

Is otolith science transformative? New views on fish migration

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Abstract Publications focused on fish otolith applications grew exponentially from 1981–2000 but have subsequently stabilized, suggesting maturation of otolith applications. Over the past 30 years >3,500 primary journal publications were identified prompting the question, how have otoliths fundamentally changed our understanding of fishes and their environment? Has otolith science in this way been transformative? I use Harden Jones' 1968 *Fish Migration* as a benchmark of fish migration concepts prior to Pannella's 1971 breakthrough paper on otolith microstructure. For case study species I highlight how otolith science has informed migration concepts including, (1) parent stream theory (Atlantic bluefin tuna), (2) adoptive homing (Atlantic herring), and (3) partial migration (European eel). Harden Jones' overall conclusion that life cycle closure leads to population structure (also known as the migration triangle) is a first principle in fisheries science, but in recent years has been challenged by otolith science. In particular, a transformative discovery attributable to otoliths is that life cycles vary substantially *within* populations. New avenues of otolith science are now exploring the causes and consequences of this life cycle diversity, and large advances are expected through integration of otolith approaches with electronic tagging, genetics,

field manipulations, and modeling that will permit migration concepts to be tested at multiple ecological scales.

Keywords Biodiversity · Life cycle · Migration · Otolith science · Stock structure

Why should otolith science be transformative?

Broad scientific interest in fish otoliths emerged three decades ago with Pannella's discovery of daily increments (Pannella 1971), resulting now in four dedicated conferences and thousands of scientific papers on otolith research and applications. A recent survey of the fisheries literature using Aquatic Sciences and Fisheries Abstracts © (ASFIS 2007; Fig. 1) indicated a nearly twofold expansion of otolith science during the period 1981–1995, followed by a stable period where otolith applications comprised c. 0.6% of the literature base. During the entire period (1981–2008), the literature base recorded 3,615 primary literature contributions in otolith science. This pattern of early growth followed by stability suggests maturation of otolith applications.

Although the discipline may now be mature, supporting numerous important applications across diverse disciplines (e.g., Campana 2005), otolith science remains somewhat obscure, particularly among the public. How does one explain otolith science to the layperson? One tactic, perhaps over-ambitious, is to show how otoliths have changed our

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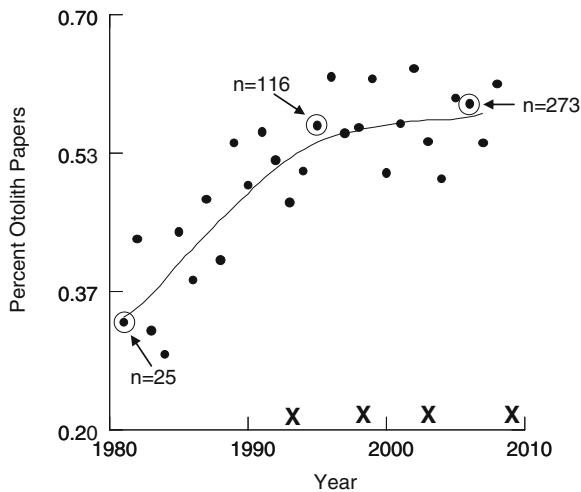


Fig. 1 Relative growth of otolith literature from 1981 to 2009. Percent otolith papers references total number of otolith papers (keyword = otolith*) divided by entire reference database for Aquatic Sciences and Fisheries Abstracts (peer-reviewed journals). Growth rate fitted with a LOWESS smoothing function, tension = 0.6. Benchmark numbers of otolith papers are given for years 1981, 1995 (first year $n > 100$), and 2006 (peak number). Past International Otolith Symposia are indicated by X symbols. Total numbers of otolith and database papers over this period were respectively 3615 and 682 075

world view. Research funding agencies have long asked us to consider broader impacts, most recently requesting that applicants pursue transformative science. The U.S. National Science Foundation defines transformative science as, *research that has the capacity to revolutionize existing fields, create new subfields, cause paradigm shifts, support discovery, and lead to radically new technologies* (NSF 2007). Other agencies are promoting similar views. The US National Institute of Health seeks to support ... *exceptionally innovative, high risk, original and/or unconventional research projects that have the potential to create or overturn fundamental paradigms* (NIH 2009). Such directives are humbling to the individual scientist. How does one do transformative science—through persistence, a fresh outlook, epiphany, serendipity? The answer in fact may originate in humility: through introspection, by making the implicit explicit.

