHD, making it possible to test the hypothesis that increased habitat quantity, quality, or diversity leads to increased life history diversity.

Although many diversity indices and applications in ecology exist (e.g., Anderson et al., 2011; Frosini, 2004; Koleff et al., 2003, and Tuomisto, 2012), to our knowledge none has been explicitly applied to indexing attributes of ELHD for Chinook salmon. Many authors addressed or alluded to life history diversity, but none offered a quantifying approach. For example, Beechie et al. (2006) related environmental attributes to life history diversity. Gustafson et al. (2007) quantified extinctions of salmon populations, but not life history diversity per se. A possible approach was reported by the National Marine Fisheries Service (NMFS, 2007) in an application of the ecosystem diagnosis and treatment model. The model measured salmon performance using three indicators: abundance, productivity, and life history diversity (Lichatowich et al., 1995). By their definition (NMFS, 2007), life history diversity was the proportion of total historical life history trajectories that are presently successful, where a "...trajectory is a life history pathway that starts in one of the spawning reaches and moves through time and space in the environment that was defined by the reach structure and environmental attribute ratings." This approach is not suitable for an ELHD index because the trajectories are subjective and require accurate, detailed historical knowledge that is usually unavailable.

In this paper we used an index to quantify the ELHD of Chinook salmon that incorporates measurements of biological traits exhibited during seaward migration. Overall, we were guided by Hill's (1973) assertion that "Simple and well-understood indices should be used." We strived for an ELHD index meeting the following criteria:

- applies to multiple life history strategies using the same suite of readily measurable traits;
- incorporates fish abundance, density, or catch per unit effort data;
- incorporates both richness (number of species or traits) and evenness (equitability of proportional frequencies);
- is readily understandable and interpretable;
- supports comparisons across like locales and examinations of trends through time at a given locale, where locale is a prescribed area of a river or estuary; and
- builds on the extensive body of prior research in ecology regarding the relative merits of alternative diversity measurements.

This paper documents the steps taken to develop an ELHD index for Chinook salmon, the quantitative rationale for the index, and our recommendations for application of the index as a high-level monitored indicator of salmon performance that can be applied to assess ecosystem restoration program effectiveness at locales including tributary streams, main-stem dams, tidal freshwater rivers, and estuaries. To develop an ELHD index, we began with a characterization and prioritization of early life history traits to identify appropriate, measurable index dimensions. We then studied the diversity index literature for overarching concepts and indices suitable to apply as an ELHD index. Finally, we tested indices from the literature review using case studies involving juvenile salmon catch data from the LCRE. Based on these steps, our recommended method for indexing ELHD of Chinook salmon applies "true" diversity approach, also termed effective number (Jost, 2006 and Tuomisto, 2012), modified to account for missing time-size trait combinations and sample coverage (Chao and Shen, 2003).

2. Index development

2.1. Early life history strategies and traits

Early life history strategies reflect a combination of interacting traits influenced by environmental and genetic factors. The categorization of early life history strategies for Chinook salmon has focused primarily on traits such as migration timing, size of fish as they enter habitats in the river–estuary–ocean continuum, residence time, growth rate, and habitat associations (Bottom et al., 2005a; Burke, 2004; Fresh et al., 2005, and Roegner et al., 2012). The categorization of traits these has been particularly focused toward describing the life history strategies of Chinook salmon in estuaries spanning the North American coast from the State of Oregon to Vancouver Island in British Columbia (Beamer et al., 2005; Bottom et al., 2005a,b; Carl and Healey, 1984; Healey, 1991; and Nicholas and Hankin, 1989); this is likely because Chinook salmon have the broadest variation in life history strategies of all salmon species and make extensive use of estuarine habitats (Quinn, 2005). The traits observed vary among populations and individuals, and include timing of onset of emigration from natal streams; timing of entry into tidal freshwater, estuarine water, and the ocean; age and size of fish as they enter particular habitats; and residence times in tidal freshwater and estuarine waters. Factors affecting the expression of life history traits include genetic stock, distance upriver of the ocean, habitat availability, physical conditions (e.g., temperature

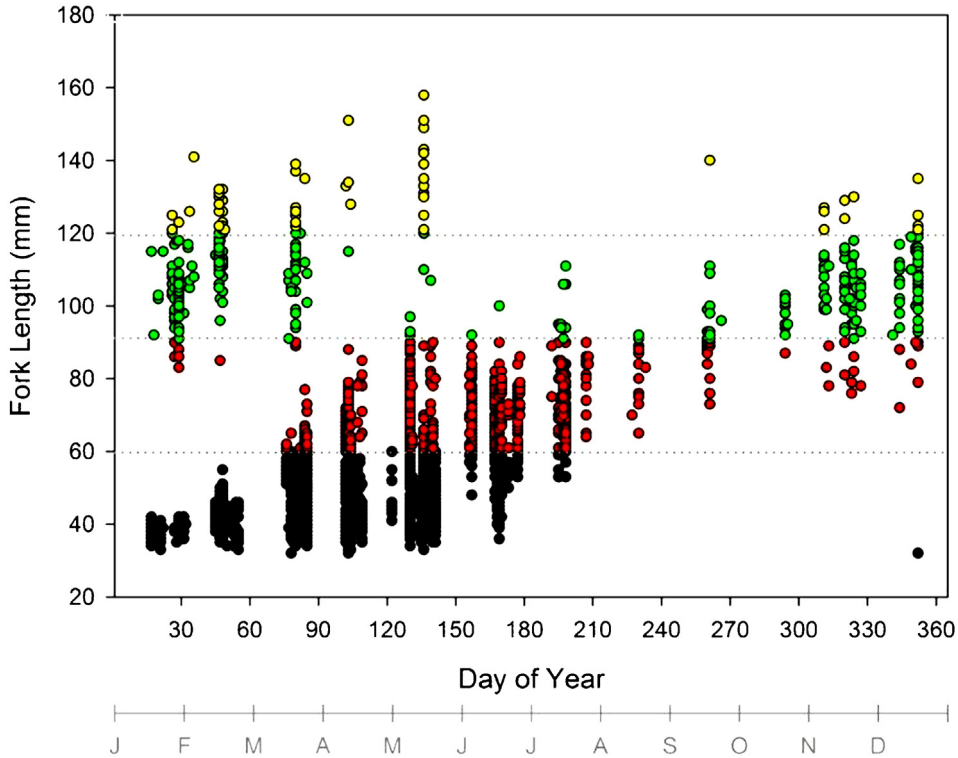

Fig. 1. Fork length of unmarked Chinook salmon sampled at the Sandy River delta (LCRE rkm 188–202) study area during 2007–2012 (Sather et al., 2011). Horizontal dashed lines and colors depict size class categories used for index calculations.

and water velocity), and, ecological conditions (e.g., prey availability and predator distribution).

