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Lexicon of Life Cycle Diversity in Diadromous and Other Fishes

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Abstract.—In the study of species life histories and the structure of diadromous populations, an emerging trend is the prevalence of life cycle diversity—that is, individuals within populations that do not conform to a single life cycle pattern. A rapid rise in publications documenting within-population variability in life cycles has resulted in the use of numerous terms and phrases. We argue that myriad terms specific to taxa, ecosystem types, and applications are in fact describing the same phenomenon—life cycle diversity. This phenomenon has been obscured by the use of multiple terms across applications, but also by the overuse of typologies (i.e., anadromy, catadromy) that fail to convey the extent of life cycle variations that underlay population, metapopulation, and species dynamics. To illustrate this, we review migration and habitat-use terms that have been used to describe life cycles and life cycle variation. Using a citation index (Cambridge Scientific Abstracts © Aquatic Sciences and Fisheries Abstracts), terms were tallied across taxonomic family, ecosystem, type of application, analytical approach, and country of study. Studies on life cycle diversity have increased threefold during the past 15 years, with a total of 336 papers identified in this review. Most of the 40 terms we identified described either sedentary or migratory lifetime behaviors. The sedentary-migratory dichotomy fits well with the phenomenon of partial migration, which has been commonly reported for birds and Salmonidae and is postulated to be the result of early life thresholds (switch-points). On the other hand, the lexicon supports alternate modes of migration, beyond the simple sedentary–migratory dichotomy. Here more elaborate causal mechanisms such as the entrainment hypothesis may have application. Diversity of life cycles in fish populations, whether due to partial migration, entrainment, or other mechanisms, is increasingly recognized as having the effect of offsetting environmental stochasticity and contributing to long-term persistence.

Introduction

Spatial management and population connectivity across freshwater, estuarine, and marine ecosystems is a priority theme within fisheries science and management. With the maturation of approaches that yield longitudinal migration data (i.e., electronic tags and otolith chemistry that record daily and seasonal migrations of individuals), recognition of life cycle diversity within populations is becoming increasingly prevalent. Many examples exist of alternate life cycles within populations, epitomized by resident males in Salmonidae (Groot and Margolis 1998) and "sea eels" in Anguillidae (Tsukamoto et al. 1998). Concepts explaining life cycle diversity include genetic polymorphism, density-dependent habitat selection, early life conditional tactics, and social transmission of learned migration behavior (Jonsson and Jonsson 1993; McQuinn 1997; Secor 1999; Corten 2002). Life cycle diversity can have consequences for mixed-stock fisheries (Fromentin and Powers 2005), classification of essential fish habitats (Kraus and Secor 2005), and spatial management tactics (Robichaud and Rose 2004). A key challenge presented by alternate life cycles is to identify commonalities across species in pattern, cause, and consequence. To aid in this, we present a brief review on theory underlying life cycle diversity

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in fishes and then examine the ways in which scientists have described life cycle diversity across a range of taxa, ecosystems, and problems.

Alternate Life Cycle Theory

In contrast to the fish literature, avian studies support a structured terminology associated with alternate life cycles, largely due to wide-scale adoption of a theory for partial migration. In partial migration, one portion of a population is migratory and the other portion is sedentary (Lack 1943; Berthold 2001). Partial migration is further subdivided into two types: (1) facultative, where migration behavior is only under environmental control; and (2) obligate, where migrations are under both genetic and environmental control (Terrill and Able 1988; Berthold 1996). In facultative migration, there typically is not a persistent migratory life cycle, but the population can respond (e.g., with irruptive or nomadic migrations) when triggered by large changes to the environment. Obligate partial migration is believed to be more prevalent among birds and is thought to be maintained through a conditional strategy: one based upon early life thresholds (Berthold 2001). Thus, the coexistence of sedentary and migratory tactics in a single genetic population is maintained by the combined effect of an individual's fitness and trade-offs associated with each behavior (Lundberg 1988).

This theory of partial migration (Table 1) has been adopted to describe the diversity of migration patterns observed in Salmonidae but has not been widely used outside this family. As in birds, the choice of alternative life cycles (resident versus migrant) within many salmonid populations is hypothesized to be under the control of a genetically defined developmental switch-point, which causes the individual to follow one or another conditional strategy (Thorpe 1989; Mangel 1994; Thorpe et al. 1998). For instance, individual growth rate relative to a growth threshold has been shown to be a cue that can either initiate or preclude migration depending upon species (Secor 1999). In addition to growth rate, partial migration has been postulated to be regulated by early physiological state and behavior (e.g., feeding hierarchies; Metcalfe and Thorpe 1992; Økland et al. 1993).

An alternative theory has been proposed to describe the return to diverse spawning habitats by Atlantic herring *Clupea harengus*. Atlantic herring populations show a diverse pattern of intrapopulation spawning habitat use, which has stimulated debate on population structure, life cycle closure, and alternate migration behaviors (Iles and Sinclair 1982; Sinclair 1988; McQuinn 1997). Strong circumstantial evidence has been documented for the role of learned behaviors in conserving multiple migration circuits within herring populations. The so-called "adopted migrant" or "entrainment" hypothesis (Table 1) postulates that behaviors associated with a particular life cycle circuit are learned by juveniles (aka subadults) from adults during periods of spatial overlap (McQuinn 1997; Corten 2002; Petitgas et al. 2007). Thus, a certain number of juveniles are entrained into an already established life cycle. Without association with older age-classes, juveniles can establish novel migration circuits through exploration, although the adoption of novel life circuits is expected to be much less efficient than the adoption of already established circuits. As populations decline, behavioral entrainment into minority groups is postulated to become less efficient, and entire circuits and associated patterns of habitat-use can be lost (Table 1). As a population expands, density-dependent habitat selection can promote exploration of new habitats and establishment of novel migration circuits by juveniles. The diverse patterns of winter, forage, and spawning habitat use in Norwegian, North Sea, and Scotian Shelf populations of Atlantic herring have been explained in terms of the entrainment hypothesis, and it could have more general application for other coastal species (Petitgas et al. 2007).