We can gain perspective from the setting of the 4th International Otolith Symposium, Monterey California, which was a hard-edged, culturally diverse industrial port centered on a hugely productive sardine fishery in the early 20th Century. The writings of John

Steinbeck characterize the hard scrabble lives of the personalities and families that once lived on *Cannery Row* (Steinbeck 1945). In describing the lives of outcasts and misfits, Steinbeck brought attention to larger social issues. By making hidden elements in society explicit, his “literary realism” created new insights and broader understanding (Barrish 2008). Literary realism is analogous to what educational specialists term transformative learning, where we make the implicit explicit either through introspection or through social interactions (Mezirow 2000). As otolith scientists, we should be much more comfortable with this definition—this characterizes much of what we do. We are fundamentally empiricists seeking to more accurately test and measure fundamental properties and processes of fishes, those previously obscured.

Consider the founder of modern otolith science, Giorgio Pannella, a Yale geologist who took notice of the 2-micron “concentric shells” within otoliths that fisheries scientists had noticed for decades but had never attached ecological significance. Pannella made a bold suggestion that these increments might in fact be formed daily and concluded that, *the information recorded in otoliths will be invaluable to the marine biologist*. This quote should alert readers that otolith science is indeed transformative. The hundreds of scientists represented at the 4th International Otolith Symposium and the thousands of others who work with otoliths (Fig. 1) have made this prediction an extreme understatement.

Otolith science speaks volumes on fish migration

Fish migration is but one process where otolith science has provided unique insights. Most fish display a complex life cycle: fish leave natal areas for juvenile and adult habitats and then return. Populations often overlap in juvenile and adult distributions, yet remain discrete so long as natal regions do. Otolith daily increment (Pannella 1971) and otolith tracer approaches (Radtke 1984) have provided what Gilbert (1914) termed certificates of origin for fish. The natal origin of fish is fundamental to our understanding of population dynamics—it is the pivot point that permits fishery removals to be matched with production (recruitment) (Cadrin and Secor 2009). Natal homing permits life cycle closure, a first principle in fisheries assessment.

In this essay, I use Harden Jones' compendium of case studies and migration concepts published as *Fish Migration* in 1968, as a baseline for subsequent discoveries and concepts brought about by otolith science. In his seminal argument for life cycle closure, Harden Jones reviewed migration patterns of diverse species and found that they could be generalized as a simple triangular pattern between spawning, nursery, and adult habitats. In his transformative treatise, Harden Jones made tacit knowledge explicit proposing a general picture of life cycle closure for marine fishes—that patterns of early natal dispersal and adult natal homing were supported by underlying oceanography and evidence for breeding philopatry in some species, namely Pacific salmon. Also contained in that volume are early results from nascent approaches including genetics, electronic tagging, hydroacoustics, and the use of otoliths as certificates of origin. Perhaps less well recognized in this volume is Harden Jones' critical articulation of ideas and controversies related to minority life cycle behaviors. Here, I review how otolith science has influenced the 'fit' of the migration triangle to populations of Atlantic bluefin tuna, Atlantic herring, and European eels. An important personal motivation in this exercise is the view that pioneering historical works such as *Fish Migration* represent a wellspring for new ideas. In doing so, I am using my own interpretations, which are subject to a personal perspective and other sources of bias.

Are Atlantic bluefin tuna Pacific salmon?

Harden Jones devoted a single paragraph in his book to otoliths as certificates of origin, but these early applications were not without uncertainty. The optical nature of annuli was featured as a means to detect differences between populations spawned between seasons or regions, yet the mechanism behind these differences was unknown, as was the accuracy of these certificates. Developments in otolith science during the past 30 years have provided more robust certificates of origin, where otolith composition can represent natal habitats (Campana et al. 2000; Elsdon et al. 2008). The capacity to directly test natal homing by assigning adults to habitat of natal origin is a transformative development (Thorrold et al. 2001), yet surprisingly few applications exist (Gillanders 2002; Almany et al. 2007; Rooker et al. 2008a, b). Here I review nearly a

decade of research and development to test natal homing in Atlantic bluefin tuna *Thunnus thynnus* to show how such applications are not straightforward.

For Atlantic bluefin tuna, restricted spawning in the Gulf of Mexico and Mediterranean, life history differences in adult spawners, and concentrated fisheries in shelf waters have supported a two-stock management strategy by the International Commission for the Conservation of Atlantic Tunas (Fromentin and Powers 2005; Rooker et al. 2007). The premise of homing to western Atlantic and Mediterranean natal areas has been used to justify separate assessments and management actions on either side of a 45° meridian since 1982. Also important was the assumed generality of the migration triangle (breeding philopatry): *In temperate seas, fish return to the same spawning ground each year at the same season much as do Pacific salmon...* (Cushing 1995). Since 1982, fisheries on either side of the Atlantic have evolved separately. Western fisheries are characterized as 10-fold depleted over the last 25 years in comparison to historical abundances, with no sign of recovery despite strict quotas designed for rebuilding (SCRS 2008). Landings from eastern fisheries have been higher by comparison, despite much higher exploitation levels. Many think that failure of the western stock to recover is due to misspecification of population structure. Indeed, the U.S. National Academy of Science recommended a concerted effort to test natal homing in Atlantic bluefin tuna (Magnuson et al. 1994).

In 1997, a workshop was held to develop and apply otolith tracer studies to Atlantic bluefin tuna natal homing, sponsored by National Marine Fisheries Service (Secor and Chesney 1998). Atlantic bluefin tuna are moderately long-lived and a chief challenge was to develop a certificate of origin that would not deviate substantially among year-classes. A program to test temporal stability of otolith tracers for juveniles from the two primary nursery areas commenced that resulted in 8 years of collections. Parallel to this effort, milling procedures were developed to extract otolith material from adult otoliths corresponding to the first year of life. For both juvenile and adult otoliths, critical issues were bias and precision. Bias is incurred by contamination through otolith collection, preparation, and analysis; imprecision can occur through deviations in procedure between investigators/laboratories. Using nested comparisons between paired sagittae, we conducted a series of experiments where otoliths were

deliberately contaminated and cleaned to test decontamination procedures (Rooker et al. 2001a; Secor et al. 2001; Arslan and Secor 2008). We adopted a strategy of rigorous cleaning rather than clean room collection procedures (Thresher 1999), which were not realistic for a multi-investigator, multi-region, multi-year study (including archived samples). These experiments were considerably aided by the availability of a certified otolith reference material (Yoshinaga et al. 2000). Tests between independent laboratories showed that protocols that minimized bias could be replicated with high precision (Secor et al. 2001).

The typical suite of alkaline and earth metals used as elemental fingerprints (Campana and Thorrold 2001) showed poor interannual stability and for any particular year, moderate (60–70%) classification success (Rooker et al. 2001a, b; Secor et al. 2001). With the help of analytical chemists, novel preconcentration and separation methods were developed to include a larger set of transition and heavy metals (Arslan and Paulson 2003). These provided moderately improved discrimination but still showed considerable interannual variability (Arslan and Secor 2008). Finally, we turned to stable isotopes, which were advantageous in that aqueous $\delta^{18}\text{O}$ was known to differ appreciably between the two principal nursery areas. This tracer gave us what we were looking for: good discrimination (>90%) within most years and consistent discrimination (>87%) among years (Rooker et al. 2008a, b). Ironically, stable isotope analysis is unaffected by metal contamination, a central issue in our earlier research.

Results from the application of stable isotope tracers on otolith samples collected throughout the Western Atlantic Ocean and Mediterranean Sea supported the assumed population structure with greater than 90% natal homing, and trans-oceanic migrations and mixing during the juvenile period between two populations (Rooker et al. 2008a, b). In samples of large adults taken in the NW Atlantic or spawners taken in the Gulf of Mexico, we observed that otolith $\delta^{18}\text{O}$ overlapped broadly with the natal juvenile range, indicating natal homing (Fig. 2). Similarly otolith $\delta^{18}\text{O}$ of adults from the Mediterranean overlapped with natal (age 1) juveniles in their stable isotope values. Interesting, for older juvenile bluefin tuna ranging 2–10 years in age and collected in US shelf habitats, c. 50% of these originated from the Mediterranean. Molecular and contaminant tracer studies supported this same general

pattern of natal homing by adults and mixing by older juveniles (Carlsson et al. 2007; Dickhut et al. 2009).

Another recent effort to test population structures of bluefin tuna emphasized development and application of satellite pop-up tags and archival tags. Early electronic tagging studies did not fit the two-stock picture. Lutcavage et al. (1999), using satellite pop-up tags, observed large adult bluefin tuna in the central Atlantic when they were supposed to be spawning. This suggested mis-specified reproductive schedules (aka skipped spawning; Secor 2008) or perhaps, a third spawning area (Lutcavage et al. 1999). These results generated substantial controversy because they conflicted with other archival tagging results, which showed expected movements of adults to Gulf of Mexico or Mediterranean spawning areas (Block et al. 2005). Stokesbury et al. (2004) suggested that the early generation tags used by Lutcavage et al. did not perform as intended, although subsequent research by this group of researchers with improved satellite pop-up showed much the same result (Wilson et al. 2005; Galuardi et al. 2010).

