

Otolith microstructure reveals ecological and oceanographic processes important to ecosystem-based management

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Abstract Information obtained from fish otoliths has been a critical component of fisheries management for decades. The nature of this information has changed over time as management goals and approaches have shifted. The earliest and still most pervasively used data are those of annual age and growth used to calculate the demographic rates of populations in single-species management strategies. Over time, the absence of simple stock-recruitment relationships has focused attention on the youngest stages, where otolith microstructure resolved on a daily basis has become a valuable tool. As management has transitioned to more ecosystem-based approaches, the need to understand ecological and oceanographic processes has been advanced through the analysis of daily otolith microstructure. Recent field examples illustrate how otolith microstructure data have been used to reveal environmental influences on larval growth, traits that lead to higher survivorship, mechanisms of larval transport, dynamics of dispersal and population connectivity, determinants of recruitment magnitude, carry-over processes between life stages, habitat-specific juvenile survival, and identification of natal sources. Daily otolith-derived data collected at an individual level are increasingly combined with data

from other disciplines and incorporated into individual-based models, which in turn can form the building blocks of complex models of ecosystem dynamics. A mechanistic understanding of the ecology of young stages is particularly necessary in light of a rapidly changing ocean environment, as we need to be able to predict individual and population responses to perturbations. Otolith microstructure analysis is an important tool in our management arsenal, contributing to a broader understanding of the oceanographic and ecological processes underlying ecosystem dynamics.

Keywords Fisheries oceanography · Population connectivity · Early life history · Larval and juvenile fish · Otolith increments · Larval age and growth · Larval transport

Introduction

Approaches to fisheries management have undergone major shifts over the past several decades. Traditional, single-species approaches have morphed into broader, more comprehensive ecosystem-based management. While a deep understanding of the ecology of individual species is still essential, management must now encompass other species, habitats, human usage needs, and socio-economics (Browman and Stergiou 2004; McLeod and Leslie 2009). The science needs for informing ecosystem-based management approach are vast and range from physical oceanography, larval

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dynamics, identification of habitats essential to survival, and predator-prey interactions, to coastal zone management, economics, extractive services, and socio-political constraints. See Gerber et al. (2003), Rice (2005), Francis et al. (2007), Cury et al. (2008), and Botsford et al. (2009) for more discussion.

Biological information such as longevity, age at first reproduction, and growth rates for individual fish species is based extensively on data obtained from annual otolith increments. Traditional single-species management has relied on age and growth data extracted from the analysis of the otoliths of different populations. Annual otolith increment interpretation therefore has a long and valued history in fisheries management. To date, there is still no more direct method for obtaining fundamental biological and ecological data for particular fish species. Life history data for year 1+ individuals, species, and populations remain a central component of fisheries management today. However, during the past century, recognition of the importance of early (< year 1) life stages to population dynamics has grown, generating an array of hypotheses and entire fields of research (fisheries oceanography). Testing these hypotheses and exploring the early life of fishes has been greatly enhanced through the discovery by Pannella (1971) of the existence of daily increments deposited on otoliths.

The shift to studying early life stages can be traced to Hjort (1914) who tracked a single year class of Atlantic herring over multiple years, highlighting the importance of early stages in determining recruitment¹ strength. Hjort's *Critical Period Hypothesis* maintained that recruitment was linked to first feeding by larvae and his *Offshore Transport Hypothesis* stated that ocean currents can transport larvae away from favorable feeding areas. In the mid-1970s, around the time otolith daily increments were discovered, a diversity of hypotheses explaining processes occurring during early life began to emerge. Building upon the emphasis on larval feeding, Cushing's (1975) *Match-Mismatch Hypothesis* stated that variable larval growth results from the degree to which fish spawning is temporally

synchronized with variable plankton blooms. Directly related to seasonal changes in water column stratification, plankton blooms cascade to secondary production of prey for larval fishes. Lasker's (1981) *Stable Ocean Hypothesis* suggested that larval feeding success is related to calm ocean conditions when a stratified ocean allows for sufficient larval fish food concentrations. Sinclair's (1988) *Member-Vagrant Hypothesis* emphasized that reproductive strategies favor larval retention: larvae spawned in optimal locations are retained in the population as "members"; larvae spawned elsewhere become "vagrants". Shifting from transport to survival, Houde's (1987) *Stage Duration Hypothesis* noted that larval mortality due to predation is high and therefore a shorter larval duration should enhance survival, while Miller et al. (1988) emphasized the importance of size to larval survival. The "*Bigger is Better*" hypothesis suggests that because of gape-limited predation, being larger at a given age is a survival advantage (Anderson 1988). These and other hypotheses have been and continue to be investigated by individual researchers as well as fisheries oceanographers in large research programs, beginning in the 1950s with programs such as CalCOFI (California Cooperative Oceanic Fisheries Investigations), which focused on Pacific sardine and northern anchovy, and continuing to the present with ongoing GLOBEC (Global Ocean Ecosystem Dynamics) efforts. For reviews and discussions of hypotheses and paradigms in fisheries oceanography see Chambers and Trippel (1997), Cowan and Shaw (2002), Govoni (2005), Leggett and Frank (2008), and Miller and Kendall (2009).