Partial migration and behavioral entrainment are complementary ideas in that they account for life cycle diversity through a polyphenic response rather than a genetic polymorphism. For instance, following an initial threshold switch-point, a juvenile undertakes a migratory rather than a sedentary behavior. Thereafter, at some point later in life, the individual behaviorally entrains into one of several migration circuits through its interaction with already entrained age-classes in common wintering or feeding habitats. Genetic polymorphism—the idea that different life cycles represent discrete subpopulations—can only be maintained through isolating mechanisms such as assortative mating. Such subpopulation structure has been associated with sedentary and migratory components of populations of

Table 1.—Description of two theories describing alternative life cycles within fish populations.

Partial migration hypothesis	Entrainment hypothesis
Background	
Explanation for migratory and sedentary forms of Atlantic salmon and other salmonids (Thorpe 1989).	Explanation for persistent homing to multiple spawning banks within the same population of Atlantic herring—also known as conservatism of life cycles (McQuinn 1997).
Theory related to frequency dependent mating success among migratory types for birds and salmon (Hutchings and Myers 1994; Berthold 2001) that commonly exhibit partial migration.	Theory related to schooling and learned behavior in animals (Helfman and Schultz 1984; Petitgas et al. 2007).
Concept of population life cycle organization	
Same spawning unit uses different nursery, feeding, and wintering habitats.	Different spawning units share nursery, feeding and wintering habitats.
Sedentary/migratory behaviors during first year of life result in divergent life cycles.	Overlap of juvenile and adult habitat permits opportunity for adopted migration behavior.
Dispersive contingent more likely to colonize new habitats or stray into adjacent populations.	Juveniles that do not adopt an adult behavior are vagrants and can colonize novel habitats.
Life cycle closure achieved through natal homing.	Life cycle closure achieved through entrainment.
Statement of hypotheses	
Adoption of migratory behavior occurs during first year of life, with subsequent conservatism of life cycle throughout subadult and adult period.	Conveyance and conservation of migration behavior occur through transmission of behaviors from repeat spawners (adults) to recruit spawners (juveniles).
Conditional responses to the larval/juvenile environment (thresholds and developmental switches) result in adoption and subsequent conservatism of life cycle behaviors. Conditional response thresholds can differ among populations.	Juveniles adopt adult life cycles after their distributions initially overlap.
Environmental factors during the first year of life will influence the frequency of life cycle pattern in a year-class. Overlapping generations will determine how climate and other conditions affect the frequency of life cycle patterns within populations.	The dominant spawning unit will influence the dominant life cycle pattern. Loss of a life cycle can only be recovered through recolonization.

Atlantic salmon *Salmo salar* and Atlantic cod *Gadus morhua*, but results have been inconsistent for the same study populations or for other populations of the same species (Verspoor and Cole 1989; Jonsson and Jonsson 1993; Ruzzante et al. 1997, 2000; Beacham et al. 2002; Klemetsen et al. 2003).

Life Cycle Typologies and Lexicon

In this paper, we suggest that discourse among fisheries ecologists on life cycle diversity has been hindered by terms used to describe this phenomenon. First, terms used to ascribe general life cycles at the species level (typologies) tend to obscure the phenomenon of life cycle diversity. On the other hand, terms used to describe life cycle diversity within species and populations are themselves diverse, which potentially limit cross-taxa and cross-system generalities because the dialogue is too restricted (e.g., straying salmon versus vagrant herring). Here, we examine patterns of term use with the intent to not be prescriptive or authoritarian, but rather to illustrate that across diverse taxa, ecosystems, methodologies, and applications, life cycle diversity is increasingly recognized as a common phenomenon, one deserving of dedicated investigation related to its general patterns, causes, and consequences.

At both the species and within species level, a literature search for the period 1975–2006 was conducted to identify terms used to describe life cycles and life cycle diversity of fish. Terms were analyzed for underlying patterns of usage associated with taxonomic group, ecosystem, discipline, analytical approach, study nationality, and precedence.

Methods

Terms and phrases that apply to alternate life cycles were searched using Cambridge Scientific Abstracts Aquatic Sciences and Fisheries Abstracts (ASFA). The database covers more than 4,500 periodicals and gray literature reports and was selected based upon its inclusion of journals pertinent to fish biology and ecology and fisheries science (http://www-md2.csa.com/factsheets/aquclust-set-c.php). It has substantial coverage across all aquatic, ecological, and evolutionary biology journals and includes high impact periodicals such as Science and Nature. Boolean operators were applied to both restrict and broaden searches of terms that occurred anywhere in the record (e.g., title, abstract, key words). Several spot checks conducted using the more inclusive ISI Web of Knowledge (http://isiwebofknowledge.com/database) yielded nearly identical search results.

For each record attributable to bony fishes (Osteichthyes), the abstract was read to determine whether usage was a species descriptor or used to describe individual behaviors within populations or species. For instance, the term "nondiadromous" was used only as a species or population descriptor rather than a reference to individuals that were sedentary within a diadromous population. For a minority of keywords, searches yielded too many records (>500) to be reviewed for term usage (e.g., "migrant," "migratory," and "anadromous") and were excluded. While this meant that our review was not absolutely all-inclusive, coverage was likely representative and captured the prevalence of life cycle studies and the numerous terms used. We tallied the incidence of terms by taxonomy, the ecosystems connected by migration, study type, methodological approach, and the country where the work was done. Ecosystems were broadly classified according to population (rather than groups or individuals within a population) into 10 categories. River–Coast represented most diadromous species that migrate between freshwater and marine ecosystems (e.g., Salmonidae and Anguillidae). Here, coast represents both neritic (continental shelf) and oceanic environments. River was broadly used to indicate all freshwater fluvial habitats, including streams and tidal freshwater. Dashed Ecosystem categories (e.g., Estuary–Coast) indicate species migrations between the two opposed ecosystems in either direction.

Applications were tallied according to a subjective decision based upon content of the reviewed abstracts. For instance, a study noting increased straying within a population of salmon augmented by hatchery releases was identified as a hatchery application. Conservation applications were driven by concerns of species extirpation, but also often included issues related to impact of invasive caged salmon on natural populations. Population structure applications were usually easily defined but, on occasion, overlapped with studies that only described patterns of behavior (Behavior category) or Conservation (e.g., when concerned with metapopulation structure). In such instances, if there was an effort to discriminate or otherwise quantify within-population groups, the record was assigned to population structure. The Evolution category was used to describe studies on mechanisms associated with alternate life cycles. The Habitat category pertained to those applications centered on altered habitats (e.g., river impoundments). Fisheries applied to papers that related to stock structure and its effect on population dynamics in exploited species. Oceanography dealt with climate and oceanographic forcing on key life cycle attributes. Ecosystem category included community dynamics and multispecies interactions.