When we are presented with anomalous or conflicting results, it may be useful to return to first principles: what are the processes that contribute to population structure? Processes and terms have been idiosyncratically used in the fisheries science literature (Secor and Kerr 2009), so I borrow from avian ecology, where more consistent terminology occurs (Pearce 2007). Here, terms related to philopatry are applied in a hierarchical manner: (1) Breeding philopatry or just plain philopatry refers to multi-generational return to the same spawning area—most often this is inferred indirectly through use of neutral genetic markers and applied to an entire population or sub-population (e.g., Carlsson et al. 2007). (2) Natal homing is the return of an individual to a spawning or nursery area whence that individual originated. Otoliths as natural tags (Campana et al. 2000) have provided direct evidence for this behavior. Finally, (3) spawning site fidelity is the multiple return of an adult to the same spawning area—evidence for this often comes from conventional or electronic tagging. In this hierarchical framework, natal homing selects for spawning fidelity and breeding philopatry selects for natal homing. Depending upon the aim of the ecological or assessment question at hand, some or all of these processes may be relevant.

For Atlantic bluefin tuna, an otolith application supports the remarkable finding that bluefin tuna can

Fig. 2 Notched box plots of $\delta^{18}\text{O}$ distributions for different population components of Atlantic bluefin tuna. Grey and white fills respectively indicate Mediterranean or Western Atlantic natal origin. Notch indicates median, box shoulders are 25th and 75th percentiles and bars represent 10th and 90th percentiles; asterisks and circles are outliers. Modified from Rooker et al. (2008a, b)

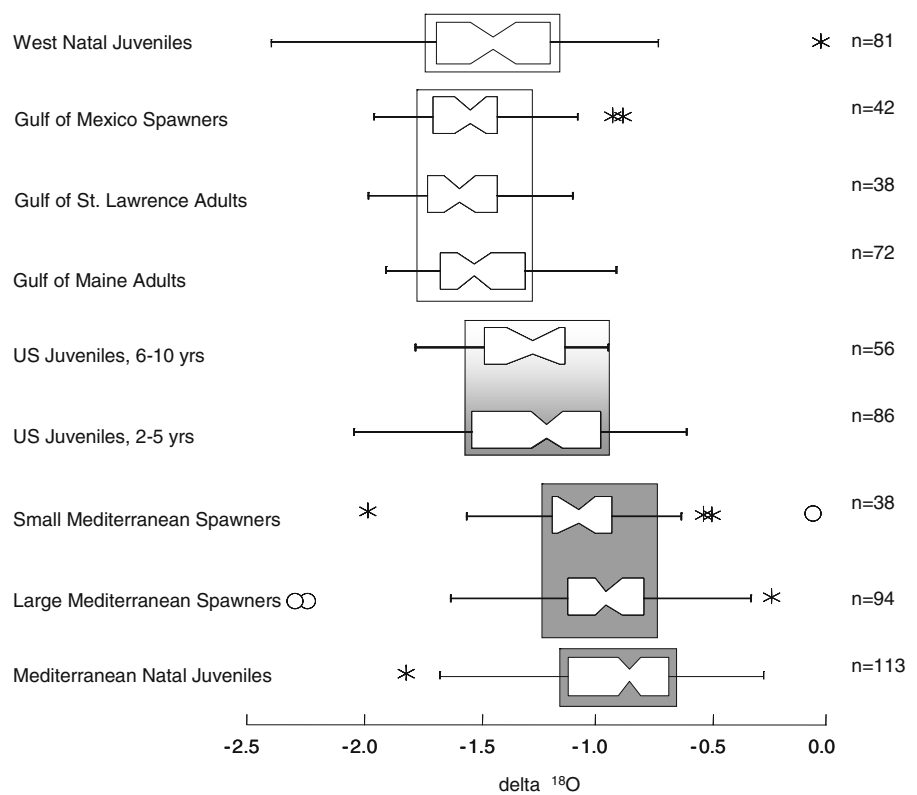


exhibit natal homing rates similar to Pacific salmon. Other types of evidence support natal homing in Atlantic bluefin tuna as well (Block et al. 2005; Carlsson et al. 2007; Dickhut et al. 2009). In this sense, they conform to the Harden Jones concept of life cycle closure, a surprising result given their highly migratory behaviors. Thus, we can think of natal homing as a necessary element of life cycle closure and philopatry. More definitive links between spawning fidelity and natal homing remain to be discovered but could be made if otolith chemistry data were matched with archival geolocations for the same adults. Such efforts are feasible and merit priority to better understand how diverse migration behaviors by adults contribute to natal homing and philopatry.