The daily microstructure of otoliths allows us to shine a light into the larval "black box" and identify ecological and oceanographic processes that are important to population replenishment and fisheries recruitment. Such processes not only influence larval fish survival but also have the potential to affect a variety of other organisms and our understanding of these processes underlies many of the scientific data needs for ecosystem-based management. For example, at the heart of spatial management (e.g., establishing marine protected areas, MPAs) is the need to quantify population connectivity, or the degree to which local populations exchange reproductive propagules (reviewed in Cowen and Sponaugle 2009). Movements of other segments of the population are also important to define—from the settlement of pelagic larvae to benthic habitats and movement of juveniles among nursery habitats, to the

¹ The term 'recruitment' is used loosely to indicate entry of young into the population. For many studies cited here, this entry point refers to the transition from larvae to juveniles and is measured at some point during juvenile life. For studies of more commercially important fishery species, 'recruitment' may refer to the point when fish appear in the fishery.

sometimes-extensive spawning migrations of adults. These, together with patterns of fishing pressure, all contribute to the degree to which MPAs adequately sustain populations, maintain fishery yields, and promote ecosystem health (Botsford et al. 2009). However, successful population replenishment is not simply the movement of propagules between natal and nursery habitats. Offspring must grow, develop, and survive the journey both as larvae and then as juveniles to reach reproductive maturity. Particular habitats have differential value to different species and life stages, as evident in variation in growth and survival. It is also necessary to identify the various ecological interactions within and among species. Essentially, we need to have an understanding of population and community dynamics in a spatial context. To obtain these data a wealth of tools must be brought to bear, one of which is combining data from multiple disciplines with data from the daily microstructure of fish otoliths. This tool continues to reveal a diversity of ecological and oceanographic processes that are important in the early life of marine fishes and can help inform ecosystem-based management.

The goal of this paper is to simply highlight how data from daily otolith increments have contributed to our understanding of processes that underlie the

maintenance of viable marine ecosystems. It is not intended to be a thorough review of the topic, but is instead an introduction to a series of empirical studies of a variety of fish species from multiple marine ecosystems that were selected to illustrate the widespread value and applicability of such studies to ecosystem-based fisheries management. The focus is entirely on field studies of species that spend all or a portion of their life in marine or estuarine systems. In many cases, otolith microstructure studies from the 1980s and 1990s have made significant contributions to our understanding of such processes, but to emphasize recent advances, examples have been drawn exclusively from literature published during the past decade (2000–2010). See Fig. 1 and Table 1 for geographic coverage and species listings of cited examples.

Recent highlights

Influence of environment on larval growth

Temperature

Otolith microstructure analyses have allowed new insight on how temperature affects not only individual



Fig. 1 Geographical location of field studies cited here as examples of studies using daily otolith microstructure data to examine oceanographic or ecological processes occurring in marine or estuarine ecosystems. Note that in several cases a single point represents multiple studies. Thus the density of

points is not representative of the number of studies cited from a given area. Studies may also encompass a broader area than indicated by a single point, but only in the very broadest situation do two separate points represent a single study

Table 1 Fish species and their study region for cited examples of the use of daily otolith microstructure data to examine processes occurring during early life of marine and estuarine fishes

Order	Family	Species	Common name	Region	Reference
Anguilliformes	Anguillidae	<i>Anguilla bicolor pacifica</i> , <i>A. celebesensis</i> , <i>A.</i> <i>borneensis</i> , <i>A.</i> <i>marmorata</i> , <i>A. bicolor</i> <i>bicolor</i> , <i>A. mossambica</i>	Eels	SW Indian Ocean; W Pacific Ocean; Indonesian Sea	Kuroki et al. 2006; Robinet et al. 2008
	Anguillidae	<i>Anguilla anguilla</i> , <i>A. rostrata</i>	Atlantic eels (European, American)	Maine, USA; Portugal	Arai et al. 2000
	Congridae	<i>Conger conger</i>	Conger eel	Azores	Correia et al. 2002
Clupeiformes	Clupeidae	<i>Brevoortia tyrannus</i>	Atlantic menhaden	North Carolina and New Jersey estuaries; Delaware Bay, USA	Warlen et al. 2002; Light and Able 2003
	Clupeidae	<i>Clupea harengus</i>	Atlantic herring	Barents Sea; Irish Sea; Celtic Sea; North Sea; W Baltic Sea	Ottersen and Loeng 2000; Brophy and Danilowicz 2002; Clausen et al. 2007
	Clupeidae	<i>Ethmalosa fimbriata</i>	Bonga	W Africa estuaries	Panfili et al. 2005
	Clupeidae	<i>Sardinops melanostictus</i>	Japanese sardine	W North Pacific	Takasuka et al. 2007
	Clupeidae	<i>Sardinops sagax</i>	Sardine	E Indian Ocean, SW Australia	Muhling et al. 2008
	Clupeidae	<i>Sprattus sprattus</i>	Sprat	Baltic Sea; Irish Sea	Baumann et al. 2006, 2007; Lee et al. 2006
	Engraulidae	<i>Engraulis anchoita</i>	Anchovy	SW Atlantic, off Brazil	Castello and Castello 2003
	Engraulidae	<i>Engraulis encrasicolus</i>	Anchovy	Bay of Biscay	Allain et al. 2003
	Engraulidae	<i>Engraulis japonicus</i>	Japanese anchovy	Kuroshio-Oyashio region; Taiwan coastal waters, W North Pacific	Takahashi et al. 2001; Chen and Chiu 2003; Takasuka et al. 2004, 2007; Takahashi and Watanabe 2005
	Engraulidae	<i>Engraulis ringens</i>	Anchoveta	Central Chilean coast	Castro and Hernandez 2000
Salmoniformes	Salmonidae	<i>Oncorhynchus</i> <i>tshawytscha</i>	Chinook salmon	West coast U.S.A.	Barnett-Johnson et al. 2007
	Salmonidae	<i>Oncorhynchus</i> spp.	Pacific salmon	Southeastern Alaska, N Pacific Ocean	Courtney et al. 2000
Aulopiformes	Synodontidae	<i>Saurida suspicio</i>	Caribbean lizardfish	San Blas Archipelago, Panama	Lemberget and McCormick 2009
Gadiformes	Gadidae	<i>Boreogadus saida</i>	Arctic cod	Greenland Sea	Fortier et al. 2006
	Gadidae	<i>Gadus morhua</i>	Atlantic cod	Icelandic Sea; Barents Sea; North Sea; Georges Bank, NW Atlantic Ocean	Marteinsdottir et al. 2000; Ottersen and Loeng 2000; Green et al. 2004; Nielsen and Munk 2004; Munk 2007
	Gadidae	<i>Melanogrammus</i> <i>aeglefinus</i>	Haddock	Barents Sea; North Sea	Ottersen and Loeng 2000; Green et al. 2004; Lapolla and Buckley 2005; Wright and Gibb 2005
	Gadidae	<i>Micromesistius</i> <i>poutassou</i>	Blue whiting	NE Atlantic	Brophy and King 2007
Scorpaeniformes	Sebastidae	<i>Sebastes capensis</i>	Rockfish	Southern Chilean fjords and coastal waters	Landaeta and Castro 2006
	Sebastidae	<i>Sebastes melanops</i>	Black rockfish	NE Pacific (Oregon, USA)	Miller and Shanks 2004
Perciformes	Moronidae	<i>Dicentrarchus labrax</i>	Sea bass	Portugal estuaries	Vinagre et al. 2009
	Moronidae	<i>Morone americana</i>	White perch	Chesapeake Bay, USA	Kraus and Secor 2004; Kerr and Secor 2009