Twelve broad categories of analytical approach were chosen, which emphasized the increased application of longitudinal methods in recent years. The Distribution category broadly included catch and survey data analysis and basic demographic characterizations of fish populations. Physiology represented laboratory and field measurements of energetic and physiological state. Tagging studies were broken down into a Conventional tag category, where tags were externally applied; an Electronic tag category, which includes microchip, acoustic, radio, datalogging ,and satellite tags; and a Natural tag category. Natural tags referred to meristics, morphometrics, parasites, and other tracers of environmental origin. Because otolith chemistry has become a dominant approach in uncovering patterns of life cycle diversity, it was treated separately from the Natural tag category. Other categories of approaches included Genetic studies and Review.

Papers were identified in terms of country of study site. Authors often use multiple terms related to alternate life cycles within the same paper. These instances were identified to ensure that individual papers were not redundantly tallied across classifications.

Results and Discussion

Life Cycle Typologies

At the species level, life cycle descriptions have generated two typological approaches based upon habitat use or migration (Table 2). The two typologies share their basis in the characterization of the salinity habitats utilized by species. Habitat-use types emphasize the area where fish spend most of their lives (e.g., freshwater, estuarine, and marine habitats), with qualifiers describing the degree of residency in these environments (e.g., resident, migrant, straggler, etc.; Whitfield 1999). Migration types characterize the movement of fish between habitats utilized for growth, breeding, or other purposes (Myers 1949; McDowall 1988). The migration typology is well accepted in the literature, as indicated by numerous citations (Table 2), with few synonyms in use. The two typologies have been deliberately developed with terms generalizing important seasonal, ontogenetic, and lifetime trends in habitat use. Substantial literature and scholarship support these typologies as valid ways of describing assemblages and communities across zoogeographical and geological scales.

Beyond species descriptors, the typologies do not accommodate the well-documented within-population diversity in life cycles of diadromous fishes. Additionally, the unique terminology used for diadromous fishes cannot be extended to characterize life-cycle patterns in marine and freshwater species. For instance, important migration cycles occur for marine fishes; yet, these populations are simply classified as marine or oceanodromous types because migrations do not traverse salinity zones.

Life Cycle Lexicon

For the period 1975–2006, the search identified 336 studies within which occurred 40 terms pertinent to life cycle diversity that were used in 401 instances (Figures 1 and 2). Zero to 10 papers appeared during the period 1975–1990, but over the past 15 years, publications have increased threefold to more than 30 papers per year in recent years. In contrast, during the same period, total papers across all fishes and other taxa reported by ASFA increased 80% from 829 in 1992 to 1489 in 2006. Prior to 2000, papers related to Salmonidae (predominately *Oncorhynchus* and *Salvelinus*) dominated the life cycle diversity literature, but in the most recent decade, papers constitute an increasing diversity of species and families (Figures 2 and 3), representing fishes from all major ecosystem types (Figure 4A).

Terms were grouped into four categories: (1) migration patterns and modalities, (2) migration process, (3) dispersive modes, and (4) retentive (sedentary) modes (Figure 1; Table 3). Here and elsewhere, we use the term mode to imply groupings or variants within populations. Modalities represent multiple groups. Within each category, repeated terms included migratory, type, ecotype, form, and history. Common process-oriented phrases included facultative, which specified alternate life cycles, and vagrant, which related to tests of the member-vagrant hypothesis on life-cycle evolution (Sinclair 1988). The most common term was stray, which has a long history of use in questions related to Salmonidae (Tables 3 and 4). Other commonly used terms that were predominately applied to anadromous salmon populations included ocean type, stream type, nonanadromous, and nonmigratory.

Terms that were searched, but not applied to life cycle diversity studies, included ecomorph, straggler, wanderer, dispersive, and facultative anadromy; with the exception of facultative anadromy, these terms did occur in our search but were applied at the species level or pertained to attributes unrelated to alternate life cycles. The absence of the terms ecomorph and facultative anadromy in the life cycle diversity literature was unexpected. Ecomorph would seem an apt term to describe morphological variation among sedentary and migratory forms in

Table 2.—Habitat use and migration typologies that describe fish life cycles at the species level. In the choice of terms to define, we considered the precedence and common usage of the term and included less utilized synonyms in parentheses. We used primary sources of term definitions and also used more recent review articles that synthesized terminology. The definitions appear verbatim as found in the bolded citations (however, in some of these cases terms where defined in illustrations, and in those instances, the definition was excerpted and summarized from figures and associated text). One paper from a peer-reviewed journal was chosen to illustrate the application of each term. The number of citations for each term, as determined by a Cambridge Scientific Abstracts Aquatic Sciences and Fisheries Abstracts (ASFA) term search of abstracts and titles of peer-reviewed journals (1975–2006), was recorded to evaluate usage of the term.

Term	Subcategory	Definition	Application	Number of citations (ASFA)
Habitat typology				
Marine resident		Species that utilize ocean habitat at all life stages (inferred definition; not formally defined).	Tsukamoto and Arai 2001	3
Oceanodromous		Truly migratory fishes that live and migrate wholly in the sea (**Myers 1949**).	Khalaf 2005	1
Marine stragglers (Marine adventitious visitor, marine visitors, local marine species, nondependent marine species, occasional marine visitor)		Marine species where only a small proportion of the overall population makes use of estuaries (Potter et al. 1986, 1990; Whitfield 1999).	Valesini et al. 1997	7
Marine migrant (Marine immigrant, seasonal marine migrant, dependent marine species, marine estuarine dependent, estuarine transient, temporary residents, marine estuarine-opportunist)		Marine species that make extensive use of estuaries during juvenile and/or adult life stages (**Whitfield 1999**).	Vorwerk et al. 2003	6
	Marine estuarine-opportunist	Marine species of teleost that enter estuaries regularly and in at least moderate numbers (**Potter 1990**).	Potter et al. 1997	7
	Marine estuarine-dependent	Marine species that enter estuaries in large numbers (**Potter et al. 1986**).	Laffaille et al. 2000	2
Estuarine resident (resident, true estuarine species, permanent resident, estuarine, inshore nonmigratory, truly estuarine species)		Truly estuarine resident species that spend their entier lives in the estuary (McHugh 1967; **Elliott and Dewailly 1995**; Whitfield 1999).	Knieb and Knowlton 1995	27

Table 2.—Continued.

Term	Subcategory	Definition	Application	Number of citations (ASFA)
Estuarine migrant		Fish species, usually of marine origin, that breed in estuaries but have a marine or freshwater aspect to their life cycle. Estuarine migrants often have marine or freshwater breeding populations (Whitfield 1999, 2005).	Whitfield 2005	1
Freshwater resident		Species that utilize freshwater habitat at all life stages (adopted term)	Secor et al. 2001	40
Freshwater straggler (freshwater adventitious, freshwater species, freshwater migratory species)		Freshwater fish species that sometimes enter estuaries when conditions are favorable (Elliott and Dewailly 1995; Whitfield 1999).	Whitfield 2005	1
Freshwater migrant (freshwater species, freshwater migratory species)		Freshwater species that are often in estuaries, retreating into catchment rivers when conditions become unfavorable (Whitfield 1999, 2005).	Whitfield 2005	0
Migration typology				
Potamodromous		Truly migratory fishes that live and migrate wholly within freshwater (Myers 1949).	Mallen-Cohen and Stuart 2003	18
Diadromous		Truly migratory fishes that migrate between the sea and freshwater (Myers 1949; McDowall 1988).	Tsukamoto et al. 2002	143
Anadromous		Diadromous fishes that spend most of their lives in the sea and that migrate to freshwater to breed (Myers 1949; McDowall 1988).	Wedemeyer et al. 1980	985
Semi-anadromous		Diadromous fishes that spend most of their lives in saline water and that migrate to, or almost to, freshwater for spawning (Cronin and Mansueti 1971).	Hoeksema and Potter 2006	7

Table 2.—Continued.

Term	Subcategory	Definition	Application	Number of citations (ASFA)
Catadromous		Diadromous fishes that spend most of their lives in freshwater and that migrate to the sea to breed (Myers 1949, McDowall 1988).	Sang et al. 1994	71
Semi-catadromous		Diadromous fishes that spend most of their lives in freshwater and that migrate to the estuary to breed (Whitfield 2005).	Tzeng et al. 2000	0
Amphidromous		Diadromous fishes whose migration from freshwater to the sea, and vice versa, is not for the purpose of breeding (Myers 1949; McDowell 2007).	Iguchi and Mizuno 1990	122
	Freshwater amphidromy	Diadromous fish whose return migration to freshwater from the sea occurs during the juvenile stage is not for the purpose of breeding (McDowell 1988; McDowall 1992).	No application found outside definition by McDowall	0
	Marine amphidromy	Diadromous fish whose return migration to the sea from freshwater occurs during the juvenile stage and is not for the purpose of breeding (McDowell 1988, 1992).	No application found ouside definition by McDowall	0

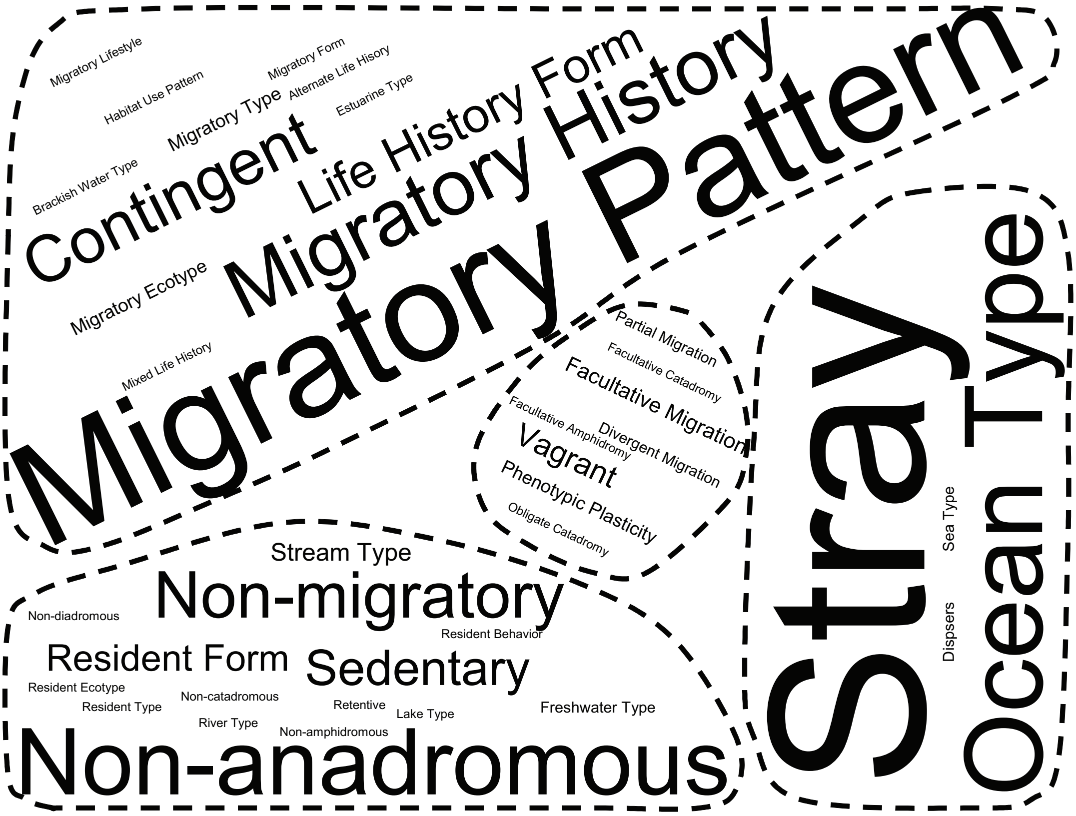

Figure 1.—Term use grouped according to lexicon categories (see Table 3) scaled by font size (e.g., Migratory Lifestyle = 1 citation; Migratory Pattern = 48 citations).

