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BOOK REVIEW

An ecological perspective on the migrations of marine fishes

Reviewing: David Hallock Secor, Migration Ecology of Marine Fishes. 2015 John Hopkins University Press, 292 pp

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The diverse movements of animals are unified by the problem that locations that are most favorable at one particular time are not likely to be the most favorable at another. This might be due to environmental variation (e.g., diurnal or seasonal changes in temperature or food availability), or it could be intrinsic to the organism, as different life-stages may have very different requirements. Owing to the periodicity of environmental variability and animal life-cycles, one might anticipate that certain locations would become favorable, lose favorability, and become favorable again at somewhat regular intervals. Migratory animals take advantage of this predictable variability across space and through time by moving between or among locations as the need arises. Migration has evolved in numerous and diverse taxa, including cnidarians, arthropods, mollusks, fishes, amphibians, reptiles, birds, and mammals. Likewise, the habitats in which migration occurs are as varied as the Earth, ranging from the deep ocean to above Himalayas and everywhere in-between. For centuries, the apparent precision and ease by which animals travel across extraordinary distances has inspired considerable awe among humans. The numerical abundance and coordinated movement, rolling in waves of biomass across landscapes, surely plays an outsized role in ecological and evolutionary processes.

David H. Secor, professor at the University of Maryland, highlights the diversity, complexity, and ecological implications of migration in his 2015 book, *Migration Ecology of Marine Fishes*. At the outset, Secor notes that the inspiration for his book came from F.R. Harden-Jones's *Fish Migration* (1968). Early in Chapter 1, Secor informs readers that his book takes up on a "loose end" of what happens to fish that breakaway from the "migration triangle" that prominently featured in the work by Harden-Jones (in which larval fish disperse from spawning to nursery habitats, juveniles migrate to adult foraging habitats, and adults travel back and forth between foraging and spawning habitats). Being a relatively new student to fishes, I had only read a few excerpts from Harden-Jones's *Fish Migration*. So, I immediately put down Secor's book and read the entire text by Harden-Jones. First, the book by Harden-Jones is a gem. I could imagine why Secor would want to pick up where *Fish Migration* left off. Harden-Jones set a rigorous standard for scientific acceptance and laid out a number of vexing challenges that had yet to be adequately resolved.

Returning to the text by Secor, it quickly became apparent that Secor was extending the work by Harden-Jones into novel areas, rather than supplanting the classic text. Secor passes on most opportunities to show how an ecological perspective and modern methods might answer some of the obstinate questions left by Harden-Jones at the doorstep of scientists-yet-to-come. Instead, Secor largely sets his own course to

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examine the causes and consequences of diversity in marine fish migration and related life-cycles. His stated aim is to "portray migrations and life-cycles as complex adaptive systems" and to consider migration from the perspective of the population, rather than the individual. The value of *Migration Ecology of Marine Fishes* is that it provides accessible avenues for researchers that do study fish movement at the individual-level (or from behavioral and physiological perspectives) to consider the emergent properties that arise at the population level.

Below, I highlight a few elements from each of the seven chapters that I found particularly pertinent in the context of present research emphases in migration biology.

In the first chapter, "Introduction: The Hidden Lives of Marine Fish," Secor gives several working definitions, migration is "collective movement that occurs chiefly through motivated behaviors, resulting in changed ecological status." His preferred topic throughout the book clearly is "partial migration", as he views those segments of the population that do not strictly follow the migration triangle as uniquely important in a number of ecological processes, perhaps most notably, population resilience. He gives partial migration the, somewhat, peculiar definition of "the coexistence of two or more life-cycles within the same population. Traditionally considers migratory and sedentary life-cycles." Taken literally, as most definitions are expected to be, partial migration might not involve migration at all.

The second chapter, "Bird and Fish Migration: Movement Ecology as a Comparative Framework", begins with a matter-of-fact and *staccato* treatment of the biomechanics of fish locomotion, saving everyone a quick trip to find an animal physiology or biomechanics textbook to get up to speed on how fish move. It also presents methods for tracking animal movement, including the strengths and limitations of each approach. I appreciate Secor including a mild admonishment to move from descriptive telemetry studies to ones that focus on ecological questions guided by experimental design. He also rightly points out that life-cycle tracers (such as stable istopoes or genetic markers) do not influence future behavior or outcomes (unlike tagging, recapture, or telemetry), but rather, provide a largely unbiased perspective of prior movements. Secor also discusses some of the latest analytical methods for studying animal movement such as state-space models and Lévy walks. While Secor is enthusiastic about a number of emerging research areas, these do not appear to fall into that category. Rather, he seems to excuse these approaches as something to do with a lot of tracking data that was initially collected for descriptive studies. Indeed, pausing to read Harden-Jones's perspectives from 1968, one wonders whether the null hypothesis of state-space models and Lévy walks (variations on a "random walk") are inappropriately applied to swimming and flying organisms. Instead, the null hypothesis of an organism's movement in a fluid might be better framed as being attributable only to the fluid's velocity. In any case, the intricate sensory ecology of fishes (discussed immediately after this section) seems in conflict with the premise of movements being attributed to randomness.