Further empirical studies and modeling can test and examine the consequences of possible mis-specification of natal homing or spawning fidelity, but an interesting alternative is that our hierarchical view of philopatry is flawed. Perhaps natal homing does not select for spawning fidelity, but rather natal homing is an emergent attribute of spawning fidelity. Here otolith science again

provides unique insights, particularly in applications on Atlantic herring *Clupea harengus*—a species that exhibits rich diversity in population structure.

Are herring creatures of habit?

Atlantic herring epitomize diverse spawning habits and controversy on mechanisms that structure populations has persisted for this species for over 100 years (Sinclair 1988). Parapatric spawning, seasonal spawning groups that utilize the same spawning habitat but can be considered separate sub-populations, is well known for herring. Harden Jones modified his migration triangle to allow for these spawning groups, which can undertake opposite seasonal migration directions between spawning, feeding, and overwintering areas. Still, he recognized that there seemed ample opportunity for mixing between these seasonal groups, as well as between spawners in the North and Baltic Seas, which were in close proximity to each other. In contrast to Pacific

salmon, he concluded that evidence for natal homing in Atlantic herring was equivocal: *Opinions differ as to whether a herring spawns in the same season as that in which it was born and whether or not it returns to spawn on the parent ground* (Harden Jones 1968).

A mismatch seems to occur between the number and diversity of spawning bank habitats which are consistently occupied over generations, and a dispersive larval period that persists in pelagic environments for many months. Given the potential for larval dispersal in the advective shelf waters of the North Sea and elsewhere, how is life cycle closure maintained? A major key in resolving this question were natural tags associated with seasonal spawning groups. Harden Jones: *The problem would be relatively simple if autumn- and winter-spawned herring could be separated by some distinct and clear-cut feature....* Thus, otoliths and scales have been used to identify seasons of spawning (natal homing), but as highlighted below these led to conflicting interpretations.

In support of natal homing, Einarsson (1951) used otolith nucleus optical properties to distinguish Icelandic summer and spring spawners. The approach was not fully calibrated but did suggest natal homing by summer spawners. In contrast, using back-calculation of annuli in scales, Burd (1962) inferred that a common pool of southern North Sea juveniles recruited to either autumn or winter spawning groups at a similar “critical” length. Thus conceivably, variable growth rates during the juvenile stage would result in mixing between the spawning groups. This led Cushing (1962) to speculate that *...stocks might be mixed on the nursery grounds...they are ‘set up’ at recruitment and [maintain] their identity throughout their adult lives.* Under this view, spawning fidelity causes generation after generation return to natal areas rather than some form of larval or juvenile imprinting.

During the past three decades, advances in coupled biophysical observing systems and modeling have altered the view that larvae are merely dispersed after spawning. Sinclair (1988) in particular has emphasized that spawning and larval behaviors can cause retention of larvae within meso- and macro-scale current systems, leading to natal homing and population structure. For Atlantic herring, he concluded *The common denominator for the diverse spawning locations of the separate populations is the geographic predictability of an oceanographic or geographic*

system that will permit persistence of the larval distribution for a few months after hatching. Thus, larval retention by Atlantic herring should lead to natal homing and philopatry (Fig. 3a).

The controversy on whether spawning fidelity or natal homing drives philopatry in Atlantic herring persists with recent otolith applications. Using otolith Sr:Ca as a natural tag of thermal conditions Townsend et al. (1989) showed that estuarine retention areas for Gulf of Maine larvae can serve as ecological traps during cold winter months. They observed that spring-time larval recruits to the study estuary came from adjacent coastal regions rather than from larvae that had entered estuaries in the previous fall and persisted there. Similar to Einarsson’s application, McQuinn (1997a) used otolith nucleus dimension to distinguish fall and spring natal origins for western Newfoundland coastal stocks. He observed that many fall-spawning adults originated from spring-spawned larvae but once a fall or spring spawning behavior was adopted, that spawning behavior was maintained throughout the adult’s life. Both of these two studies support the earlier work by Burd (1962) that allowed for potential mixing of larvae from different spawning grounds where spawning site fidelity drives natal homing rather than natal homing driving the adult migration circuit (Fig. 3b). As McQuinn (1997b) postulated in his adopted migration hypothesis, *Local population integrity is thus maintained by behavioural isolation of adults, through repeat homing to traditional spawning grounds.*

I view McQuinn’s (1997b) interpretation as transformative, in that it challenged our tacit acceptance of the parent stream theory for marine species and our incomplete understanding of natal homing and philopatry: *The orthodox view is that fish have an innate ability to imprint to their natal spawning site. ...Naïve first-time spawners, after migrating often long distances to feeding and overwintering areas, must then find and recognize home to complete the life cycle within their local population. This corresponds to the well-established salmon model; however, is this the general case?* The adopted migration hypothesis emphasizes social transmission of behaviors, adults to juveniles, generation after generation, as in migrating birds. This mechanism seems quite plausible, but lacks direct evidence. Can adults entrain juveniles that don’t necessarily share the same natal origin?

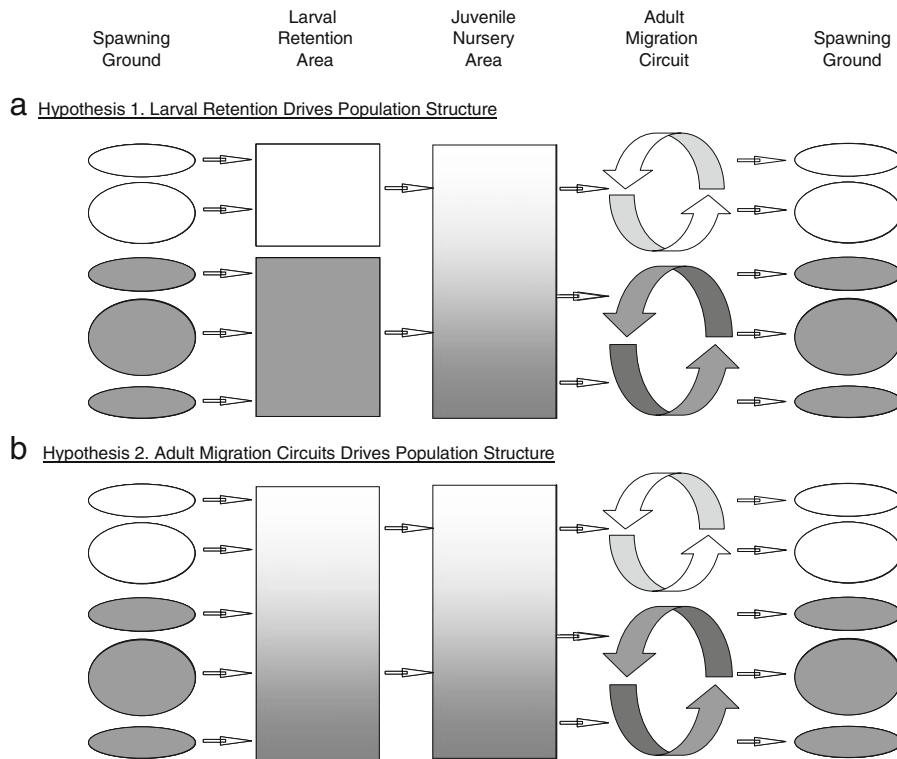


Fig. 3 Diagrams showing life cycle closure under two hypotheses. White and grey shading is used to indicate spatial segregation of individuals among ontogenetic stages and associated habitats; graded shading indicates mixing of individuals. Under the first hypothesis spawning behaviors (locations) are selected by adults to ensure larval retention (and separation) within stable oceanographic features generation

after generation leading to natal homing and philopatry. Under the second hypothesis, mixing can occur following spawning and juveniles are entrained into an established adult migration circuit so that migration pathways are socially transmitted generation after generation leading to philopatry without natal homing. Diagrams adapted from Smedbol and Stephenson (2001)

Arguably the only direct test of the adopted migration hypothesis is a study on mixing between Celtic and Irish Atlantic herring populations by Brophy et al. (2006). Here, detailed otolith microstructural analysis was coupled with careful delineation of adult spawners on spawning grounds. They observed that some Celtic Sea larvae dispersed into the Irish Sea and mixed with fall spawners there. Once there, Celtic Sea-origin juveniles only encountered Irish Sea adults, yet did not subsequently spawn in the Irish Sea but exhibited natal homing to the Celtic Sea. Brophy et al. (2006) concluded, *The results of this study...show that naïve juveniles do not need to encounter repeat spawners to locate their parental areas.*

Dynamic changes in Atlantic herring population structure (Corten 2002; Petitgas et al. 2010) have confounded attempts to apply a general theory of migration for this species. In a careful reading of Harden Jones, one finds that he too recognized this

problem, although the take-home by many readers—the migration triangle—has often supported a rather narrow typological view on the role of migration in maintaining population structure (Cadriu and Secor 2009). Rather in his epilogue Harden Jones states that *...the general picture of homing and migration is clear. But there are several instances where there is a reasonable doubt concerning important matters of fact, and until these problems are resolved, progress in the interpretation and the understanding of the mechanism of homing and migration will be slow.* By devoting a third of his book to mechanistic studies, Harden Jones calls attention to the need for increased understanding of larval imprinting and dispersal, social and/or genetic transmission of migration behaviors, orientation, and movement ecology. We now have mature applications to pursue these research priorities—otoliths as certificates of origin (natal homing), electronic tags that provide insight on movement

ecology (spawning fidelity), and genetic markers that say something about lineage (philopatry). These approaches and related processes can now be productively integrated to test mechanisms associated with population structure.