Salmonid populations (Groot and Margolis 1998). Facultative is commonly used to modify other types of diadromy (catadromy and amphidromy), and alternate life cycles are well known for many anadromous species.

Taxonomy and Applications

More than 25 species representing species from stream, lake, river, estuary, and coastal ecosystems were represented (Figure 4; Table 4). The lexicon was clearly dominated by Salmonidae, with most of these applications pertinent to anadromy (River–Coast ecosystem). Nondiadromous families include Centrarchidae, Cyprinidae, Esocidae, Gadidae, Mugilidae, Pleuronectidae, Pomatomidae, Scombridae, and Sparidae. Although alternate life cycles are best known among anadromous species, numerous studies across diverse species and ecosystems suggest that life-cycle diversity is common in teleosts.

Life cycle diversity terms were most frequently applied in Population structure, Behavior, Habitat, and Hatchery studies (Table 4). Application of these terms was also, although less frequently, used in the study of Physiology, Evolution, Fisheries, Conservation, and Pollution. Most studies were aimed at describing behaviors (n = 117), evaluating population structure (n = 104), or addressing habitat issues (n = 46). Otolith chemistry was a dominant approach in these applications, used in 41% of the Behavior studies, 26% of the Population structure studies, and 32% of the Habitat studies. Genetics was used in 41% of the Population structure studies. Conventional tagging and Distribution approaches were also commonly used across these applications. Hatchery applications mostly involved issues related to hatchery recruits straying into adjacent

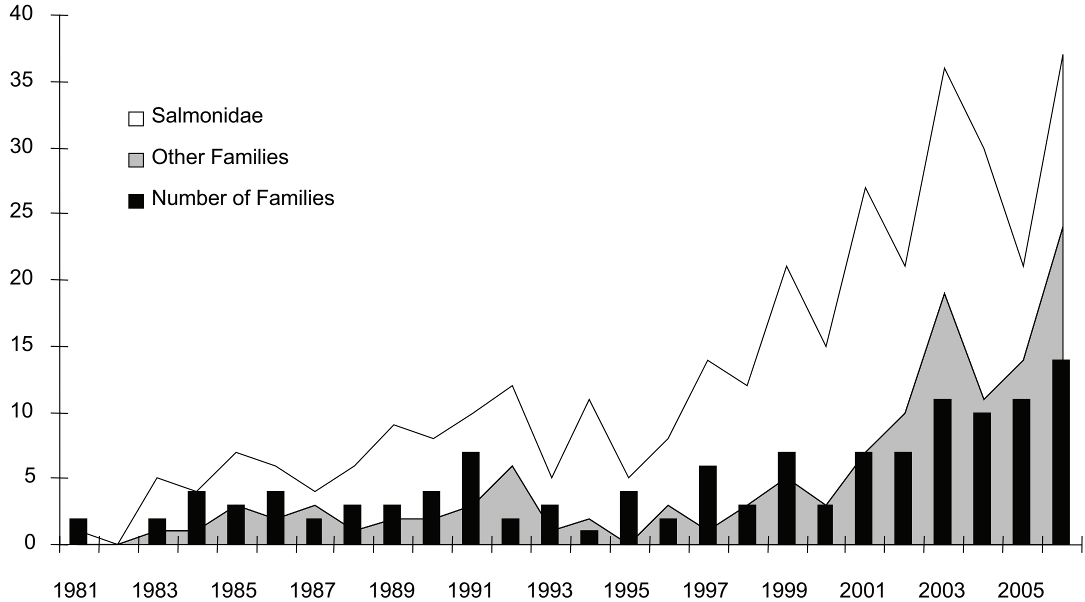

Figure 2.—Number of studies reviewed for life cycle lexicon from 1981 to 2006 using Cambridge Scientific Abstracts Aquatic Sciences and Fisheries Abstracts.

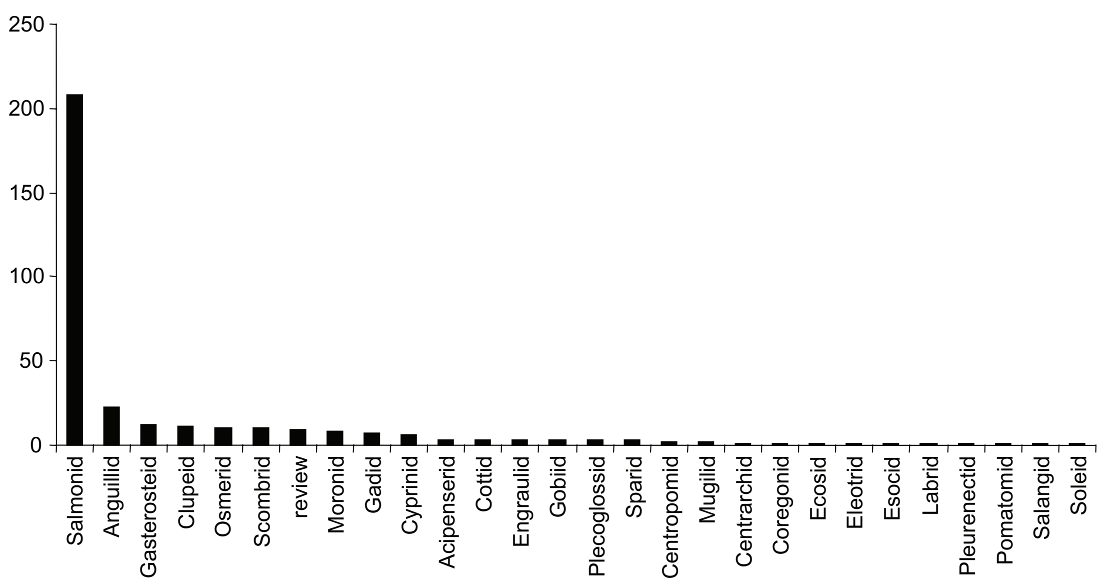

Figure 3.—Distribution of taxonomic families in life cycle lexicon.

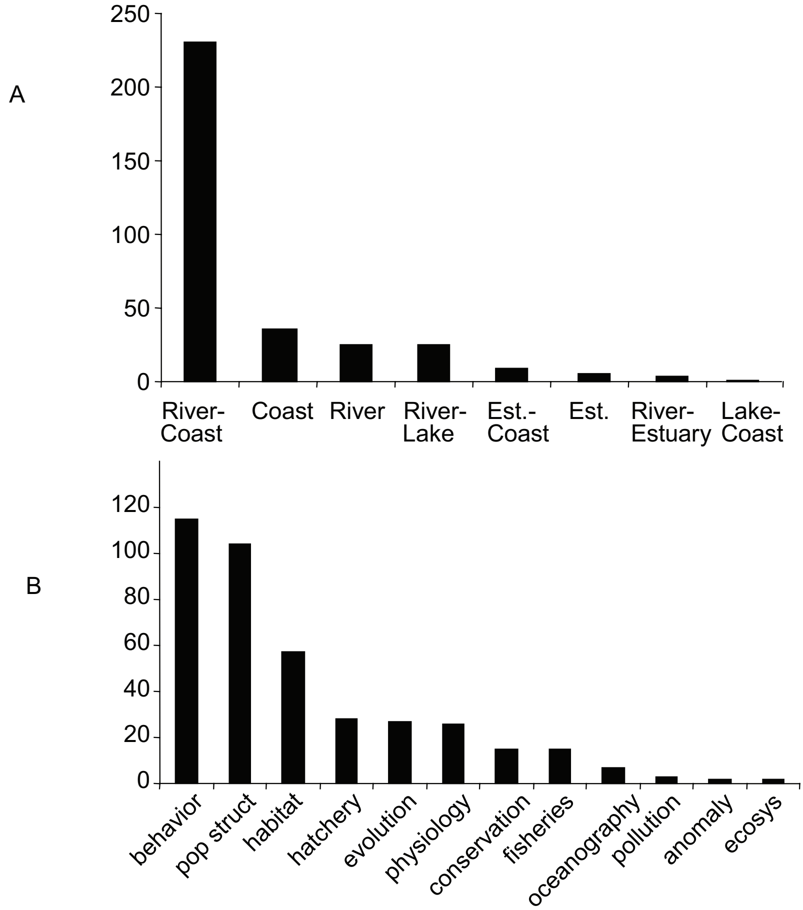

Figure 4.—Distribution of ecosystems (A) and applications (B) in life cycle lexicon. Est. = estuary. For details on categories, see Methods.

populations and principally involved Conventional tagging approaches.

Below are several examples of term use across applications:

- Nonanadromous, resident, migatory, and nonmigratory terms were collectively used in an examination of population structure of rainbow trout *Oncorhynchus mykiss* (Zimmerman and Reeves 2000). In this study, reproductive isolation between anadromous and nonanadromous life history forms was suggested by spawning surveys and otolith microchemistry.
- Facultative catadromy was used in a study of the migratory behavior of Japanese eel *Anguilla japonica* (Tsukamoto and Arai 2001). Otolith chemistry revealed remarkable flexibility in migratory pathways by Japanese eel in this behavioral study.
- Partial migration was used in the description of physiological differences between migratory and resident forms of brook trout *Salvelinus fontinalis* (Morinville and Rasmussen 2003). The study provided evidence for bioenergetic trade-offs in life history strategy. Migratory forms of brook trout exhibited higher consumptions rates prior to dispersal compared to resident forms; however, this gain in energy up take was balanced by higher metabolic costs.
- Straying was used in an examination of the significance of this life history tactic in Salmonidae from an evolutionary perspective (Thorpe 1994). The study highlighted the im-

Table 3.—Lexicon of terms and phrases used to describe life cycle diversity within species and populations. A total of 40 terms were distributed among four lexicons centered on migration pattern or process and degree of dispersive or retentive behaviors. More than 300 citations were distributed among terms. Alternate search strings are shown in parentheses.

Term grouping	Term or phrase	Citations
Patterns/modalities (13)	Migratory pattern (migration pattern)	48
	Migratory history (migration history)	26
	Contingent(s) (migratory contingents)	21
	Life history forms (___types, ___modes)	16
	Migratory ecotype (migration ecotype)	6
	Migratory type (migratory type)	6
	Habitat use pattern(s)	4
	Migratory form(s)	4
	Brackish water type(s)	3
	Alternate life history(ies)	2
	Mixed life history(ies)	2
	Estuarine type(s)	1
	Migratory lifestyle	1
Migration process (8)	Vagrants (member-vagrant)	10
	Facultative migration (___migrants)	7
	Phenotypic plasticity	6
	Divergent migration(s)	5
	Partial migration	5
	Facultative catadromy	4
	Facultative amphidromy	1
	Facultative anadromy	0
	Obligate catadromy	2
	Obligate anadromy/___amphidromy	0
Dispersive modes (4)	Stray(s)	70
	Ocean type(s)	35
	Sea type(s)	4
	Dispersers	1
Retentive modes (15)	Nonanadromous	30
	Nonmigratory	21
	Sedentary	16
	Resident form(s)	12
	Stream type(s)	8
	Freshwater type(s)	5
	Resident type(s)	4
	River type(s)	4
	Lake type(s)	3
	Nonamphidromous	2
	Resident behavior(s)	2
	Noncatadromous	1
	Nondiadromous	1
	Resident ecotype	1
	Retentive	1

Table 4.—Term usage in life cycle diversity lexicon. Number of times a term was used in a given application is shown for more than five citations for patterns of use across taxonomic family, ecosystem, application, approach, and study nationality. Migr = migration or migratory; LH = life history; Facult = facultative; P Plastic = phenotypic plasticity.