For our purposes, we focused on traits that are recognized as being biologically meaningful to ascribing life history strategies to juvenile salmon and readily measurable from typical field data collection efforts. Juvenile salmon can migrate through tidal areas throughout the entire year at a variety of sizes and are found in various estuarine and tidal freshwater habitat types prior to migrating to the ocean (Dawley et al., 1986; Durkin et al., 1981; Roegner et al., 2012; and Sather et al., 2011). For Chinook salmon, such diversity is thought to have evolved to spread the risk of mortality across habitats and years (Healey, 1991). The timing of migration into an estuary, period of estuarine residence, and size at ocean entry have all been linked to variability in the survival of Chinook salmon to the adult spawning life stage (Reimers, 1973; Claiborne et al., 2011, and Scheuerell et al., 2009). Thus, we consider migration timing (time of year, either month or season) and fish size (fork length) key traits for calculating an index for Chinook salmon; these simple traits can be used to represent an array of genetic stock groups that occupy a range of habitat types.

To define size classes of juvenile salmon for the purpose of this paper, we examined the reported sizes and length-frequency distributions of juvenile Chinook salmon collected from shallow water habitats in the LCRE, although it is understood that size class definition may have to be application specific. In composite length-frequency data collected with beach seines from 2002 through 2004 in estuarine waters, modes were present at 40 mm and 100 mm (Roegner et al., 2008). These data, while not directly applicable for addressing our inquiries because of their reduced state, provide context for validating the sizes of migrating juvenile salmon in the LCRE. Campbell (2010) characterized the residence time of juvenile Chinook salmon within the saline portion of the estuary using four size categories: <45 mm, 45–60 mm, 61–90 mm, and >90 mm. Length-frequency data from Sather et al. (2011) indicate the size categories described by Campbell (2010) in the LCRE are similar to those of fish captured in upstream tidal freshwater habitats (Fig. 1). Based on the reported values for size and timing of unmarked juvenile Chinook salmon and visual examination of size frequency distributions through time (see Fig. 1), we chose four size categories for the purposes of calculating the ELHD index: <61 mm, 61–90 mm, 90–120 mm, >120 mm. Such discrete categories, however, are necessarily an abstraction of the continuous nature of fish size data. Applying the ELHD index in areas other than the LCRE would require a similar evaluation of regionally specific data to validate size classes.

2.2. Diversity literature

We examined peer-reviewed literature on species diversity indices (hereafter also referred to as diversity indices) to identify possible approaches for an ELHD index. This was not intended to be a comprehensive review of the literature on species diversity. Rather, we focused on seminal papers that in our view influenced the state of science for species diversity along with some recent distillations relevant to the diversity of juvenile salmon. This examination of the literature established basic concepts and scope, a set of proposed ELHD indices, a richness and evenness measure, an approach for normalizing and accounting for zeros in a data set, and a method for accounting for sample coverage, as described below.

2.2.1. Concepts and scope

For an ELHD index, we were interested in quantifying the diversity of combinations of early life history traits for juvenile salmon. Given the voluminous literature on the subject of diversity, it was necessary to identify the subset of concepts most relevant to the aims of our research. Most important to life history diversity is the commonality across these diversity concepts expressed by Patil and Taillie (1979) as the "...apportionment of some *quantity* into a number of well defined *categories*, determined by the problem at hand" (italics added). In this study, quantity is equivalent to juvenile Chinook salmon abundance, expressed as counts (number

of fish) or densities (number of fish per square meter). Categories are combinations of early life history traits, i.e., the combinations of traits replace "species" typically used in species diversity indices.

Ecologists measure or derive species diversity at three scales, referred to as alpha, beta, and gamma (Ellison, 2010). Alpha is measured within a given locale, such as a plot, a creek, or a wetland (Jost, 2007). Gamma is measured from a suite of locales across a region (Jost, 2007). Beta is the variation in alpha diversity among locales in a region and is typically derived, not measured, from calculations of alpha and gamma (Jurasinski and Koch, 2011). For the purpose of quantifying early life history diversity of juvenile salmon, it would not be useful to calculate beta diversity nor partition gamma diversity into alpha and beta components (Jost, 2007 and Veech and Crist, 2010). Alpha and gamma diversity were determined to be most applicable to our investigation, because our primary focus is on quantification of ELHD for a locale or region and making comparisons across locales (not calculations of beta diversity), although we make no further distinction between them because they quantify the same phenomenon, albeit at different scales (Jurasinski et al., 2009).

Diversity consists of two elements: richness (number of species) and evenness (proportional distribution of abundance among the species) (Hurlburt, 1971; Pielou, 1966, and Tuomisto, 2012). Diversity increases as richness and/or evenness increase (Frosini, 2004). Richness alone is informative and has been used as a surrogate for diversity, although Wilsey et al. (2005) noted this is improper because it fails to account for evenness. Soininen et al. (2012) note that in aquatic ecosystems richness and evenness may respond to different environmental conditions, supporting the notion that reliance on richness alone is not an appropriate surrogate for diversity. Evenness is critical to measuring diversity of juvenile salmon because it incorporates fish abundance or density data and proportional frequency distributions. Expressions for ELHD richness and evenness are provided below.

The final ecological concept needed to establish an ELHD index regards the effective number of species, which is the same as saying the number of equally common species, and is also called "true" diversity (Jost, 2006 and Tuomisto, 2011). The concept of effective number of species was proposed by MacArthur (1965) and further espoused by Hill (1973), Jost (2006, 2007), Tuomisto (2010), and others. Notably, many refer to effective or true diversities as "Hill numbers" after his seminal paper. This is an important concept because most of the diversity indices available in the literature are in fact measures of probabilities or entropies (the uncertainty in the outcome of a sampling process; Jost, 2006), not diversities (Jost, 2006). Examples include the popular Shannon, Simpson, Gini-Simpson, and Renyi indices (Jost, 2006). These indices are generally not comparable to one another, or, for a given index, not comparable across space and time. Nor are they easily interpreted. Based on the literature we studied, we concluded that converting diversity indices to the effective number of species (as described in Section 2.2.2) is an integral step in quantifying ELHD.

For our purpose, the term "species" refers to a combination of categories of early life history traits. That is, each unique combination of early life history traits as used here is analogous to a unique species as used in the conventional sense of diversity. For example, assume we have 5 size classes (Z_1,...,Z_5) and 12 time classes (M_1,...,M_{12}), then the combination of Z_3 and M_5 represents a "species." Thus, after conversion to an effective number of species, an ELHD index value can be interpreted as the *number of equally common time-size trait combinations* representing early life history diversity.

2.2.2. Proposed ELHD indices

For an ELHD index, we adopt the concept of effective number (MacArthur, 1965) of time-size trait combinations and its generalized form (^qD) known as the Hill number (Hill, 1973; Tuomisto, 2010, Eq. (4)). The generalized form for effective number of time-size trait combinations (^qELHD) is

$$^qD = {}^qELHD = \left(\sum_{i=1}^{T} p_i^q\right)^{1/(1-q)} \tag{1}$$

where, q is the order, p_i is the proportion of total abundance for the ith time-size trait combination, and T is the total number of possible time-size trait combinations (after Jost, 2006, Eq. (1)).

The parameter q, the order for the diversity estimator, is pivotal in the calculation (Keylock, 2005). When $q < 1$, rarer time-size trait combinations are emphasized in the diversity value, as opposed to emphasizing the dominant species when $q > 1$. When $q = 1$, diversity is weighted by the proportion of abundance and does not favor rarer or more abundant time-size trait combination. Note, $q < 0$ causes the effective number of time-size trait combinations to exceed the actual number; therefore, $q < 0$ is not used due to the potential for erroneous results. Values of $q > 2$ are not common. To develop an ELHD index for juvenile salmon, we applied diversities for $q = 0$, 0.5, 1, and 2.

For $q = 0$, *ELHD* is equivalent to richness (S) of time-size trait combinations. Note, $S \leq T$ because the number of observed time-size trait combinations (S) may be less than the number of possible time-size trait combinations (T). The equation for richness is

$$^0ELHD = \left(\sum_{i=1}^{S} p_i^0\right) = S \tag{2}$$

For $q = 0.5$, *ELHD* reflects a deliberate focus on rarer time-size trait combinations as follows

$$^{0.5}ELHD = \left(\sum_{i=1}^{S} p_i^{0.5}\right)^2 \tag{3}$$

For $q = 1$, *ELHD* is based on the Shannon Index, also known as the Shannon-Wiener Index or the Shannon-Weaver Index (Spellerberg and Fedor, 2003). This commonly used index quantifies the uncertainty in the identity of a randomly chosen individual (Tuomisto, 2012). When $q = 1$, the generalized form is undefined, but its limit exists and equals the exponential function of the Shannon Index, expressed as

$$^1ELHD = \exp\left(-\sum_{i=1}^{S} p_i \ln(p_i)\right) \tag{4}$$

For $q = 2$, *ELHD* is the inverse of the geometric mean of the proportional abundances. This mean proportional abundance is also known as the Simpson concentration (Jost, 2006). The equation for *ELHD* of order 2 is

$$^2ELHD = \left(\sum_{i=1}^{S} p_i^2\right)^{-1} \tag{5}$$

The popular Gini-Simpson index is one minus the Simpson concentration (Jost, 2006) and reflects the probability of two random individuals not belonging to the same time-size trait combination (Tuomisto, 2010).

2.2.3. Richness and evenness

Richness (S) was defined above as *ELHD* when $q = 0$. Following Pielou's (1966) evenness concept, evenness can be expressed as

$$^qELHD_{even} = \frac{^0ELHD}{^qELHD} \tag{6}$$

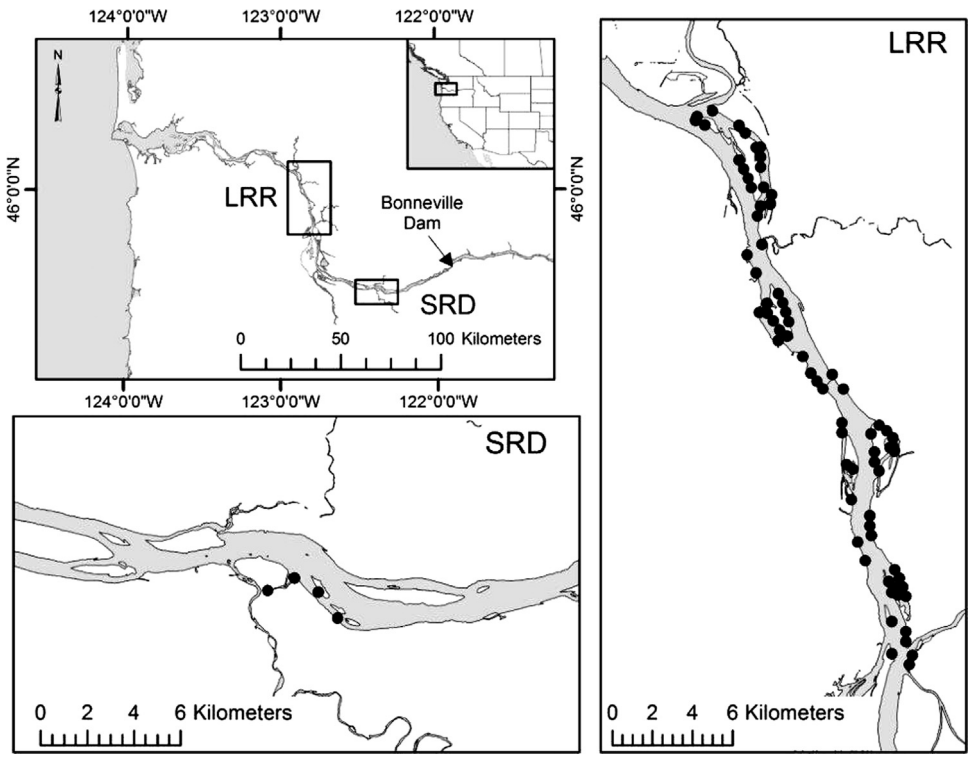

Fig. 2. Case study data collection locations: (top left panel) sampling areas in LCRE tidal freshwater; (bottom left panel) site-scale sampling sites (N, C, E, B) in the Sandy River delta (SRD, rkm 200); (right panel) landscape-scale sampling sites (yellow dots) in the Lower River Reach (LRR, rkm 110–141).

2.2.4. Normalization

Normalization converts the ELHD index to a value between zero and one by dividing the index by the maximum ELHD value possible. The maximum is the total number of possible time-size trait combinations, whether they are observed or not. This is necessary for determining the diversity values for juvenile Chinook salmon because it accounts for zeros in a data set, which is a likely occurrence given combined biotic and environmental variability in aquatic environments. Zeros are ignored in the computation of ${}^{q}ELHD$. Normalization puts the index in a common, understandable range (0–1). One can easily interpret a value of 0.75 as meaning ELHD is 75% of the total possible time-size trait combinations. For a given q (0.5, 1, or 2), the equation is

$$ {}^{q}ELHD_{norm} = \frac{{}^{q}ELHD}{T} \tag{7} $$

2.2.5. Chao–Shen modification

Richness, and therefore diversity, depends on sample size (Hurlburt, 1971). Ecologists use rarefaction techniques to account for sample size differences in richness measures (Olszewski, 2004). For the Shannon Index, which incorporates richness and evenness, Chao and Shen (2003) developed a nonparametric estimator that "makes sampling criticisms less relevant" (Jost, 2007). Their estimator incorporates the Horvitz–Thompson adjustment (Horvitz and Thompson, 1952) for missing species and a factor to account for the level of sample effort. The equation for ELHD, modified from (Chao and Shen, 2003; their Eq. (8)) to use our terms and transformed into a true diversity using Eq. (4) above, follows

$$ {}^{1}ELHD_{\mathrm{mod}} = \exp\left(-\sum_{i=1}^{T} \frac{\hat{C}p_i \log(\hat{C}p_i)}{1-(1-\hat{C}p_i)^{n}} I(A_i) \right) \tag{8} $$

where, n = number of individuals sampled, $\hat{C} = 1 - (f_1/n)$, f_1 = number of time-size trait combinations with one individual sampled, and $I(A_i) = 1$ when the event is true and 0 when it is false, thereby preventing division by zero.

3. Case studies

3.1. Description

We used case studies to examine whether the ELHD indices capture and portray attributes of the early life history of Chinook salmon in a meaningful and useful manner. An initial examination of a simulated data set revealed basic features of the indices. We then developed three case studies representing a variety of possible ELHD index (q = 0.5, 1, and 2) applications for juvenile salmon abundance or density data: monthly sampling, site-scale data; seasonal sampling, landscape-scale data; and genetic stock composition data (Fig. 2, Table 1). This section closes with a comparison of ${}^{1}ELHD$ and ${}^{1}ELHD_{\mathrm{mod}}$.

The case study data are from beach seine samples collected to examine the migration characteristics of juvenile salmon in the shallow tidal freshwater in the LCRE (Fig. 2) (Sather et al., 2011, 2012, and unpublished data). The number of matrix cells (combinations of trait categories) per ELHD calculation ranged from 4 for the Lower River Reach case study to 48 for the Sandy River delta case study (Table 1). Total sample sizes, expressed as the total number of unmarked juvenile Chinook salmon used in a given case study, were 1896 for the Sandy River delta, 4085 for the Lower River Reach, and 523 for the genetics case study. We present additional details about sampling methods under each case study.

3.2. Simulated data

To probe the indexing approach, we analyzed simulated data scenarios using the same total density (50 fish/m^2) for three diversity orders (q = 0.5, 1, 2), where the scenarios include extreme situations of species richness and evenness levels: rich and even;

Table 1
Sample characteristics for the case studies.

Case study	Number of index dimensions (trait combinations)	Number of matrix cells per ELHD Calculation	Total number of sites sampled	Total number of unmarked juvenile Chinook salmon sampled
Simulated	1 (Species)	10	NA	50
Sandy River delta	2 (Timing and size)	48	4	1896
Lower River Reach	1 (Size)	4	77	4085
Genetics	2 (Timing and size)	32	77	523

Table 2
Simulated data for ten species (top panel) and *ELHD* results (bottom panel) with three diversity orders ($q = 0.5, 1, 2$) for four scenarios: (1) rich and even; (2) half as rich and even; (3) rich but uneven; (4) somewhat rich and somewhat uneven.

Species Id.	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Abundance (proportion)				
A	5 (0.1)	10 (0.2)	41 (0.82)	20 (0.4)
B	5 (0.1)	10 (0.2)	1 (0.02)	10 (0.2)
C	5 (0.1)	10 (0.2)	1 (0.02)	6 (0.12)
D	5 (0.1)	10 (0.2)	1 (0.02)	5 (0.1)
E	5 (0.1)	10 (0.2)	1 (0.02)	4 (0.08)
F	5 (0.1)	0	1 (0.02)	3 (0.06)
G	5 (0.1)	0	1 (0.02)	1 (0.02)
H	5 (0.1)	0	1 (0.02)	1 (0.02)
I	5 (0.1)	0	1 (0.02)	0
J	5 (0.1)	0	1 (0.02)	0
Total	50 (1.0)	50 (1.0)	50 (1.0)	50 (1.0)
q	${}^{q}ELHD$ (${}^{q}ELHD_{norm}$)			
0.5	10.0 (1.0)	5.0 (0.5)	4.75 (0.47)	6.52 (0.65)
1	10.0 (1.0)	5.0 (0.5)	2.38 (0.24)	5.48 (0.55)
2	10.0 (1.0)	5.0 (0.5)	1.48 (0.15)	4.25 (0.43)

half as rich and even; rich but uneven (skewed); and, somewhat rich and somewhat uneven. For perfectly even distributions (Scenarios 1 and 2), ELHD equaled the total number of species (richness) for each of the three q-orders (Table 2). In the scenarios in which an uneven number of species was portrayed, ${}^{0.5}ELHD$ was always greater than ${}^{1}ELHD$, which was always greater than ${}^{2}ELHD$. Scenario 3 maintained the same richness as Scenario 1 ($S = 10$) but was extremely uneven to one dominant species and nine rare species. In this scenario, unevenness resulted in reduced index values compared to the even case (Scenario 2); using ${}^{1}ELHD$ as an example, the index value for Scenario 3 (uneven) was 52% of that for Scenario 2 (even). The effect of $q = 0.5$ resulted in a diversity value of 4.75, over three times as high as ${}^{2}ELHD$ of 1.48 in Scenario 3. The diversity values for Scenario 4 with $S = 8$ and moderate skew were greater than those for Scenario 3, reflecting the contribution of increased evenness in Scenario 4. Normalization (${}^{q}ELHD_{norm}$) resulted in patterns similar to ${}^{q}ELHD$; normalized values ranged from 0 to 1, as expected.

3.3. Monthly sampling, site-scale data

We collected site-scale juvenile Chinook salmon density data at the Sandy River delta (Fig. 2) using a beach seine during 47 months from January 2008 through August 2012. This particular data set included only unmarked fish, as determined by intact adipose fins and the absence of a coded wire tag. Density estimates for the four recurring sampling locations in the Sandy River delta were totaled by size class for each month. The resulting month (47) by size class (4) matrix of densities, i.e., the combinations of time and size traits, was used to calculate ${}^{q}ELHD$ for each year 2008–2012. Over the 47 months of data, total density of unmarked juvenile Chinook salmon was highest for the <61-mm fork length size class (2.11 fish/m^2), intermediate for the 61–90-mm and 91–120-mm classes (0.50 and 0.14 fish/m^2, respectively), and lowest for the >120-mm size class (0.01 fish/m^2). There were zero values in 59% of the 188 cells in the matrix.

At the Sandy River delta, ${}^{q}ELHD$ was highest during 2010 and lowest during 2012 (Fig. 3). Note, however, monthly sampling effort among years was not equal; e.g., 2012 has lowest diversity values and was incompletely sampled (only 19 site-month sampling events). Rare traits appear dominant for 2010 at the Sandy River delta compared with other years. For the three diversity orders ($q = 0.5, 1, 2$), the values for ${}^{q}ELHD$ were always highest for $q = 0.5$ and lowest for $q = 2$, although their magnitudes varied depending on the year. The richness values ($q = 0$) followed the same trend as the ${}^{q}ELHD$ values. When normalized, ${}^{q}ELHD$ was lowest for 2008 instead of 2012.

3.4. Seasonal sampling, landscape-scale data

Across the 31-km landscape of the Lower River Reach (Fig. 2), beach seine samples were collected for the purpose of estimating juvenile salmon densities (Sather et al., 2012). Sampling at 15–18 locations each season was conducted using a random-stratified, rotating-panel design (Skalski, 2011). Density estimates for unmarked juvenile Chinook salmon were averaged across the sampling locations for each size (fork length) class for each season sampled. The season (12) by size class (4) matrix representing the early life history trait combinations includes 48 cells. We calculated ${}^{q}ELHD$ for each seasonal sampling episode using density data combined over all sampling locations.

During winter 2009 at the Lower River Reach, ${}^{q}ELHD$ was higher than all other sampling events during all years (Fig. 4). ${}^{q}ELHD$ increased from winter-spring to summer months in 2009, 2010, and 2012 (summer was not sampled in 2010). Large differences in diversity between ${}^{0.5}ELHD$ and the two other q-levels were apparent in winter (February) 2010, 2011, and 2012. The richness values ($q = 0$) were 3 or 4, reflecting the number of size classes represented in a given season. Normalized diversities were highest for the three q-levels (0.5, 1, and 2) at 0.86, 0.76, and 0.63, respectively, in January 2009.

3.5. Genetic stock composition data

Genetic stock identities were estimated for a subset ($n = 523$) of juvenile Chinook salmon captured during eight seasonal Lower River Reach sampling episodes (Sather et al., 2012). The five most common stocks were West Cascade Fall, West Cascade Spring, Willamette Spring, Spring Creek Fall, and Upper Columbia Summer/Fall. Density data for unmarked juvenile Chinook salmon were apportioned into season (8) by size class (4) combinations for each of the five genetic stocks. The resulting five, 32-cell matrices had a combined total of 65% zeros. For this case study, we chose to calculate diversity within a given stock with genetic stock identification data, although it would have been equally informative to examine the diversity of stocks for different time periods. The West Cascade Fall group had the highest ${}^{q}ELHD$ (11.7) compared to other stock groups in the Lower River Reach (Fig. 5). For $q = 0.5$, the lowest diversity was for the Spring Creek Fall group (4.7). Rare trait combinations were most predominant in West Cascade Fall and Upper Columbia Summer/Fall groups. Normalizing reduced the differences among q-levels.

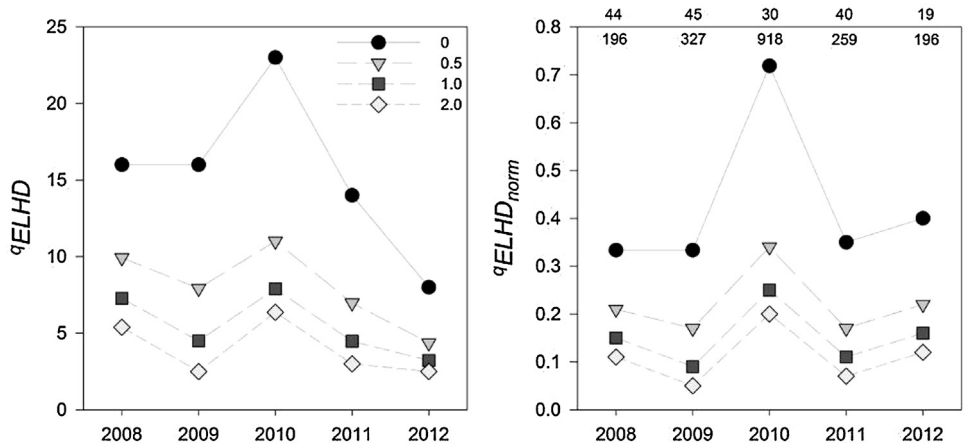

Fig. 3. Yearly *ELHD* diversities (left panel) and normalized diversities (right panel) using the time (month) by size class trait combinations for three diversity orders ($q = 0$, 0.5, 1, 2) for site-scale data from the Sandy River delta collected during 47 monthly sampling episodes from January 2008 through August 2012. At the top of the right panel, the rows above and below the line contain the number of site-month sampling events and the total number of juvenile Chinook salmon used in the index, respectively, for a given study year.

3.6. Chao–Shen modification

Using the Sandy River delta data to compare the true diversity for the Shannon entropy (^1ELHD) and the modified version ($^1ELHD_{\mathrm{mod}}$) based on Chao and Shen (2003) revealed that values of the latter equal about one-third those of the former (Table 3). The trends across years were similar between the two methods.

4. Discussion

4.1. Overview

Indices collapse data into a single value resulting in simplification of the underlying information. In ecology, Green and Chapman (2011) assert the interactions between biotic and abiotic elements

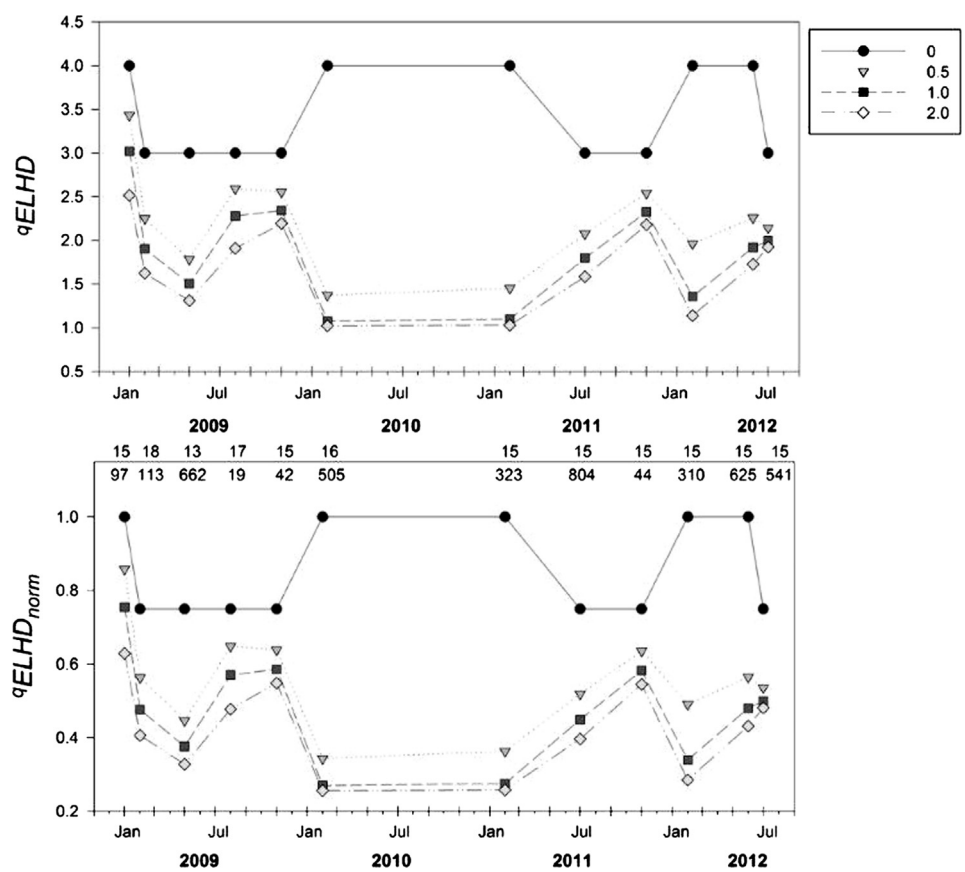

Fig. 4. Seasonal *ELHD* diversities (top panel) and normalized diversities (bottom panel) using the size class trait for three diversity orders ($q = 0$, 0.5, 1, 2) for landscape-scale data from the Lower River Reach collected in 12 seasonal sampling episodes from January 2009 through July 2012. In the bottom panel, the numbers along the upper border contain the number of site-month sampling events (above the border) and the total number of juvenile Chinook salmon (below the border) used in the index for a given sampling episode.