What should we call these saltwater eels?

A transformative discovery was that so-called “freshwater” eels (*Anguilla anguilla*, *A. japonicus*, *A. rostrata*) could in fact complete their life cycle in marine or brackish waters (Tsukamoto et al. 1998; Daverat et al. 2006). Otolith Sr:Ca profile analysis of temperate yellow (late juvenile stage) eels have shown sustained elevated Sr:Ca levels, indicative of residence in coastal or brackish waters throughout the juvenile period (Daverat et al. 2006). The traditional view of their life cycles held that after spawning in large open ocean habitats, larvae (leptocephali) drifted for months to perhaps years (depending on species), and then early stage juveniles (glass eels and elvers) all made their way across continental shelves, estuaries and upriver where they persisted in diverse freshwater habitats (yellow eel stage) until emigration as adults. This rigid concept of a freshwater growth phase was firmly accepted by Harden Jones (1968): *Eels grow up in freshwater ... Their freshwater life is of little interest to the migration problem*. Clearly otolith science has transformed our view on eel life histories.

The discovery of differing life cycles within the same population of eels seemed to require a new way of thinking—what do we call groups of individuals that undertake different life cycles but occur in the same population? What do these groups represent? At the first International Otolith Symposium held in 1993, Dr. Tsukamoto asked my advice about what we should call eels that don’t enter freshwater. The best we could come up with at the time was “facultative catadromy” (Tsukamoto et al. 1998; Tsukamoto and Arai 2001). Later as I encountered examples of life cycle diversity in other species, I resurrected the term contingent (Secor 1999), which was originally used by Hjort (1914) to describe migratory groups of North Sea herring. Since that time >100 authors have used dozens of terms to describe intra-population diversity in migration behaviors (Fig. 4; Secor and Kerr 2009). This idiosyncratic use of terms (mea culpa) emphasizes that we may not be seeing the forest for the

trees: that common causes and consequences may be associated with this new form of biodiversity that we are failing to recognize.

An important concept in bird ecology that may have general application to fishes is partial migration, where some individuals remain in their natal area and others migrate to distant wintering or feeding areas. Whether an individual becomes resident or migratory is a conditional strategy, depending on an early life switch point. This switch point interacts with the environment, leading to varying proportions of migrants within bird populations. As an example consider the house finch *Carpodacus mexicanus*, which was introduced to the U.S. east coast from a mostly sedentary population in Southwest California. After introduction to New Jersey, environmental conditions favored the migrant fraction, which contributed to irruptive growth and colonization of this species throughout the eastern U.S. (Able and Belthoff 1998). Another example is the blackcap warbler *Sylvia atricapilla* in Europe and Northern Africa where the proportion of migratory individuals among sub-populations varies with winter severity (Berthold 1999). Here and elsewhere, the machinery of partial migration is believed to underlay much of the ecology and evolution of bird migration (Berthold 1996). In fishes, partial migration has been principally applied to salmonids, where juvenile (parr) condition affects an individual’s subsequent migratory fate (Jonsson and Jonsson 1993). More recently, partial migration has been suggested for other species such as striped bass, white perch, and European eels (Kerr et al. 2009).

Recent research on European eels has suggested that a switch point occurs as glass eels reach the head of tide—the interface between fluvial and estuarine systems (Edeline 2007; Edeline et al. 2007). Ingress of glass eels up-estuary is facilitated by selective tidal stream transport, but in encountering freshwater currents, juvenile eels either have the physiological wherewithal to continue or they must fall back. Interestingly, the “migratoriness” of glass eels is something that can be identified through hormonal levels and behavior in the laboratory (du Colombier et al. 2008; Imbert et al. 2008), suggesting that eels could become a very important model species for the study of partial migration in fishes.