Table 1 (continued)

Order	Family	Species	Common name	Region	Reference
	Serranidae	<i>Mycteroperca microlepis</i>	Gag	NE Gulf of Mexico	Strelcheck et al. 2003
	Serranidae	<i>Paralabrax clathratus</i>	Kelp bass	California coast, USA	Shima and Findlay 2002
	Sillaginidae	<i>Sillaginodes punctata</i>	King George whiting	S Australia	Fowler et al. 2000; Jenkins et al. 2000; Jenkins and King 2006
	Pomatomidae	<i>Pomatomus saltatrix</i>	Bluefish	W Atlantic Ocean; New Jersey, USA	Hare et al. 2002; Taylor et al. 2007; Callihan et al. 2008
	Sciaenidae	<i>Micropogonias undulatus</i>	Atlantic croaker	North Carolina estuaries, USA	Searcy et al. 2007
	Sciaenidae	<i>Sciaenops ocellatus</i>	Red drum	Galveston Bay, N Gulf of Mexico	Stunz et al. 2002
	Scombridae	<i>Scomber scombrus</i>	Atlantic mackerel	S Gulf of St. Lawrence	Robert et al. 2007
	Scombridae	<i>Scomberomorus niphonius</i>	Japanese Spanish mackerel	Seto Inland Sea, Japan	Shoji and Tanaka 2005, 2006
	Scombridae	<i>Thunnus orientalis</i>	Pacific bluefin tuna	NW Pacific Ocean	Tanaka et al. 2006; Satoh et al. 2008
	Scombridae	<i>Trachurus japonicus</i>	Jack mackerel	Sagami Bay, Japan	Xie and Watanabe 2007
	Istiophoridae	<i>Makaira nigricans</i>	Blue marlin	Bahamas, Straits of Florida	Sponaugle et al. 2005a, 2010
	Cichlidae	<i>Sarotherodon melanotheron</i>	Tilapia	W African estuaries	Panfili et al. 2005; Diouf et al. 2009
	Pomacentridae	<i>Amphiprion akindynos</i>	Anemone-fish	Great Barrier Reef, N Australia	Gagliano and McCormick 2004
	Pomacentridae	<i>Chromis chromis</i>	Damselfish	NW Mediterranean Sea	Macpherson and Raventos 2005
	Pomacentridae	<i>Chromis viridis</i>	Damselfish	Gulf of Aquaba, Red Sea	Ben-Tzvi et al. 2007, 2008
	Pomacentridae	<i>Dascyllus marginatus</i>	Damselfish	Red Sea	Ben-Tzvi et al. 2007
	Pomacentridae	<i>Neopomacentrus filamentosus</i>	Damselfish	Dampier Archipelago, Western Australia	Vigliola et al. 2007
	Pomacentridae	<i>Pomacentrus ambonensis</i>	Ambon damselfish	Great Barrier Reef, N Australia	Gagliano and McCormick 2004; Hoey and McCormick 2004; McCormick and Hoey 2004; Gagliano et al. 2007, 2008
	Pomacentridae	<i>Pomacentrus coelestis</i>	Damselfish	E Indian Ocean, W Australia	Meekan et al. 2003
	Pomacentridae	<i>Pomacentrus moluccensis</i>	Damselfish	Great Barrier Reef, Australia	Brunton and Booth 2003
	Pomacentridae	<i>Stegastes partitus</i>	Bicolor damselfish	San Blas, Panama	Wilson and Meekan 2002
	Labridae	<i>Thalassoma bifasciatum</i>	Bluehead wrasse	Barbados; Florida Keys; St. Croix, US Virgin Islands	Searcy and Sponaugle 2001; Sponaugle and Pinkard 2004; Grorud-Colvert and Sponaugle 2006; Sponaugle and Grorud-Colvert 2006; Sponaugle et al. 2006, 2009; Hamilton et al. 2008
	Labridae	<i>Xyrictys novacula</i>	Pearly razorfish	W Atlantic Ocean	Hare et al. 2002
	Stichaeidae	<i>Ulvaria subbifurcata</i>	Radiated shanny	Newfoundland	Dower et al. 2002
	Tripterygiidae	<i>Forsterygion lapillum</i>	Triplefin	New Zealand harbor and coastal waters	Shima and Swearer 2009
	Blenniidae	<i>Lipophrys trigloides</i>	Blenny	NW Mediterranean Sea	Macpherson and Raventos 2005
	Acanthuridae	<i>Acanthurus chirurgus</i>	Doctorfish	Panama	Bergenius et al. 2002
Pleuronectiformes	Pleuronectidae	<i>Limanda limanda</i>	Common dab	Irish Sea	Lee et al. 2006
	Pleuronectidae	<i>Pleuronectes platessa</i>	Plaice	Irish Sea	Fox et al. 2007
	Pleuronectidae	<i>Pseudopleuronectes americanus</i>	Winter flounder	New Jersey estuaries, USA	Sogard et al. 2001

Table 1 (continued)

Order	Family	Species	Common name	Region	Reference
		Generic fish or meta-analysis of multiple species		All Oceans; Caribbean Sea; SE US coast	Benoît et al. 2000; Lester and Ruttenberg 2005; Cowen et al. 2006; Laurel and Bradbury 2006; Edwards et al. 2007; Bradbury et al. 2008

larval growth rates, but the underlying phenology between oceanographic conditions and recruitment. An excellent example of the often-tight correlations between growth of larvae in the field and *in situ* water temperatures is illustrated by Baumann et al. (2006). Using a combination of hydrodynamic modeling and otolith microstructure analysis, standardized growth of young of the year sprat in the Baltic Sea was correlated with temperatures they likely experienced. Mean daily otolith increment widths closely tracked daily temperatures estimated from Lagrangian particle simulations. In another study off the coast of Japan, Takasuka et al. (2007) measured optimal temperatures of maximal growth for multiple cohorts of larval Japanese anchovy and sardine. Comparison of recent otolith growth revealed that larval growth of Japanese anchovy peaks at a higher temperature than that of Japanese sardine, potentially explaining their differential abundance during alternate environmental temperature conditions. Temperature was also found to be a primary driver of growth for the reef fish *Pomacentrus coelestis* in Western Australia. Comparing larvae collected during two summers of contrasting oceanographic conditions, Meekan et al. (2003) found that larval growth was determined more by temperature differences than prey abundance. Larval growth was lower during the summer when upwelling brought cooler temperatures and higher zooplankton biomass onto the shelf, and higher during the following summer when water temperatures were higher and prey more scarce. The strong dependence of larval growth on ambient water temperatures results in important environmental effects on recruitment magnitude (see below).

Spawning season

The tight relationship between temperature and larval growth also enables the pattern of increment widths in otoliths to uniquely record seasonality and spawning

events. Brophy and Danilowicz (2002) provide a clear example of this. Analyzing the otoliths of juvenile Atlantic herring collected in the Irish Sea, they were able to distinguish slow-growing larvae spawned in the autumn from fast-growing larvae spawned in the winter. Based on the proportions of juveniles with these life histories, they hypothesized that faster-growing larvae had been spawned in the Celtic Sea where temperatures were warmer and were transported into the Irish Sea, mixing with slower growing Irish Sea-spawned fish to create a heterogeneous pool of juveniles.

Water masses

Similarly, otolith microstructure can serve as a natural tag for water masses. Three-dimensional complexity in the ocean influences the distribution and growth of larval fishes, and patterns found within the otoliths can reveal this complexity. Reef fishes settling to the upstream Caribbean island of Barbados typically encounter oceanic waters except when low salinity mesoscale rings pinch off from the North Brazil Current, entrain Amazon River water, and propagate northwestward through the Caribbean. An 18-month time series of bluehead wrasse recruitment was compared to a concurrent record of salinity to distinguish larvae that encountered a low salinity current ring during their larval period from those that did not (Sponaugle and Pinkard 2004). Larvae that encountered a ring during at least half of their larval period grew more slowly and attained smaller sizes-at-age than larvae that encountered only oceanic conditions, demonstrating that encounter with particular oceanographic features has direct (in this case negative) consequences for larvae. Larval encounter with other features can be positive: Cod larvae collected in the vicinity of a hydrographic front in the North Sea exhibited faster growth than larvae collected farther away (Munk 2007). On a larger

spatial scale, Atlantic blue marlin larvae from two neighboring but distinct oceanographic areas—Exuma Sound, Bahamas, and the Straits of Florida—had different patterns of growth rates (faster in the Exuma Sound), although the underlying cause of this variation among water masses was unclear (Sponaugle et al. 2005a). In another example, larval anchovy in the southwest Atlantic off Brazil had increasing growth rates in upwelling areas whereas growth rates of larvae in areas with more stable water columns decreased over time (Castello and Castello 2003). Water masses can have clear effects on larval growth and survival, and otolith microstructure data allow us to track these relationships.

Distance from shore or prey availability

Daily otolith growth records have revealed that larvae distributed at various distances from shore or feeding on different prey exhibit different growth rates. Analysis of the otoliths of Japanese anchovy larvae and early juveniles collected in the Kurashio-Oyashio transition region demonstrated that mean and recent larval growth declined from inshore to offshore waters (Takahashi et al. 2001). This pattern was not due to temperature differences, but was most likely related to higher copepod abundances in inshore waters. However, a subsequent study identified inter-annual differences in the pattern of inshore-offshore growth and suggested that these were a function of both prey availability and water temperature. Recent growth of larval Japanese anchovy appeared to be determined primarily by water temperature in waters <math><16^{\circ}\text{C}</math>, but primarily by prey availability in warmer waters (Takahashi and Watanabe 2005). In another oceanographically dynamic region, larvae of a common Caribbean reef fish distributed across the Straits of Florida had higher growth and fuller guts towards the western side of the Straits where their prey were more abundant (Sponaugle et al. 2009). Recent growth of zooplanktivorous blue marlin larvae in the same area was also higher in the west, but this was related not to gut fullness, but to prey composition (Sponaugle et al. 2010). Similarly, off southern Chile, rockfish larvae on the shelf and outer portions of fjords grew faster than larvae in the inner fjords, co-occurring with higher abundances of larger calanoid copepod prey (Landaeta and Castro 2006). Variation in prey availability does not always translate into

spatial patterns of growth, but may be evident over temporal scales. Growth and feeding incidence of larval Japanese Spanish mackerel in the Seto Inland Sea were higher in a year when their clupeid prey were more abundant, leading to higher recruitment (Shoji and Tanaka 2005). Otolith-derived growth rates for larval cod on Georges Bank were higher in late spring of a year when early copepodites were more abundant due to variation in the timing of seasonal warming (Green et al. 2004). In contrast, Lee et al. (2006) used a combination of otolith microstructure and RNA/DNA ratios to determine that patterns in dab and sprat larval growth did not reflect food availability, but instead were highly heterogeneous, suggesting a complex relationship between production and larval growth. Growth of anchoveta larvae off central Chile, was similarly not food-limited (Castro and Hernandez 2000). High larval growth does not always lead to high larval abundances or recruitment. Although larval sardine growth rates were surprisingly high off southwestern Australia, larvae spawned during peak productivity periods were rapidly advected southward by the Leeuwin Current, resulting in low population abundances (Muhling et al. 2008).

Selective mortality: who is surviving & why?