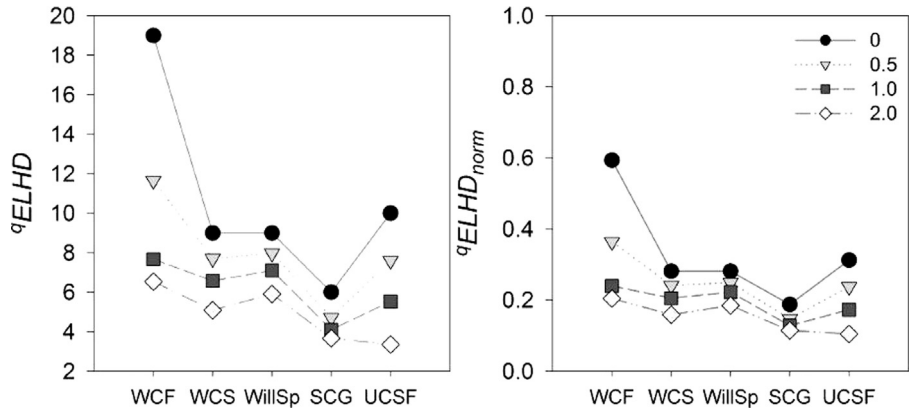

Fig. 5. *ELHD* diversities (left panel) and normalized diversities (right panel) for five genetic stocks using season by size class trait combinations for all sampling episodes combined for three diversity orders (q = 0, 0.5, 1, 2) for landscape-scale data from the Lower River Reach collected in eight seasonal sampling episodes from January 2009 through July 2011. Genetic stock groups are defined as follows: WCF = West Cascade Fall, WCS = West Cascade Spring, WillSp = Willamette Spring, SCG = Spring Creek Group, and UCSF = Upper Columbia Summer/Fall.

Table 3
Parameters and results for the Chao–Shen modification to the Shannon entropy as applied to yearly *ELHD* diversities using the timing (month) by size class trait combinations for site-scale data from the Sandy River delta. Notation: f_1 = number of species with one individual sampled, n = number of individuals sampled, $\hat{C} = 1 - (f_1/n)$.

Year	f_1	n	$\hat{C}$	${}^1ELHD$	${}^1ELHD_{mod}$
2008	3	196	0.9847	7.73	2.49
2009	3	327	0.9908	9.54	2.70
2010	7	918	0.9924	7.70	2.46
2011	3	259	0.9884	6.81	2.34
2012	2	196	0.9898	3.87	1.83

across numerous spatial and temporal scales are too complex to be simplified into a numerical index. This depends on the purpose of the index and the underlying data used for calculations. In some cases, indices are useful for the purpose of generating simple, interpretable values to communicate to the public, such as conveying financial and economic data. Our contention is that an index designed to serve a specific purpose can be useful as long as it is not taken out of context and misused; this point is pertinent to the ELHD index.

We developed an approach to index the ELHD of juvenile Chinook salmon. This was accomplished by first characterizing early life history traits and prioritizing *time* and *size* as two appropriate, and readily measurable dimensions for an ELHD index. Within the context of these selected traits, we then identified an approach based on the effective number of species (Jost, 2006 and Tuomisto, 2012) and adapted it for use on juvenile Chinook salmon in the LCRE. Finally, we tested several variations of the "true diversity" calculations for performance and usefulness, in case studies using juvenile Chinook salmon catch data from the LCRE. We were able to make reasonable interpretations of ELHD index values calculated for the case studies. The case studies showed the following:

- ${}^0ELHD > {}^{0.5}ELHD > {}^1ELHD > {}^2ELHD$ for all scenarios;
- all four q-levels produced tractable, understandable ELHD values;
- ${}^0ELHD$, the richness of time-size trait combinations, was informative and would be useful if only fish presence-absence data could be obtained;
- sensitivity of ${}^{0.5}ELHD$ to rarer time-size trait combinations was evident;
- as expected, patterns in the results were similar before and after normalization;
- normalization was useful because it produced proportions of maximum diversity that were easy to understand and interpret while accounting for zero observations in a data set;
- time-size trait combinations made sense biologically for the early life history phases of Chinook salmon;
- an ELHD index based on the effective number of time-size trait combinations appears to have utility irrespective of q-level; and
- the Chao and Shen modification has promise by accounting for unequal sample sizes.

4.2. Limitations and cautions

We recognize that relying on two early life history traits, timing and size, presents a simplified view of the early life history of juvenile salmon. The selection of these traits for the ELHD index was based on well-established characteristics (Bottom et al., 2005a and Groot and Margolis, 1991), and the particular size class distinctions we made (<61 mm, 61–90 mm, 91–120 mm, >120 mm) used the best available data for juvenile Chinook salmon in the LCRE (Campbell, 2010; Sather et al., 2011; Roegner et al., 2012). Nevertheless, the size class distinctions for LCRE applications may need further evaluation as new data on age structure and location of capture become available. For applications of the ELHD index in regions outside the LCRE, such as Puget Sound or Columbia River basin tributaries, it will be necessary to reassess the juvenile salmon size (length) classes.

An important consideration for calculating and interpreting the ELHD index is its dependence on sampling method and sample coverage. Differences in sampling methodologies are driven by research objectives as well as sampling locations, which will ultimately influence fish catch rates and detection of life history trait combinations. For example, in a given habitat such as a shallow water wetland, a snorkel survey and a beach seine may produce different results for densities and size class distributions. Each method is inherently biased for fish capture/encounter rate and efficiency, which may result in under- or over-valuing of ELHD indices. On the other hand, consider a hypothetical situation with beach seine sampling in shallow tidal freshwater habitats compared to purse seine sampling in the main channel adjacent to the beach seine site. The data on salmon species and their timing and size class distribution will likely be different between the two habitats because of an ontogenetic shift in habitat selection as juvenile salmon become bigger (Dawley et al., 1986; Levings, 1982; Levings et al., 1986, and Pearcy et al., 1989). Therefore, even though the sampling methods differ, a valid comparison of ELHD index values may be possible. Regarding sample coverage, it is well known that species richness,

and therefore diversity, is related to sample size (Magurran, 2004). In our site-scale case studies, we purposefully included the incomplete sampling from 2012 to demonstrate this point; only 5 of 12 months were sampled and the ELHD values were low compared to 2008–2011 (Fig. 3).