Term	Families	Ecosystem	Application	Approach	Country
Migr pattern	Salmonid (14) Acipenserid, Anguillid, Centropomid, Clupeid, Cottid, Cyprinid, Engraulid, Gadid, Gasterosteid, Labrid, Moronid, Mugillid, Osmerid, Pomatomid, Salangid, Scombrid, Sparid	River-Coast (20) Coast (12) Estuary-Coast, Ocean, River, River-Lake	Habitat (17) Pop Str (9) Fisheries (8) Behavior (6) Conservation, Ecosystem, Evoluation, Oceanography	Otol chem (16) Conv tag (8) Electronic (8) Acoustics, Distribution, Genetics, Model, Nat tag, Physiology, Review	USA (16) Canada (8) Japan (7) Australia, China, Finland, France, Germany, Lithuania, Norway Papua NG, Taiwan, UK, Yugoslavia
Migr history	Anguillid (7) Acipenserid, Centropomid, Cottid, Cyprinid, Engraulid, Gadid, Gasterosteid, Gobiid, Moronid, Osmerid, Salmonid, Scombrid	River-Coast (22) Estuary-Coast, Ocean, River-Estuary	Behavior (20) Habitat, Pop Str	Otol chem (26)	Japan (16) Canada, China, New Zealand, Papua NG, Russia, Spain, Taiwan, USA
Contingents	Anguillid (6) Clupeid, Esocid, Moronid, Pleuronectid, Salmonid, Scombrid, Sparid	River-Coast (8) Coast, Ocean, Review, River	Pop Str (15) Behavior, Ecosystem, Habitat	Otol chem (12) Conv tag, Distribution, Electronic, Genetics, Nat tag, Physiology	USA (8) Australia, Canada, France, New Zealand, Sweden, Taiwan, UK
LH forms	Salmonidae (16)	River-Coast (11) River-Lake	Conserv (6) Behavior, Evolution, Hatch, Pop Str	Distribution (6) Genetics (6) Electronic, Physiology Review	USA (8) Canada, Europe, Japan, Norway, Russia, Sweden

Table 4.—Continued.

Term	Families	Ecosystem	Application	Approach	Country
Migr ecotype	Salmonid (6)	River-Coast, River-Lake	Behavior, Evolution, Habitat, Pop Str	Behavior, Electronic, Genetics, Physiology, Review	Canada, Finland, Japan, Norway, USA
Migr type	Anguillid, Gadid, Mugillid, Salmonid, Sparid	Coast, River-Estuary, River-Coast	Behavior, Physiology, Pollution, Pop Str	Conv tag, Electronic, Genetics, Oto chem, Physiology	Canada Germany, Japan, Taiwan, UK
Vagrants	Anguillid, Clupeid, Gadid, Osmerid, Salmonid, Soleid	Coast, Estuary, River, River-Coast	Pop Str (6) Oceanography	Genetics (6) Distribution, Review	Canada, Mexico, Russia, Taiwan, UK, USA
Facult migr	Anguillid, Eleotrid	Estuary-Coast, River-Coast, River-Estuary, River-Lake	Behavior, Habitat	Otol chem, Review	Canada, France, Japan, New Zealand, Poland,
P plastic	Anguillid, Clupeid, Salmonid	River-Coast	Behavior, Evolution, Habitat	Distribution, Nat tag, Otol chem, Review	France, New Zealand, Norway, USA
Strays	Salmonid (60) Acipenserid, Clupeid, Cyprinid, Gadid, Moronid, Scombrid	River-Coast (57) Coast, River River-Lake	Hatch (23) Pop Str (16) Behavior (15) Conservation, Evolution, Fisheries, Habitat, Pollution	Conv tag (33) Genetics (16) Review (7) Distribution, Electronic, Electronic-otol chem, Genetics, Model, Nat tag, Physiology	USA (34) Canada (14) Norway (6) Argentina, Iceland, Netherlands, New Zealand, Spain, Sweden, UK
Ocean type	Salmonid (34) Gadid	River-Coast (34) Coast	Habitat (11) Behavior (7) Pop Str (6) Conservation, Evolution, Fisheries, Hat, Oceanography, Physiology	Distribution (16) Behavior Conv tab, Genetics, Model, Otol chem, Physiology, Review Distribution (16)	USA (26) Canada (7) New Zealand

Table 4.—Continued.

Term	Families	Ecosystem	Application	Approach	Country
Non-anadromous	Salmonid (29) Coregonid	River-Coast (29) River	Behavior (10) Pop Str (9) Evolution (6) Physiol	Genetics (10) Physiology (6) Behavior, Distribution, Nat tag, Otol chem	Canada (16) USA (8) Argentina, Finland, Japan, New Zealand, Norway, UK
Non-migr	Salmonid (14) Anguillid, Clupeid, Cyprinid, Osmerid, Sparid	River-Coast (15) Coast, River-Coast, River-Lake	Behavior (9) Physiology (7) Evolution, Hat, Pop Str	Physiology (8) Conv tag, Distribution, Nat tag, Otol chem, Review	Argentina, Australia, Canada, Denmark, France, Japan, Netherlands, New Zealand, Norway, Sweden, UK, USA
Sedentary	Anguillid, Centrarchid, Cottid, Cyprinid, Ecosid, Engraulid, Gadid, Osmerid, Salmonid	River (8) Coast, Lake-Coast, River-Coast, River-Lake	Pop Str (9) Behavior Evolution	Conv tag, Distribution, Electronic, Genetics, Nat tag, Review,	Belgium, Canada, Finland, France, Japan, Mexico, Switzerland, USA
Resident form	Salmonid (10) Osmerid	River-Coast (9) River-Lake	Behavior, Physiology, Pop str, Habitat	Distribution, Genetics, Otol chem, Physiology, Review	Canada, Japan, New Zealand, Norway, Sweden, USA
Stream type	Salmonid (8)	River, River-Coast	Habitat (5) Behavior	Conv tag Distribution,	Canada, USA, Argentina, New Zealand

portance of straying in the colonization of new habitat by modern salmon over the past 8,000–15,000 years. Implications included the need to minimize the probability of straying in released populations by ensuring that the homing process is engrained in smolts.

- Ocean-type and stream-type were applied in an oceanographic context in a study of variation in size of returning life history forms of Chinook salmon along the northeast Pacific coast. Here, Wells et al. (2006) found significant associations between adult sizes of differing migratory forms to Pacific Ocean teleclimatic indices.
- Zlokovitz and Secor (1999) described resident and migratory contingents of striped bass *Morone saxatilis* in the Hudson River. In this application, body burdens of polychlorinated bi-

phenyls in resident fish, identified through otolith chemistry, were far greater than migratory fish.

- Vagrant was used in the description of population structure of Atlantic salmon *Salmo salar* L. in a Canadian river system. Garant et al. (2000) provided genetic evidence of within-river population structure and established the importance of vagrants in population structuring and metapopulation persistence.
- Life history form was used to describe life history diversity documented in bull char *Salvelinus confluentus* in a conservation context (Nelson et al. 2002). A decline in the migratory form of bull char was documented in a Montana river drainage, with only the resident form present in several headwater streams. The absence of the migratory form of bull char was thought to be a factor in their current threatened status, and establishment of its stock was deemed an important conservation goal.