Size, age, and growth

Natural variation in larval age and growth (as due, for example, to temperature, oceanographic features, and prey availability as above) provides fodder for mortality to be non-random and otolith microstructure is an useful tool for examining mortality on a fine scale. Larvae with variable traits may be more or less susceptible to starvation or predation by gape-limited predators. For example, comparison of the early growth of Pacific bluefin tuna larvae of different ages revealed that post-flexion larvae were larger at age during the first 12 days of life than either pre-flexion or flexion stage larvae (Tanaka et al. 2006), indicating that smaller individuals were preferentially removed from the population. Similarly, juvenile anchovy collected from the Bay of Biscay grew more rapidly at early ages than larvae from the same cohort (Allain et al. 2003). Further, juveniles collected off the French coast grew more rapidly as larvae than juveniles collected off the Spanish shelf, suggesting different levels of growth-selective mortality. Growth-

and size-selective mortality were also demonstrated for North Sea cod where older individuals from each of two out of three monthly cohorts had significantly higher larval growth and larger sizes-at-age (Nielsen and Munk 2004). Growth-selective mortality was also evident in first-feeding Japanese Spanish mackerel larvae in the Seto Inland Sea, with the strength of this selectivity varying among years likely due to differential prey availability (Shoji and Tanaka 2006).

Birthdate

Otolith microstructure enables the back-calculation of birth (spawning) date for individuals and provides insight into the relationship between spawning behavior and recruitment. Survival may be selective based on spawning or hatching date and a comparison of these data among different age groups enables a determination of which portion of the spawn contributes to the population and, potentially, under what environmental conditions survival may be enhanced. Several examples demonstrate temporal variation in survival probabilities by birthdate. In one case, comparison of birthdates of settled juvenile haddock to egg densities around Georges Bank indicated selection for early and mid-season hatching (Lapolla and Buckley 2005). Similarly, when back-calculated birthdates of juvenile North Sea haddock were compared to adult egg production, it was evident that only a portion of the spawn each year survived to the juvenile stage, although the relative contributions of the different portions varied by year (Wright and Gibb 2005). In contrast, Fox et al. (2007) found a close correspondence between the back-calculated birthdates of juvenile plaice in the Irish Sea and the distributions of spawning from an egg production model, indicating the lack of selective survival. Where environmental data are also available, possible sources of variation in birthdate survival may be apparent. For example, an interaction of birthdate and water temperature likely underlies the observation that juvenile jack mackerel collected from Sagami Bay, Japan, had both successful winter and spring larval hatchdates, whereas juveniles from Fukawa Bay were typically only from later (spring) hatches (Xie and Watanabe 2007). Cooler, suboptimal winter water temperatures in Fukawa Bay are not conducive to survival of winter-recruiting fish. In another example, analysis of daily otolith increments enabled Callihan

et al. (2008) to determine that Chesapeake Bay populations of bluefish are dominated by the spring-spawned cohort, whereas the summer spawned cohort is more abundant in Maryland coastal waters. Inter-annual variation in the timing of these cohorts led to the hypothesis that patterns of vernal warming influence the degree to which bluefish spawning in the Middle Atlantic Bight occurs in discrete events. These otolith-based studies show that seasonal and interannual environmental variation can drive patterns of spawn survival that can ultimately influence recruitment. By removing particular segments of the population, fishing practices can also play a role in influencing spawning patterns, larval survival, and recruitment (reviewed in Wright and Trippel 2009).

Predation

A creative otolith microstructure approach has been used to directly point to the role of selective predation. Takasuka et al. (2004) examined the otoliths of Japanese anchovy larvae cannibalized by juvenile anchovy and those ingested by skipjack tunas and compared the larval growth of these prey larvae to the original population of anchovy larvae. Cannibalized larvae were smaller-at-age and larvae preyed upon were larger-at-age than the original population. Further, where prey sizes overlapped, juvenile anchovy selected slower growing larval prey, whereas there was no difference in the growth of larvae preyed upon by skipjack tunas.

Patch-specific rates

Many ichthyoplankton field studies integrate sampling over meso-spatial scales that fail to capture small physical and biological features. Yet, patches of larvae may have growth and mortality signatures unique to each patch and differential survival of patches could lead to heterogeneous population contributions. This patchiness element was demonstrated by Dower et al. (2002) who tracked three patches of larval radiated shanny in Newfoundland bays. Between-patch differences in growth were consistent with temperature differences but not prey availability, even though prey availability explained 38% of the variation in gut contents. The importance of patchiness was also evident in a study on bluefin tuna larvae by Satoh et al. (2008). They showed that

instantaneous mortality rates of bluefin tuna larvae in the northwestern Pacific Ocean varied significantly among three patches and were generally higher than most literature estimates. These examples illustrate how otolith microstructure analysis can provide important data for understanding how patches function as we explore dynamics at smaller and smaller spatial and temporal scales.

Larval transport mechanisms

Defining the pathways between spawning locations and juvenile habitats is critical for a complete understanding of population replenishment in organisms with complex life histories. Physical oceanography interacts with biology to bring about variability in the replenishment success of local populations (Cowen 2002, Sponaugle et al. 2002). Identifying the physical and biological processes associated with larval transport, or the movement of larvae between areas (Pineda et al. 2007), can be challenging. Daily otolith increments provide a direct measure of pelagic larval duration (PLD), which is useful in determining the potential extent of transport (see below). Daily otolith increments can also provide information on the timing of settlement to evaluate the role of particular physical transport processes. For example, by using otoliths to back-calculate the timing and magnitude of recruitment of two damselfishes to reefs in the Red Sea, Ben-Tzvi et al. (2007) found a strong correlation between recruitment magnitude and strength of downwelling flow. In another example, a very large settlement pulse of a diversity of reef fishes occurred during the nearshore passage of a mesoscale eddy by the upper Florida Keys, and otolith-derived larval ages of the more abundant taxa pointed to larval entrainment along the Keys during eddy translocation (Sponaugle et al. 2005b). Another important context for studying larval transport is that of time, or duration, over which specific processes may be acting. Otolith increments can also provide information about the time or duration larvae may be associated with particular phases of the transport process. In one illustration of this, Hare et al. (2002) hypothesized that larval fish spawned south of Cape Hatteras off the U.S. east coast are transported northward by the Gulf Stream and its associated warm core rings. They created a probability model based on hydrographic (sea surface temperature) and

drifter data coupled with a larval mortality function. Modeled larval transport times agreed closely with the age distribution of larval bluefish and pearly razorfish collected in the Middle Atlantic Bight. Another study used otolith growth patterns to infer a larval transport route: Growth rates tend to be higher for larval Japanese anchovy collected in coastal waters of Taiwan compared to larvae collected offshore (Chen and Chiu 2003). Yet coastal larvae have more variable otolith growth trajectories that include an early period of slower growth, followed by a period of faster growth, consistent with a hypothesis of offshore-to-onshore transport by a coastal current. Although not directly identifying specific transport mechanisms, Arai et al. (2000) found the PLD of the European eel to be ~40 d longer than American eel, consistent with the European eel's longer transit to separate geographical areas from common spawning grounds in the Sargasso Sea. Abundant data on the timing of eel migration has led to an integrated view of the evolution and persistence of migration pathways among different eel species (e.g., reviewed in Tsukamoto et al. 2002).

Dispersal & population connectivity

The length of time larvae spend in the plankton (PLD) prior to recruiting to the juvenile population is a primary variable in estimating dispersal and connectivity among populations and daily otolith increments provide accurate measures of PLD. Most estimates of dispersal kernels rely on models that include oceanographic data coupled with biological data on larval behavior, survival, and PLD (Werner et al. 2007). Cowen et al. (2006) constructed a matrix map of dispersal probabilities throughout the Caribbean for a reef fish with an average 28 d PLD. Running the biophysical model over multiple years provided robust estimates of connectivity among islands and identified three distinct biogeographical regions. Model runs in a different system off the southeast U.S. coast revealed that not only is PLD central to defining dispersal kernels, but spawning timing and location play an important role (Edwards et al. 2007). Benoît et al. (2000) demonstrated that temperature is the dominant influence on PLD, which decreased exponentially with increasing temperature across species and populations of marine fishes. Such temperature dependence of PLD can impart considerable spatial variability to transport outcomes and

population connectivity. For example, compiling data on PLD and genetic differentiation for a broad range of marine fish species, Bradbury et al. (2008) demonstrated that dispersal increases with latitude, adult body size, and water depth. The increased dispersal potential, PLD, and genetic homogeneity of fishes in higher latitudes points to the need for larger MPAs in those areas (Laurel and Bradbury 2006). In a meta-analysis of PLD and range for tropical fishes from different oceans, Lester and Ruttenberg (2005) found that dispersal potential and range size are positively related only in the Indo-Pacific, where the pattern is driven by the spatial distribution of habitat and dispersal barriers. Further, they found evidence that speciation rate may be negatively related to dispersal potential. Such meta-analyses are beginning to provide a more synthetic, global view of dispersal.

Empirical estimates of larval dispersal are fewer and frequently less direct. One example is the use of a combination of otolith microstructure and micro-chemistry to estimate the dispersal of black rockfish along Oregon, USA (Miller and Shanks 2004). Their results suggested that larvae did not mix during ontogeny and that dispersal distances are shorter than predicted by models of passive dispersal.

Determinants of recruitment magnitude

Difficulties predicting recruitment strength from adult population abundances largely gave rise to the field of fishery oceanography and the central focus on understanding recruitment has not diminished over time. Larval traits obtained from otolith microstructure such as size at hatching, growth and survival (including temperature-mediated), size at settlement, and condition/stress have all been correlated with recruitment.

Size at hatching and larval growth

Larger hatch sizes and faster larval growth should increase survivorship and thus result in higher levels of larval settlement or juvenile recruitment. Evidence for the former was shown for larvae of a Mediterranean blenny (but not a pomacentrid from the same region), where larvae that were larger at hatching settled to the reef in larger events (Macpherson and Raventos 2005). The importance of larval growth to recruitment was

evident in Panama, where monthly settlement strength of a surgeonfish was correlated with larval growth during the first two weeks following the onset of feeding (Bergenius et al. 2002). Similarly, larval growth as determined from otolith increments was directly correlated with postlarval abundance of King George whiting in a temperate Australian Bay (Jenkins and King 2006). Robert et al. (2007) found that strong recruitment of Atlantic mackerel in the Gulf of St. Lawrence was a function of fast larval growth and weak selection for fast growth.

Temperature-mediated growth and survival

As poikilotherms, fish are particularly sensitive to fluctuations in water temperature, and evidence of the influence of temperature on larval growth and recruitment magnitude comes from a variety of latitudes, providing a mechanistic understanding of at least one source of recruitment success. In the Greenland Sea, Arctic cod produce two cohorts of larvae that experience different rates of survival associated with temperature (encounter with $<0^{\circ}\text{C}$ water reduces larval survival; Fortier et al. 2006). The summer-spawned cohort typically has higher survival and hence, stronger recruitment, but spring-spawned larvae that survive are larger-at-age by the end of the summer, pointing to a possible selective advantage to the persistence of spring spawning. Larval size and abundance and recruitment are all strongly temperature-dependent in Barents Sea cod, haddock, and herring (Ottersen and Loeng 2000). Even at low latitudes, water temperature influences larval growth and recruitment. Variation in water temperature explained 78% of the variation in larval growth of bluehead wrasse in the upper Florida Keys, and once recruitment events associated with the passage of mesoscale eddies were removed, variation in water temperature predicted juvenile recruitment strength (Sponaugle et al. 2006).

Size at settlement

Size at settlement is a function of larval growth and PLD and can also be related to recruitment magnitude. Pulses of bicolor damselfish settlement to Panama over 18 months were strongly correlated with size-at-settlement as determined from otolith increments: larger fish settled in larger events (Wilson and Meekan 2002).

Condition, stress, and otolith asymmetry

Fluctuating asymmetry between pairs of otoliths has been suggested as a measure of condition or stress in individuals (e.g., Gagliano and McCormick 2004; Panfili et al. 2005). Recently, Lemberget and McCormick (2009) demonstrated that individual Caribbean lizardfish settling to Panama in larger pulses had lower residual otolith asymmetry. Such asymmetry has also been shown to negatively influence the ability of larvae to respond to particular sound frequencies during settlement, potentially disrupting their ability to detect suitable settlement habitats (Gagliano et al. 2008). Thus, otolith asymmetry appears to provide a unique measure of relative condition (direct or indirect) that is preserved in hard parts.

Carry-over from larval life to juvenile survival

Variation in larval life (early life history traits) not only influences survival of larvae, but can “carry-over” and influence survival of juveniles. Shima and Findlay (2002) compared instantaneous larval growth of juvenile California kelp bass of three different ages and found that older survivors were those with faster larval growth rates. Similarly, during a caging experiment on the Great Barrier Reef, juvenile *Pomacentrus amboinensis* damselfish survivors were those that were larger-at-age and grew faster during the second half of their larval period (McCormick and Hoey 2004). Interestingly, predators of different sizes had contrasting impacts on mortality patterns, which were obscured when young fish were naturally exposed to a range of predators. Comparing this same species between reefs with and without predators demonstrated that higher levels of predation led to stronger patterns of selective mortality on larval traits (Hoey and McCormick 2004). Although larval growth rate remains the most important determinant of early survival of juveniles in this damselfish, the direction of selective mortality can change during the first 8 wks of juvenile life (Gagliano et al. 2007).

Condition at the time of larval settlement to benthic habitats is a product of larval life. A measure of settlement condition is recorded in the width of the metamorphic band deposited during settlement in the otoliths of bluehead wrasse (Searcy and Sponaugle 2001; Hamilton et al. 2008). For fish settling to Barbados, the Florida Keys, and St. Croix, surviving

juveniles were those that were of higher condition at the time of settlement (Searcy and Sponaugle 2001; Sponaugle and Grorud-Colvert 2006; Hamilton et al. 2008). Hamilton et al. (2008) combined otolith microchemical signatures with otolith microstructure data to distinguish juveniles that had developed nearshore versus offshore as larvae and showed that selection for high settlement condition was greater for larvae that had developed nearshore. Events during larval life can influence juvenile behavior and consequently survival. To examine the behavioral mechanisms underlying selective mortality in bluehead wrasse, Grorud-Colvert and Sponaugle (2006) tested new recruits and found that larvae settling at higher condition levels were able, as juveniles, to evade a simulated predator threat at faster speeds. These high condition fish also exhibited less risk-taking behavior. For juvenile white perch in a Maryland estuary, a combination of otolith microstructure and microchemical data revealed that individuals with higher larval growth tended to remain in freshwater as juveniles, whereas those with lower larval growth moved to brackish waters where juvenile growth rates were higher (Kraus and Secor 2004). This brackish contingent consistently dominated the adult population.

Density dependence and post-settlement mortality

Survival of juveniles is also influenced by population density, with mortality often being related directly to juvenile traits. Such traits can be quantified with otolith microstructure data. Repeated sampling of cohorts of a damselfish on reefs of Western Australia revealed that smaller, slower-growing individuals were lost from the population over time and the strength of this selection was related to settlement density (Vigliola et al. 2007). Further, significant genetic structure between age groups indicated a relationship between phenotype and haplotype. Mortality of a damselfish on the Great Barrier Reef was also density-dependent and otolith microstructure analysis revealed the existence of size-dependent mortality, but only at sites with high mortality rates (Brunton and Booth 2003). Baumann et al. (2007) compared juvenile growth of young sprat collected in coastal waters to those collected later in offshore waters of the Baltic Sea and found that younger juveniles had a sharp decline in otolith growth not evident in the otolith growth records of older recruits.

They hypothesized that poor feeding conditions leading to juvenile starvation may be a density-dependent mechanism in coastal waters.

Habitat-specific growth of juveniles

Various juvenile habitats may be differentially beneficial to juveniles and daily growth estimates can help quantify these contributions. Stunz et al. (2002) caged red drum juveniles in three different nearshore habitats in the Gulf of Mexico and found that juvenile growth was highest in marsh and seagrass enclosures relative to non-vegetated bottoms and oyster reefs. However, there is likely substantial natural movement among different habitats as uncaged juveniles collected from the different habitats had similar growth rates. Comparisons of juvenile growth among different habitats can also be confounded by environmental variation. For example, young Atlantic croaker juveniles collected from two different North Carolina (USA) estuaries had distinct patterns of juvenile growth, but because selective mortality was stronger in one of the estuaries, comparison of juvenile growth among older survivors revealed no differences between the estuaries (Searcy et al. 2007). Such complex relationships between growth and other selective mortality processes may underlie the conflicting results Strelcheck et al. (2003) found regarding latitudinal variation in gag growth. Young juveniles appear to be larger towards the south in the eastern Gulf of Mexico, but it is not clear that these size differences are due to latitudinal patterns of growth. The role of temperature variation was similarly apparent in latitudinal variation in the growth of young sea bass from four estuaries along the Portugal coast (Vinagre et al. 2009). During ten years of recruitment to New Jersey estuaries, winter flounder juveniles consistently metamorphosed later, had higher densities, and grew faster in the northernmost of four estuaries (Sogard et al. 2001). These large-scale patterns provided a backdrop for more variable temporal fluctuations in juvenile growth among estuaries due to local-scale processes. Temperature differences rather than habitat quality per se may underlie higher growth of summer-spawned bluefish juveniles collected off New Jersey ocean beaches relative to those from neighboring estuaries (Taylor et al. 2007). In addition to temperature and latitude, salinity can influence fish growth in estuaries. Growth and

condition of juvenile tilapia over two years in West African estuaries varied directly with salinity (Diouf et al. 2009). White perch juveniles occupying brackish portions of Chesapeake Bay had higher growth rates than those resident in freshwater habitats, consistent with laboratory experiments demonstrating that the brackish contingent had higher consumption rates and a higher scope for growth (Kerr and Secor 2009). Thus, otolith microstructure enables the evaluation of habitat quality to juveniles, including the role of other environmental variables such as temperature and salinity.