Indeed, Secor seems to view one of the major advances in fish ecology is the expanded understanding of the navigational cues used by fish to orient. There are a couple of issues in this portion of Chapter 2 that might be worth clarifying in a second edition of the book. It might be beneficial to give readers, in simple terms, the idea that navigation requires a minimum of two steps, a map step (to pick a direction) and a compass step (to maintain the desired direction). In the text, these two steps, and the environmental cues that animals can use to achieve them are, at times, conflated. For instance, magnetic and celestial compasses might not only be used on a "regional basis" (p. 51), though this might be true of a magnetic or celestial map. Indeed, magnetic and celestial compasses have been shown in taxa transiting only a few meters [consider amphipods (Ugolini and Pezzani 1995) and dung beetles (Dacke et al. 2013)]. Likewise, mention of a "latitudinal compass" might be better referred to as a "latitudinal map." This section would be correct in stating that redundancy in compasses are well-established in diverse taxa, but the function and existence of redundant map information is less known. Similarly, Secor describes limitations of navigating with a geomagnetic map, rather than a geomagnetic compass as written (p. 58). Additionally, in the context of "limitations" of fishes and other animals navigating with a magnetic map, it is worth noting that bicoordinate navigation is possible with magnetic cues alone (Putman et al. 2011; Kishkinev et al. 2015). Secor attributes the advocating of a "cognitive map" in animals to Lohmann et al. (2008) (p. 52), but instead, the Lohmanns and I have rather tended to favor a broad definition of "maps" that do not presupose an animal has any mental conception or image of their location (e.g., Lohmann et al. 2007).

Chapter 3, "Mating Systems and Larval Dispersal", delves into the specifics of the ecological consequences of mating systems. Secor touts the proliferation of larval transport simulations within ocean circulation models as an invaluable tool for understanding processes of dispersal and connectivity that are difficult to directly observe. While I share his enthusiasm on the subject (and make use of such techniques myself), some additional consideration of the potential for bias and error should be mentioned (particular given the caution advocated for on pp. 109–110 related to interpreting the findings of sampling with a plankton net). While it is correct that many of the models are in agreement with available observations, care must be taken to note at what scale comparisons are made. *Reductio ad absurdum*: a completely unrealistic oceanic model could do a good job of predicting the distribution of larvae if the "grid cell" of comparison was an entire ocean basin. Secor emphasizes that the combination of behavior (especially, vertically-oriented swimming) and water currents drive larval movement. Additionally, he brings anthropogenic effects to the equation: fishing pressure can act as a selecting agent on mating systems, behavior, and distribution. The mechanisms of behavior (e.g., whether they are under genetic control or are culturally mediated) will shape to what extent human perturbations influence mating systems and thus fish migration. Unfortunately, these mechanisms of behavior are too poorly known to currently predict outcomes, which Secor convincingly argues is an important reason to increase basic research on fishes for successful management. In the middle of this chapter it feels like Secor finds his rhythm, voice, and an easy comfort with the subject matter that persists through the end of the book.

Chapter 4, "Complex Life Cycles and Marine Food Webs: Migrating Through Size Spectra", provides a useful contextualization of marine food webs by comparing them to their terrestrial counterparts. Secor does a particularly good job introducing "size spectrum theory", an important aspect of understanding the timing of fish reproduction and its role in population dynamics, in an intuitive and accessible manner. The designation of "r" and "K″ selected species (Pianka 1970) and optimization theory (Roff 1992) poorly explain teleost life-history traits and their "careless application" to fishes clearly raise the ire of Secor. He goes on to present a very nice factor analysis, original to the book, to bolster his view that fish possess three, somewhat continuous, life-history types (designated as periodic, opportunistic, and equilibrium) (pp. 118–119). He rounds out the chapter with an insightful description of schooling ecology and "the storage effect" - why managing for diversity in age structure is important for population resilience.

In Chapter 5, "Population Structure: Closed and Open Life Cycles", provides examples of the remarkable homing abilities in five case studies: Fraser River sockeye salmon, Celtic Sea Atlantic herring, Atlantic Bluefin tuna, reef fish, and elasmobranchs. Secor notes that the mechanisms that allow for this are sketchy, but are typically attributed to environmental imprinting or genetically inherited tendencies. In other species, however, migration might not be centered on the natal site and could be adopted through associations with different schools, through "tradition", or "ecological inheritance." These later migratory types have received scant consideration from the animal navigation community, but given that the mechanisms by which animals make movement decisions can greatly influence population-level processes (e.g., Putman et al. 2014), work in this area is sorely needed. From, Secor's description of different means by which migratory movements at the population-level emerge, coalesce, and diverge, the argument for spatially explicit stock models are cogent. Likewise, within this argument, the need to conserve multiple biological diversity metrics in populations (e.g., age, behavioral, and genetic) becomes unequivocal.

In Chapter 6, "Propagating Propensities: Partial Migration", Secor more strongly argues that the "migration triangle" proposed by Harden-Jones poses serious problems. In a strictly academic sense, I quite like the triangle. It elegantly explains a large proportion of the variation in life-cycles in marine fishes with three simple vertices. However, trouble often arises when taking a conceptual model as "True" rather than viewing it as a convenient simplification of reality. Secor correctly argues that explicit attention to partial migration (life-history diversity) is necessary given that humans' interactions with fish are not primarily an academic exercise. In the chapter that follows, he nicely shows how consideration of diversity in fishes (behavioral, spatial, age, etc.) can be used to manage for fish populations that are more likely to be resilient to external forces.

Additionally, he uses the lens of partial migration to tackle one of the major challenges that Harden-Jones put forward in 1968, "the eel problem." How do North American (*Anguilla rostra*) and European eels (*A. anguilla*), spawning in sympatry in the Sargasso Sea, retain population structure and reach developmental habitats on opposite sides of the Atlantic? I was very

excited to see Secor taking the challenge on this topic, as I had been hoping that throughout the book Secor would show how modern methods had been able to resolve those stubborn questions articulated by Harden-Jones. Secor puts forth an intriguing argument centered on "larval duration constituting a liability trait leading to initial niche partitioning and subsequent speciation." However, one piece of the argument rests on Iceland, the (presumably) lone location where *A. rostra*, *A. anguilla*, and their hybrids recruit. Citing Kuroki et al. (2008), he states that in Iceland, "larval durations are intermediate between American and European eels." