An assessment of terminology for intra-specific diversity, with a focus on "ecotypes" and "life histories"

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Abstract

Understanding and preserving intra-specific diversity (ISD) is important for species conservation. However, ISD units do not have taxonomic standards and are not universally recognized. The terminology used to describe ISD is varied and often used ambiguously. We compared classical and authoritative definitions of terms used to describe ISD with terms used in recent studies of three fish taxa: sticklebacks (Gasterosteidae), Pacific salmon and trout (Oncorhynchus spp., "PST"), and lampreys (Petromyzontiformes). Our review revealed the terminological ambiguity of "races" and "subspecies", found similar definitions of "subspecies" and "ecotype", and of "ecotype" and "reaction norms". "Species pairs" describes two phenotypes; however, in some situations more than one phenotype may occur. "Ecotype" was originally used to describe patterns in genes and ecology, and recent studies employing this term tend to report a genetic basis in ISD. Ecotype is used most frequently in genetic- and evolution-based journals. By contrast, "life history" includes biological parameters that affect population growth and decline, and this term tends to be used in organismal- and ecology-based journals. When the genetic or demographic components of ISD are not well understood, a conservative approach would be to refer to expressions of this diversity as "phenotypes". The nature of human interests in particular taxa could influence how these organisms are studied, and hence the ways in which their ISD is understood, described, and conserved.

Introduction

It is incumbent on any scientist, no matter the field of inquiry, to adhere to (or at least specify) definitions. (Patten 2015)

Intra-specific diversity (ISD) represents the "evolutionary potential within a species" (Haig et al. 2006) and understanding and preserving this diveristy is an important conservation goal (Ford 2004). However, units of ISD do not have taxonomic standards, are not universally recognized, and thus are more contested than species (Ginsburg 1937; Hubbs 1943; Haig et al. 2006; Patten 2015). Intra-specific diversity can be challenging to understand, given the variable roles of phenotype, genotype, and phenotypic plasticity (interactions of the genotype with the environment): $\text{Variability}_{\text{Phenotype}} = \text{Variability}_{\text{Genotype}} + \text{Variability}_{\text{Environment}} + \text{Variability}_{\text{Genotype X Environment}}$ (DeWitt and Scheiner 2004). Some researchers use holistic assessments of phenotypic expression relative to genotype and particular environments. However, an easier, and therefore more common strategy among researchers is to focus on components of this relationship. Given these challenges, it is perhaps not surprising that the terminology for describing ISD is often used ambiguously. The ambiguous use of terminology to describe ISD ironically creates another impediment to understanding and thus preserving this diversity.

The scientific literature includes a plethora of terms to denote ISD. These include morphotypes (Lessios and Weinberg 1994; Chavarie et al. 2013; Collyer et al. 2015); ecotypes (Gregor 1944; Arostegui et al. 2018; Cruz-Font 2019); species pairs (Taylor 1999); satellite species (Salewski 2003); ecomorphotypes (Baker et al.

1998; Segura-Trujillo et al. 2018; Kloh et al. 2019); ecophenotypes (Schönborn and Peschke 1988; Sorensen and Lindberg 1991; Proćków et al. 2018); polymorphisms (Skúlason and Smith 1995; Skúlason et al. 2019; Jamie and Meier 2020); and life histories (Stearns 1989; Winemiller and Rose 1992). Several of these terms have common roots, and are often used inter-changeably or in combination (e.g., Baker et al. 1998; Chavarie et al. 2013; Brannon et al. 2004; Wood et al. 2008; Palacios et al. 2012). The use of these terms may suggest perceived or actual novelty, a unique take on biological phenomena, or an attempt to follow precedents of other published works. Although a diverse terminology can be useful in describing the existing diversity of evolved or expressed phenotypes, careful use of terms could improve knowledge transfer and clarity of understanding among scientists, policy makers and fisheries managers. Here, we assess the use of terms to describe ISD in the peer-reviewed scientific literature. We focused on two ISD terms that we believe have been used inconsistently and interchangeably — life histories and ecotypes.

Our goals were to assess the terminology for ISD and make recommendations for future use of these terms. Our four objectives were to: 1) define key terms for intra-species diversity using classical and authoritative sources that set a precedent and articulate clear definitions; 2) provide a meta-review of evolution, traits, and ISD for the three aforementioned taxa; 3) analyze trends over the last three decades (1990 – 2019) in the use of the terms "life history" and "ecotype" in the peer-reviewed literature; and 4) compare the authoritative definitions with the trends in use of life history and ecotypes and make recommendations on future term use. For objectives 2 and 3, we focused on three fish taxa, including sticklebacks (Gasterosteidae), Pacific salmon and trout (*Oncorhynchus* spp., herein, "PST"), and lampreys (Petromyzontiformes) that represent a rich history of classical ecology and evolutionary studies (Bell and Foster 1994; Woottton 2009; Hendry et al. 2013; Groot and Margolis 1991; Hendry and Stearns 2004; Quinn 2005; Hardisty 2006; Docker 2015; 2019; Orlov and Beamish 2016a, b).

Methods

Objective 1: Definitions

We found authoritative uses of the terms ecotypes and life history in the literature. In papers that make a distinction across various animal taxa, we focused on information provided for fishes, for example as by Haig et al. (2006). Our literature search included locating the first use of the term "ecotype" in the early 1900s and key publications by Stearns (1992), who is a recognized authority on life history studies in animals. In addition, we found authoritative definitions for other terms that have been used synonymously with ecotype and life history.

Objective 2: Meta-review of fish taxa

We conducted broad and succinct reviews of sticklebacks, PST, and lampreys that focused on books, book chapters, review articles, and other peer-reviewed literature to provide and describe the number of species, their evolution, trait diversity, and use of terms to describe ISD. We chose to do a meta-literature review because the exponential increase in articles for these species (e.g., Wootton 2009) rendered exhaustive reviews untenable for the scope of this paper.

Objective 3: Trends in use of "life history" and "ecotype"

We conducted three independent searches for the use of the terms, "ecotypes" and "life history" for sticklebacks, PST, and lampreys using the advanced search option in the Web of Science search engine for articles in English, over 30 years (for years 1990 – 2019). Each search included the words "stickleback" or "*Oncorhynchus* " or "lamprey", with at least one of the words "ecotype life history" in the title of the article, using the operators: (TI=(ecotype OR life history) AND TI=(stickleback)). The same was done for "*Oncorhynchus* " and "lamprey". These searches were executed between November of 2020 and February of 2021. Each article was reviewed to determine the focal species and phenotypes assessed; whether a genetic basis was identified for the diversity in phenotypes; and whether an article used both terms (ecotypes and life history) interchangeably; or both, but independently; or used only one of the terms. Finally, the frequency of term use was calculated and compared among papers.

Objective 4: Compare definitions with term use and make recommendations

We compared classical and authoritative definitions (Objective 1) with the meta-review (Objective 2), and trends in use of the terms ecotypes and life history (Objective 3). We addressed the questions: Are there clear patterns in how terms are used in particular contexts? Do redundancies or ambiguities exist in the use of some terms that suggest that some terms ought not to be used?

Results and Discussion

Objective 1: Definitions

In our search for classical and authoritative definitions of ecotype and life history, it became apparent that several terms are used more-or-less synonymously (e.g., "species pairs", "ecotypes", and "life histories" in Taylor 1999 and "races", "phenotype", "types", and "subspecies" in Brannon et al. 2004). This entanglement of phenotypic terms was noted over eight decades ago: "The questions of what is a species, or a subspecies, any classificatory category of specific or lower rank, cannot be disassociated from one another" (Ginsburg 1937).

We compiled definitions of common terms used to describe ISD (Table 1). Generic terms used to describe ISD include "form" and "type" (Table 1). Our review revealed the ambiguity of terms such as "races" and "subspecies", and the extent to which these two terms appear to be used less by scientists now than in the past. Classification of subspecies is controversial among taxonomists (Haig et al. 2006; Patten 2015; de Queiroz 2020), and a common accepted definition of the subspecies remains elusive (Haig et al. 2006). Subspecies have recently been defined as components of a species that are incompletely speciated (Patten 2015; de Queiroz 2020; Table 1). We also found an overlap in definitions between subspecies and ecotypes, and a striking similarity between the terms, ecotype and reaction norms. Ecotype was originally used to describe patterns in traits (genes) and ecology in the early 1900s (Turesson 1922; Gregor 1944). Life history, by contrast, includes biological parameters that affect abundance and population growth or decline, including parameters related to birth, survival, reproductive timing, reproductive investment, and mortality (Stearns 1992). The terms paired species/species pairs have been used to describe a dichotomy of two different phenotypes such as benthic versus limnetic sticklebacks or freshwater resident kokanee versus anadromous sockeye salmon (*O. kisutch* ; Taylor 1999) and freshwater resident, non-feeding brook lampreys vs. anadromous and parasitic lampreys (Salewski 2003; Docker 2009; Docker and Potter 2019). The term, satellite species is generally used to describe situations in which one lamprey species yields two or more derived species (Vladykov and Kott 1979; Salewski 2003; Docker 2009). Evolutionary Significant Units (ESUs) have been used primarily for PST.

Objective 2: Meta-review of fish taxa

Sticklebacks

Research on sticklebacks has focused primarily on one species, the threespine stickleback, *Gasterosteus aculeatus* , with fewer studies on ninespine stickleback, *Pungitius pungitius* (e.g., Table 2). Within species, the divergence of populations is suggestive of population structuring. The threespine stickleback has been a model organism for studying behavior, host-parasite relationships, morphology, evolutionary ecology, and speciation (e.g., Bell and Foster 1994; McKinnon and Rundle 2002; Baker et al. 2008; Hendry et al. 2009, 2013; Wootton 2009; Schluter 2010). The overall trend with studies on the threespine stickleback has been the identification of numerous species, followed by lumping into one species, followed by a return to splitting the phenotypes back out into individual species in some geographical areas.

In the early 1900s, taxonomists struggled with the wide phenotypic diversity of threespine stickleback and several phenotypes were initially believed to be separate species (Wootton 2009). This diversity is captured in the following quote: "Race ranking may be accorded forms, like local types of *Gasterosteus aculeatus* , which are so confusingly numerous or so complex in characters, and so complicated in genetic and geographical relationship, as to transcend any ordinary scheme of zoological nomenclature" (Hubbs 1943). It has since been argued that the threespine stickleback is a "raceme" (persistent lineage [marine phenotype] out of which multiple lineages [anadromous and freshwater phenotypes] diverge and quickly end in extinction) or "species complex", composed of thousands of diverse populations that have evolved numerous times in particular locations (Bell and Foster 1994; Schluter and Conte 2009; Wootton 2009; Hendry et al. 2013). Others refer to the diversity within threespine stickleback by calling the species a "superspecies" (Baker et al. 2008).

Stickleback speciation is complex and involves multiple traits. This speciation occurs rapidly in diverse geographical areas. Natural selection, sexual selection, standing genetic variation, mutation, and genetic recombination have led to rapid reproductive isolation and speciation that has occurred since the last glaciers ca. 9,000 – 13,000 years ago (McKinnon and Rundle 2002; Schluter and Conte 2009; Wootton 2009; Schluter 2010; Hendry et al. 2013). In the mid- to late-1900s, research on sticklebacks examined the variation and adaptive significance of phenotypic traits including body shape and size, body armor (bony plates), spines and skeletal structure, spawning coloration, life history characteristics, and behavior. In the latter part of this period, research focused on the adaptive radiation and reproductive isolation of sticklebacks in lakes. In the 2000s, genomic studies on sticklebacks revealed insights into associations between phenotype, genotype, and selective factors (Wootton 2009).

Phenotypic and genotypic differences in threespine stickleback have been found among marine, anadromous, freshwater resident populations (lakes and streams), and between phenotypes within these habitats (e.g., limnetic vs. benthic phenotypes/species; Table 2). This diversity has been identified as "species pairs" (Taylor 1999; Hendry et al. 2009; Wootton 2009), "ecomorph pairs" (Wootton 2009), and "ecotypes" (Table 2; Taylor 1999; Hendry et al. 2013), although life history diversity has been examined and so "life history" has also been used (Table 2; Baker et al. 2008). Some of these phenotypes of threespine stickleback show sufficient reproductive isolation and phenotypic and genotypic differences to warrant calling them separate species, although they still bear the same scientific name (Wootton 2009; Schluter 2010). For example, "limnetic" and "benthic" phenotypes/species have been shown to be adaptive in the littoral zone (benthic species/phenotype) and limnetic zone (limnetic species/phenotype) within some lakes (Schluter 2010) and phenotypes associated with different lake substrates (lava vs. mud; Kristjánsson et al. 2002) in ways that reduce competition for resources (Schluter 2010). In addition, some phenotypic and genotypic divergence in lakes has been attributed to predators and prey (Millet et al. 2013; Miller et al. 2019), and parasitism may also influence divergence leading to speciation between limnetic and benthic threespine sticklebacks (Schluter 2010).