Approaches and Study Nationality

Contributing to the increased observations of life cycle diversity are longitudinal methods, which enable the spatial histories of fish to be hindcast over major portions of an individual's life cycle. Electronic tagging and otolith chemistry are particularly powerful longitudinal approaches. Although electronic tagging applications did not increase markedly during the past 30 years in the lexicon (ranging between zero and four studies per year), they represent perhaps the most precise method for elaborating patterns of habitat use and migration. Recent applications have also permitted spatial behaviors to be linked to demographic fates (Hightower et al. 2001). Terms associated with Electronic tagging studies include migratory pattern (8), sedentary, and strays (four each; Table 4). Otolith chemistry applications have increased notably during the past decade with 8–25 studies per year during 2003–2006. Migratory history, an apt term initially coined by Radtke and Morales-Nin (1989), was most commonly associated with these applications (26) followed by migratory pattern (16), contingent (12), and habitat-use pattern, facultative migration, and nonmigratory (four each) (Table 4).

The term stray was most often associated with genetic applications (16), conventional tagging studies (33), and review papers (7). Physiological applications were commonly associated with the sedentary terms nonmigratory (8) or nonanadromous (6). In distribution studies, life history form was the most commonly used term (Table 4).

Terms showed few obvious trends with study site nationality. As expected, terms typically applied to Salmonidae were used most frequently in northern nations (e.g., Canada, USA, UK, Japan, Norway, Sweden, Finland, and Russia). Other terms that were used more broadly across taxa, such as migratory pattern, migratory history, contingent, and sedentary, were applied broadly across nationalities and zoogeographical provinces (Table 4).

Implications

Both habitat-use and migration typologies emphasize salinity; yet, in some ecosystems such as the watersheds and neretic regions of eastern North America, salinity gradients are broad and thresholds between freshwater, estuarine, and marine difficult to discern. Here a migration of a "marine resident" into adjacent parts of estuaries may be no more significant to that fish's ecology than movements within the coastal environment. In contrast, Hawaiian freshwater gobies, alternatively termed amphidromous (McDowall 2007) or marine anadromous (Bell 2009, this volume) encounter dramatically different freshwater and marine environments with little gradient in between (Kinzie 1988). Clearly, in this instance, populations are dependent upon diadromous life cycles. Application of typologies across diverse ecosystems and taxa will necessarily be incomplete descriptions of life cycles.

Here, we argue that continued authoritative assertions for improved meanings within life cycle typologies will be of limited value in understanding the complex life cycles of diadromous species. As indicated previously, species-level descriptors can be useful shorthand but, if exclusively relied upon, will limit discourse on mechanisms and consequences of the complex and diverse life cycles of diadromous and other fishes. As evidence, there is little indication that authors have sought to modify species typologies to describe life cycle diversity. Terms such as facultative catadromy and facultative amphidromy rarely occur, and facultative anadromy was not found in our literature survey. Rather, the lexicon of terms used to describe within population diversity shows substantial variation across taxa, applications, and approaches.

The proliferation of terms in describing life cycle diversity is likely due to the maturation of sophisticated longitudinal approaches for tracking individual migration pathways within populations of diadromous, marine, and freshwater fishes. But it is also reflective of a lack of cross-taxa, cross-application, or cross-ecosystem integration. As a result, scientists working in diverse individual settings may not sufficiently have recognized the prevalence of life cycle diversity among fishes, nor have pursued a more fundamental understanding of causes and consequences of that diversity. Thus, discourse on life cycle diversity within species has been hampered by term proliferation. Still, general modalities in life cycles emerge from the lexicon.

The lexicon shows sedentary and migratory components being recognized in many populations of diadromous, estuarine, marine, and freshwater fishes. Earlier studies focused on the dichotomy of sedentary versus migratory behaviors within populations of Salmonidae, but more recent evidence exists for this dichotomy in diverse taxa. Indeed, nondiadromous species show patterns of migration that can be coarsely described as migratory and nonmigratory. For instance, some Atlantic bluefin tuna *Thunnus thynnus* complete their life cycle centered on the Mediterranean Sea, whereas others of this same population (spawning in the Mediterranean) undertake long migrations to the western Atlantic (Rooker et al. 2007). As we track individual migrations with increasing resolution, we are likely to discover ever increasing diversity and patterns. Here, the dichotomy between sedentary and migratory forms may break down. For instance, modalities in Chesapeake Bay striped bass include resident freshwater, estuarine, and marine forms. An epitome may be Atlantic herring, which utilize myriad local spawning habitats generation after generation without strong evidence of philopatry. In describing life cycle modes (variants), we have resurrected the term contingent (noun) in our work (Secor 1999), which has strong precedence (Hjort 1914) in describing life cycle diversity. The term also has advantages as not specifying ecosystems, species types, or implicit meanings pertaining to function or migration. We humbly suggest it as a neutral term.

Regardless of term usage, the sedentary–migratory dichotomy is consistent with the phenomenon of partial migration, which may be as general to fishes as it is to birds. Other modalities are likely and the entrainment hypothesis is an intriguing and untested theory that could have broad application to fish. Testing among these and other hypotheses has received very little treatment in fish studies, with the exception of very strong experimental research on Salmonidae (e.g., Nordeng 1983; Thorpe 1989; Metcalfe and Thorpe 1992), which supports the obligate partial migration hypothesis. While much science has focused on describing patterns of life cycle diversity, proportionately little scientific effort has been devoted to the causes and consequences of this diversity.

Diversity of life history tactics in fish populations is increasingly recognized as having the effect of offsetting environmental stochasticity and contributing to long-term persistence (Secor 2007). Contingents within populations should show some degree of independent response to environmental conditions because each contingent is responding to a different subset of those conditions (e.g., Kraus and Secor 2005; Fodrie and Mendoza 2006). Particular contingents can differ in their vulnerability to exploitation, habitat degradation, and climate change (Secor 1999, 2007; Cadrin and Secor, in press). Thus, diversity of life cycles within populations hedges against environmental uncertainty and contributes to population persistence.

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