Partial migration is fascinating, because it implies that events that occur early in life can have far reaching consequences to population dynamics. One

Fig. 4 Terms used to describe life cycle diversity scaled to font size (Migratory Pattern = 48 citations; Alternate Life History < 4 citations). Modified from a literature review by Secor and Kerr (2009)



line of cascading effects suggested for European eels is that recent warming in the Sargasso Sea has led to reduced primary production and growth and survival of leptocephali (Bonhommeau et al. 2008). Glass eels might then arrive in estuaries and freshwater environments in depleted condition due to poor oceanic growth. This in turn would lead to reduced distribution across habitat types (Bureau du Columbier et al. 2008). Thus, reduced use of freshwater habitat by eels could be the result of how partial migration is affected by ocean conditions, rather than effects directly attributable to freshwater habitats (dams, water quality degradation, etc.).

A diminished expression of a freshwater behavior in an eel population (reduced biodiversity [for pertinent biodiversity definition see Hengveld 1996]) should have consequences to population yield stability and resilience (Kerr et al. 2010). Consider research on American eels, which showed that juvenile freshwater eels cannot effectively traverse vertical impoundments >2 m (Machut et al. 2007). Accordingly, at least 80% of the historical freshwater habitats have been lost to American eels (Busch et al. 1998). Thus in this instance, direct impacts on freshwater habitats have curtailed expression of partial migration. What are the consequences? The population may persist because it can complete its life cycle outside of freshwater habitats (USFWS 2007), but if we only invest in a marine/estuarine life cycle, we've essentially put all our eggs in one basket. Alternatively, if

we manage for recovery of a freshwater life cycle, which itself shows large diversity—rivers, streams, marshes, ponds, lakes, etc.—then we promote varying outcomes, thereby minimizing risks due to future environmental changes. Here for instance, we know that freshwater eels often show great longevities that could span periods of poor oceanic conditions (Cairns et al. 2009).

Prognosis for transformative otolith science

Otoliths were well remarked upon in Harden Jones' *Fish Migration*, but their application served to confirm accepted ideas about fish migration rather than prompt new theory and debate. Harden Jones proposed otoliths as ideal certificates of origin in natal homing studies, but so far there are surprisingly few definitive applications (Thorrold et al. 2001; Rooker et al. 2008a, b) indicating that this remains a critical and understudied application for otolith science. As highlighted for Atlantic bluefin tuna above, evaluating temporal and spatial stability in natal tags can take years of research and development. Still, otolith studies are currently the state of the art method for determining natal homing and, when coupled with other approaches (electronic tagging and genetic technologies), such applications promise new discoveries on the relationships between philopatry, natal homing, spawning fidelity, and life-cycle closure.

Otolith science is now at the center of debates on population structure. For Atlantic bluefin tuna, otolith tracers indicate that bluefin tuna show strong natal homing and population structure in accordance with Harden Jones' Migration Triangle, yet one set of electronic tagging studies indicates deviation from the expected pattern of spawning fidelity (Lutcavage et al. 1999; Wilson et al. 2005; Galuardi et al. 2010). For a Canadian Atlantic herring metapopulation, the use of otolith microstructure as a natal tag suggested that social transmission of adult migration resulted in life-cycle closure (McQuinn 1997a, b), yet for a Celtic-Irish Sea metapopulation a similar otolith application rejected this hypothesis (Brophy et al. 2006). In these and other systems, we must move beyond markers of lineage (breeding philopatry) for insight into the causes and consequences of population structures. Otoliths have shown promise as markers in measures of natal homing (Jones et al. 1999; Thorrold et al. 2001; Rooker et al. 2008a, b). But, beyond simply (or not so simply) demonstrating a generation's return to a natal area, we must understand the within-generation interactions among individuals and environment. In particular, I see new discoveries on the horizon in studies that manipulate social and environmental interactions in the field, through transplant experiments for instance. Otolith and electronic tagging approaches will be critical in designing such experiments.

Otolith tracer studies have suggested that life-cycle diversity may be common within fish populations as it is in birds. Increasingly, partial migration has been implicated as a cause of persistent sedentary and migratory behaviors within populations. Otolith science is ideally suited for resolving key components of partial migration because one can use the same otolith to evaluate early life history switch points and their consequences to adult distribution and growth patterns (Kraus and Secor 2004; Kerr and Secor 2009).

During the past 30 years or so, otolith scientists have uncovered fascinating patterns of diversity not only in migration and life-cycle patterns but also in patterns of auditory processing, demographic modalities such as longevity and skipped spawning, early life history events, environmental exposures, and physiological capabilities. In my view, this diversity in life history, life cycles, and physiological and sensory responses is the single most transformative discovery associated with otolith science. In past otolith research and applications, we have

observed such patterns of diversity and published furiously (Fig. 1). In the coming years, our collective challenge will be to make sense of this diversity, to move beyond otolith research and application and begin generalizing, and testing new hypotheses related to the causes and consequences of the important forms of biodiversity that otolith science has uncovered.

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