The appropriate terminology for describing threespine stickleback diversity may depend on the population(s) in question. This is because speciation within sticklebacks occurs along a continuum, from "continuous variation within panmictic populations" on one end to "complete and irreversible reproductive isolation" on the other, with factors affecting the divergence of populations along this continuum (Hendry et al. 2009). Hendry et al. (2009) reported that most stickleback populations are on the front end of this spectrum, "...even though some of these [populations] show evidence of disruptive selection and positive assortative mating".

Oncorhynchus

The genus *Oncorhynchus* includes five species of Pacific salmon and seven species of Pacific trout (Quinn 2005; Penaluna et al. 2016). Pacific salmon and trout (PST) are iconic and important species culturally, economically, and recreationally (Lichatowich 1999; Behnke 2002; Penaluna et al. 2016). Research on PST has been important for informing biology and fisheries management (Groot and Margolis 1991; Behnke 2002; Penaluna et al. 2016), and ecology and evolutionary processes (Stearns and Hendry 2004; Hendry and Stearns 2004; Quinn 2005; Waples and Hendry 2008).

Modern PST are approximately 6 – 20 million years old, and further speciation and intra-specific diversification has been occurring ever since (Stearley and Smith 1993; Montgomery 2000; Waples et al. 2008; Penaluna et al. 2016). Significant geologic activity, including tectonic action, volcanism, and cycles of glaciation and de-glaciation occurred and thus has been implicated in influencing the speciation of PST (Montgomery 2000; Penaluna et al. 2016). This geologic activity would have also resulted in creation of river drainages and thus geographical isolation that influenced PST speciation (Montgomery 2000). Pacific salmon and trout exhibit a general pattern of isolation-by-distance, with populations near each other being more closely related than those further away (apart from sockeye salmon *O. nerka* ; Waples et al. 2008; Wood et al. 2008). Pacific salmon and trout home to their natal streams and lakes, and this results in structured populations that are locally adapted to particular environments (Waples et al., 2001, 2008; Brannon et al. 2004; Hendry et al. 2004a; Quinn 2005). Pacific salmon and trout have been described as "...different populations [that] represent ecological types referred to as spring-, summer-, fall and winter-run segments, as well as stream- and ocean-type, or stream- and ocean-maturing life history forms" (Brannon et al. 2004).

Important ISD in PST occurs below the species level (Behnke 2002). Traits of PST that diverge at the intra-specific level include run timing (Groot and Margolis 1991; Brannon et al. 2004), anadromy / freshwater residency (Hendry et al. 2004b; Quinn and Myers 2004), ocean residency, fecundity, territoriality, iteroparity / semelparity, and precocity versus larger and older spawning types (Table 2; see also Fleming and Reynolds 2004; Quinn and Myers 2004; Quinn 2005). This ISD is a continuum determined by a suite of traits that are influenced along temporal clines. One key temporal cline is water temperature, which affects larval development, juvenile residence, and spawn timing (Waples et al. 2001; Brannon et al. 2004; Quinn and Myers 2004). The diversity in life histories and genetics within PST exhibits a direct and strong correlation (Waples et al. 2001). In addition, life history traits in PST are directly related to evolutionary fitness and thus are subjected to strong and consistent selection (Hutchings 2004; Carlson and Seamons 2008). Nevertheless, many questions remain about the extent to which the ISD in PST is a result of phenotypic plasticity versus genetic adaptation (Waples et al. 2001; Hendry et al. 2004b; Waples and Hendry 2008).

Several terms have been used to describe ISD in PST, including "morphotypes", phenotypes, populations, stocks, "life history forms", "life history types", "ecological types", "races", "phenotype", "forms", "types", and "subspecies" (Healey 1991; Waples et al. 2001; Behnke 2002; Brannon et al. 2004; Penaluna et al. 2016) — and this list is not exhaustive. The prevailing use of the term "life history" can be found in key tomes (e.g., Groot and Margolis 1991; Behnke 2002). Some authors combine use of terms such as "life history ecotypes" (Wood et al. 2008). In addition, some PST populations have received the designation of "Evolutionary Significant Units" (ESUs; Table 1). This designation enables tracking of demographic characteristics relative to population status.

Lampreys

Lampreys are a basal vertebrate (Janvier 2008; Docker et al. 2015) that first appeared in the fossil record 360 million years ago (Gess et al. 2006) — long before bony fishes (teleosts) like PST and sticklebacks appeared. Forty-two to 45 species of lampreys exist (Maitland et al., 2015; Potter et al., 2015; Riva-Rossi et al. 2020), including 23 – 26 species that are freshwater resident "brook" lampreys without a parasitic life stage, nine freshwater resident parasites, and 10 anadromous and parasitic species (Maitland et al., 2015; Riva-Rossi et al., 2020).

Phenotypic diversity in lampreys has been characterized by the feeding (parasitic vs. non-feeding) and migratory behavior (anadromous or resident; Vladykov and Kott 1979; Salewski 2003). This includes freshwater resident species that do not feed after transformation into the adult life stage (i.e., the so-called "brook lampreys"), and closely related anadromous species that feed parasitically as adults (Docker 2009; Docker and Potter 2019). The brook lampreys are relatively small in body size and females exhibit low fecundity, whereas the anadromous lampreys are relatively large and exhibit correspondingly higher fecundities (Salewski 2003; Docker 2009; Docker and Potter 2019). The closely related pairs or groups of brook and anadromous lampreys have been termed "paired species" or "species pairs", "satellite species" (more than one species), "life histories" (Vladykov and Kott 1979; Salewski 2003; Docker 2009; Docker and Potter 2019) and recently "ecotypes" (Rougemont et al. 2017; Docker and Potter 2019). A review of studies on parasitic and non-parasitic species pairs of lampreys identified a continuum of genetic and phenotypic divergence within species pairs, with the term "ecotype" being used to indicate different phenotypic expression *and* partial or full reproductive isolation, whereas life history was used to indicate trade-offs in body size and fecundity associated with feeding type (parasitic or non-feeding) and anadromy versus freshwater residency (Docker and Potter 2019).

The level of genetic relatedness between species pairs depends on the geographic location and circumstances. In some situations, closely related resident and anadromous lampreys can reproduce together; thus they may more aptly be called phenotypes of the same species. In other situations, these phenotypes or paired species exhibit discrete genetic differences. Nevertheless, these phenotypes were originally identified as separate species (Vladykov and Kott 1979; Docker 2009). Resident brook lampreys are expected to display more population structure within a particular river basin than anadromous lampreys, as demonstrated for western brook lamprey (*Lampetra richardsoni* ; Spice et al. 2019). Anadromous lampreys do not home to their natal streams, and so they display less stock structure (Bergstedt et al. 1995; Bryan et al. 2005; Spice et al. 2014a).

More recently research into Pacific lamprey, *Entosphenus tridentatus* , has revealed another vector of phenotypic diversity beyond feeding and migratory behavior: bimodal differences in maturation timing. Research into body morphology, gonado-somatic index (GSI), and maturation levels (determined by gonadal histology) revealed phenotypic differences in maturation timing, which were named "stream maturing" and "ocean maturing" Pacific lamprey (Clemens et al. 2013). It was hypothesized that the less-mature life history or phenotype was the commonly recognized stream maturing phenotype that would be expected to spawn one or more years after entering freshwater, whereas the formerly unrecognized ocean maturing form (which is more sexually mature upon entering freshwater) might spawn within the same year of entering freshwater (Clemens et al. 2013). The ocean maturing phenotype was found in the Klamath River estuary (at the river mouth, river kilometer 0). A separate study conducted at this same location used Single Nucleotide Polymorphism markers and GSI verified the existence of the two phenotypes, stream maturing and ocean maturing. This phenotypic diversity was initially referred to as "life histories" (Clemens et al. 2013), and then more recently as "ecotypes" (Parker et al. 2019).

In summary, closely related parasitic and non-parasitic lampreys have been called paired species, species pairs, satellite species, life histories, and ecotypes. And stream maturing and ocean maturing phenotypes of Pacific lamprey have been called life histories and ecotypes.

Objective 3: Trends in use of "life history" and "ecotype"

Our literature search yielded 120 articles, including 46 that focused on sticklebacks, 61 on PST, and 13 on lampreys (Table 2). Nine articles found by the Web of Science literature search were omitted from our analyses because these papers focused on life stage differences rather than intra-specific phenotypic differences. Journals with a general focus on organismal biology and ecology tended to use the term(s) "life history / life histories", whereas journals focusing on evolution and genetics tended to use the term "ecotype(s)" (Figure 1). Studies that used the term ecotype(s) tended to report a genetic basis for the phenotypic differences (Figure 2). The literature on sticklebacks tended to use both life history / life histories and ecotype(s) in equal amounts (Figure 3A), whereas the literature on PST and lampreys tended to use life history / life histories to a greater extent (Figures 3B and 3C). Taken together, this information suggests that sticklebacks have been a field and laboratory model for evolutionary and genetic research, whereas PST have tended to be the focus of fisheries-related research and management, and lampreys have experienced comparatively much less research.