The presence of hatchery-origin fish in samples would likely affect the diversity values and confound their interpretation. Hatchery fish typically have a relatively narrow size frequency distribution and are released in large quantities in a short period of time. Such practices would influence the ELHD index we developed, which relies on timing and size trait combinations. The presence of hatchery fish also validates not using an ELHD index with diversity order $q = 2$, because of its emphasis on dominant size classes in the samples.

4.3. Application considerations and further development of the ELHD index

Based on the limitations and cautions described above, we offer the following suggestions for best practice when applying the ELHD index: (1) distinguish between hatchery- and wild-origin juvenile salmon; (2) differentiate among juveniles from different sources or stocks, to the extent feasible because technical improvements in genetic analyses provide increased identification accuracies (e.g., Hess et al., 2011); (3) clearly define ELHD index dimensions; (4) document the source data; and (5) compare index values using data sets generated with similar or comparable methods and sampling designs.

The ELHD index can be applied at various locales or habitats. Examples of sampling approaches and locations in which the ELHD index can be applied include studies to assess migration characteristics using screw traps in interior basin tributaries, juvenile bypass sampling systems at a main-stem dams, purse seines in lower estuary and main-stem channels, and trap nets in a tidal wetlands. Specifically, we recommend testing the ELHD index with existing and new smolt monitoring data from Bonneville Dam (Martinson et al., 2006), screw trap data from the Snake and Willamette River tributaries (Keefer et al., 2011), and purse seine research at the mouth of the Columbia River (Weitkamp et al., 2012). Other existing collections of data (e.g., Dawley et al., 1986) might also be examined to establish historical trends using the ELHD index. Such investigations will help managers and researchers understand the utility of the ELHD index, especially in the context of the limitations and cautions mentioned previously. Comparisons of ELHD index values, however, should be made carefully and methods to account for unequal sample sizes should be applied. As (Tuomisto, 2010, p.858) said, "To obtain meaningful results on diversity, comparisons have to be limited to similar datasets. . .".

The index we developed provides one approach to evaluating the change in aspects of juvenile salmon life history diversity through time and could serve as a high-level indicator in large-scale ecological restoration efforts. For example, it has regional applications to the Northwest Power and Conservation Council's Fish and Wildlife Program, where a high-level indicator is defined as a quantitative metric used to communicate progress. The Independent Scientific Advisory Board reviewed the Council's high-level-indicator effort and recommended more emphasis on diversity as opposed to abundance (ISAB, 2012a,b). Although the importance of diversity has been recognized, high-level-indicator for it has not yet been identified; the ELHD index could fill this need. For example, the ELHD index may offer a mechanism for tracking responses to hatchery reform, a current management need in the Columbia River basin (ISAB, 2012a).

Although the case studies involved in the development of the index applied one or two dimensions, multiple index dimensions are possible. We presented seasonal ELHD for the size class trait (one dimension, Fig. 4) and yearly ELHD for the timing by size class trait combinations (two dimensions, Fig. 3). We also demonstrated that other dimensions can be incorporated by using genetic stock identification for Chinook salmon. The dimensions are necessarily crossed with proportional frequencies being computed for each cell out of the total in a multi-dimensional matrix. In our case, the trouble with more than two dimensions is the increased likelihood of zero observations. Thus, while multiple index dimensions are mathematically possible, there are practical reasons for simplifying matters and using one or two dimensions, although this will depend on the application and data at hand. The choice of dimensions in an ELHD index is flexible, but must be specified clearly and a given dimension must be measurable for individual fish. A comprehensive diversity index relying solely on salmon species as a dimension is also feasible. Furthermore, future ELHD indices might include additional attributes of early life history, such as weight, fish condition, or residence time. Incorporating additional traits into the index calculations is possible as long as the traits can be measured from individual fish and valid inferences can be made to the population level, which depends largely on the sampling scheme. Finally, there is need for additional research connecting differing life history types with growth and survival.

5. Conclusion

The ELHD indices are applicable for evaluating life history strategies of juvenile Chinook salmon using readily measurable traits of migration timing and fish size. The approach incorporates fish abundance, richness, and evenness. The ELHD values were understandable and interpretable, and should support comparisons across like locales and examinations of trends through time at a given locale. We recommend ${}^{1}ELHD_{\mathrm{mod}}$ for use as an index of early life history for Chinook salmon based on fish density data by timing-size trait combinations for the following reasons. First, ${}^{2}ELHD$ places more emphasis on dominant time-size trait combination than we believe is warranted for an index intended to track improvements (increases) in ELHD from restoration and other management actions to benefit diminished Chinook salmon populations. Second, ${}^{0.5}ELHD$ is attractive because of its sensitivity to the abundance of rarer time-size trait combinations, thereby reflecting early life histories that fisheries managers are trying to recover. An issue with ${}^{0.5}ELHD$, though, is its lack of an approach to account for sample coverage. Most collections of juvenile salmon end up with unequal sample sizes despite the best intentions and sampling designs. Third, the Chao–Shen modification accounts for unequal sample sizes and was strongly positively correlated with ${}^{2}ELHD$, the index upon which the modification was based. In conclusion, we recommend applying ${}^{1}ELHD$ using Chao and Shen's (2003) nonparametric estimator, although in situations where fish density data are not available, but presence-absence data are, ${}^{0}ELHD$ could be applied.

The recommended ELHD index offers a quantitative approach for evaluating biologically relevant life history attributes of juvenile Chinook salmon, and is based on the best available science. Careful consideration of data limitations when applying this tool is essential because of the complex and highly variable biotic and abiotic conditions associated with juvenile salmon and their environments. Future applications of the ELHD index should demonstrate its value as a long-term, high-level indicator of salmon performance in the LCRE, the Columbia River basin, and potentially other regions where recovering salmon life history diversity is a goal.

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