Identification & importance of natal sources

Identification of natal sources of marine larvae is at the heart of understanding population connectivity. The most direct techniques to identify natal sources involve the use of natural or artificial otolith microchemical tracers [see Campana and Thorrold (2001), and Elsdon et al. (2008) for reviews], but studies that use otolith microstructure or a combination of otolith microstructure and microchemistry are making valuable contributions to the field. Hatchery-reared Chinook salmon in California can be easily distinguished from wild populations by the existence of wider, more uniform otolith increments immediately following the onset of exogenous feeding (Barnett-Johnson et al. 2007). Thermally induced marks on the otoliths of juvenile Pacific salmon from southeastern Alaska suggested that most juveniles were sourced from hatcheries in southeastern Alaska (Courtney et al. 2000). Marteinsdottir et al. (2000) compared hatch dates of juvenile cod collected from the north, west, and east coasts of Iceland with known spawning dates from the main spawning grounds along the south–southwest coast and found that surviving juveniles were actually sourced from other areas. Otolith microstructure data on hatching season also allowed classification of stocks of Atlantic herring in the North Sea and western Baltic Sea (Clausen et al. 2007). Adult blue whiting in the northeast Atlantic could be separated into two distinct stocks based on their larval growth histories: fish transported from south of the spawning grounds grew faster as larvae than fish transported from the north (Brophy and King 2007). Similarly, differences in otolith growth histories could be used to distinguish eels taking different migration pathways in the Indian Ocean (Robinet et al. 2008),

and in the Indo-Pacific (Kuroki et al. 2006). In the Atlantic, consideration of otolith-derived measures of PLD in the context of the regional currents indicated that conger eels from the Azores could not be sourced from known Mediterranean spawning grounds and suggested the existence of a more proximal spawning ground (Correia et al. 2002). Back-calculated birth-dates and known local temperatures led to the conclusion that winter-spawned juvenile Atlantic menhaden in Delaware Bay (Light and Able 2003) and New Jersey estuaries (Warlen et al. 2002) originated south of Cape Hatteras where waters are sufficiently warm for spawning and larval development. Otolith-derived estimates of PLD and hydrodynamic modeling pointed to the existence of a single spawning stock of King George Whiting in Victoria, Australia (Jenkins et al. 2000), but multiple local sources for populations located farther to the west (Fowler et al. 2000). A combination of otolith microchemistry and microstructure analysis revealed that northern populations of a Red Sea pomacentrid are sourced from populations distributed along the Saudi and Sinai coasts (Ben-Tzvi et al. 2008). Such results clearly have important regional management implications. A similar combination of otolith microstructure and microchemistry data was used in New Zealand to distinguish the relative contributions of larval sources from transport pathways for a coastal triplefin (Shima and Swearer 2009). These authors found that larval dispersal history was more important than natal source in influencing larval quality: Larvae retained within a nutrient-enriched harbor were of higher quality than those dispersed along the coast. Together, these examples illustrate how otolith microstructure analyses can provide valuable data for interpreting sources of larvae to local populations.

Conclusions and future directions

The goal of this review was to demonstrate, through recent examples from the literature, how otolith microstructure analysis has and should continue to provide critical data on ecological and oceanographic processes occurring during the early life of fishes. As with any tool, otolith microstructure analysis is not without problems and requires careful use and interpretation [see technical reviews such as Panfili et al. (2002, 2009), Sponaugle (2009), Vigliola and

Meekan (2009) for details], but when applied appropriately, results can provide unique data to reveal processes in the ocean and inform the management of marine ecosystems. When otolith microstructure data are combined with data from other disciplines, it is apparent that detailed age and growth records can help pinpoint key events occurring during the earliest stages. Examples cited here include studies that have combined otolith microstructure data with data from fields of oceanography, hydrodynamic modeling, microchemistry, larval behavior, predator and prey dynamics, benthic ecology, and genetics. Of course, there is room for new avenues of multidisciplinary studies, such as those combining otolith microstructure data with genomics and larval physiology to explore, for example, individual performance and response to contaminants and stressors. All of these approaches will need to be utilized and eventually integrated to consider the impacts of future global climate change predictions, from changes in extractive patterns and altered coastal habitats to the effects of ocean acidification.

As we continue to link more fields together, the ultimate step will be to build models that incorporate ecosystem processes. Simply describing ecosystems today is insufficient. We need to understand how ecosystems *function* to enable predictions of responses of individuals and populations to perturbations. Individual-based models are a positive step towards this end and in some cases are well developed and even imbedded in some population and ecosystem models (e.g., Folkvord 2005; Fiksen et al. 2007; Megrey et al. 2007; Daewel et al. 2008; Kühn et al. 2008). Including physical oceanographic and nutrient-phytoplankton-zooplankton (NPZ) models within ecosystem models will enable the tracking of changes in ocean temperature, chemistry, food, and predators over long time frames. The observed larval growth and mortality responses to these factors, as identified through otolith studies, provides a critical tool for evaluating the early life history of fish populations in an ecosystem context. In a comprehensive review, Cury et al. (2008) broadens the field of fisheries oceanography to include ecosystem components and interactions with climate change and exploitation. “Ecosystem oceanography” encompasses the melding of a suite of models with empirical data. Some of the empirical data needs can be met with analyses of otolith microstructure.

The need for empirical data to feed into increasingly complex models should not diminish with time and some of these data will be obtained remotely. As more ocean observing networks are established, we should consider how we might revolutionize otolith tools to take advantage of these new data streams. In addition to field studies such as those cited here, laboratory experiments will continue to enable us to test the effects of variables under controlled conditions, and validate and aid our interpretation of field observations. We need to strive to be increasingly creative with how we obtain data and select new fields to link with otolith studies. Finally, successful application of results to management will require enhanced efforts at communicating the relevance and significance of understanding ecosystem processes to the management and conservation of our natural resources.

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