Objective 4: Compare definitions with term use and make recommendations

Ecotype originally was used to describe patterns in traits (gene) combinations in particular environments. This term also tends to describe a genetic basis for ISD and is often used in genetic- and evolution-based journals during 1990 – 2019. Thus, a general consistency between the classical definition and the current use of ecotype exists. Ecotype would therefore be an obvious term for geneticists and evolutionary biologists wishing to address patterns in genes associated with particular habitats. Significant overlap in meaning exists between ecotype and reaction norms, and the nuanced differences in these terms should be carefully parsed out by authors. The classical definition of "life history" is clear and straightforward on demographic trade-offs (e.g., Stearns 1989, 1992). Life history has strong demographic connotations (Table 1), and thus the general trend for its use in organismal- and ecology-based journals during 1990 – 2019 makes sense. Life history types implies discontinuity in phenotypic expressions, whereas life history pathways (e.g., Thorpe et al.

1998) implies continuity in phenotypic expression (Table 1). The term, species pairs implies two phenotypes, whereas in some species and situations, more than one phenotype or a continuum of phenotypes, akin to life history pathways, may be expressed. Race is generally synonymous with subspecies. "Satellite species" is used for lampreys, but not for sticklebacks or PST.

Although we did not assess the use of derivative terms such as morphotypes, ecomorphotypes, ecophenotypes, these terms arguably do not offer insight into ISD, and we therefore recommend that authors either should not use these terms or use them sparingly. All attempts to describe ISD would benefit from clear definitions. In situations where the genetic and demographic components of ISD are not well understood, a conservative approach would be to forego categorization of the diversity as ecotypes or life history types / life history pathways and to call them phenotypes.

We speculate that if, for some reason, cultural, recreational, and economic roles of species were reversed so that sticklebacks and lampreys became more important than PST, that perhaps the research focus of sticklebacks and lampreys would have tended more towards demographic and life history assessments and less towards evolutionary assessments — even though these disciplines are connected (e.g., Frank and Leggett 1994; Hutchings 2000; Waples and Hendry 2008). If this were to have occurred, we wonder the extent to which the diversity within sticklebacks and lampreys might be more classified by life histories, races, and subspecies, whereas the diversity of Pacific salmon and trout might be more towards ecotypes. With this simple thought experiment, we speculate that the scope and breadth of human interests in particular taxa could influence the epistemology of how these organisms are studied, and hence the way we describe their diversity. We realize this thought experiment is somewhat overly simplified, however, in that species characteristics that can determine their commercial and recreational interests (e.g., large body size and hence longer generation times, as in *Oncorhynchus* spp.) also make these animals more challenging to study (Stearns and Hendry 2004). By contrast, the relatively small-bodied sticklebacks, which do not have a known commercial or recreational interest are comparatively short-lived and this therefore makes them tractable study animals. In addition, the evolutionary histories of these three fish taxa are very different, with the oldest by far being the lampreys, followed by the PST, and then sticklebacks. Although some of the same past geological events may have influenced the evolutionary trajectories of these taxa (e.g., glaciation; Bell and Andrews 1997), these events would have worked at different time frames and to different extents. The foregoing rationale suggests that terminology to describe ISD may not be directly transferable between taxa. For example, the abundant delineation of Pacific trouts to subspecies may make more sense for that taxon, given their population structure and distribution into geographically isolated streams (that can be geologically and ecologically diverse; Behnke 2002; Penaluna et al. 2016) than it would for either sticklebacks or lampreys. On the other hand, some terminology may have broader applicability — such as life history and ecotypes (Table 2).

In conclusion, understanding and preserving ISD is important for species conservation. Ecotype was originally used to describe patterns in genes and ecology, and recent studies generally use this term in a similar way. By contrast, life history includes biological parameters that affect abundance and population growth and decline, and recent studies generally use this term in a similar way. Ecotype and life history were used equally among recent studies on sticklebacks. By contrast, life history was used more frequently than ecotype among recent studies on PST and lampreys. The nature of human interests (i.e., scientific, commercial, recreational, cultural) in particular taxa could influence the epistemology of how these organisms are studied, and hence the ways in which their ISD is understood, described, and conserved.

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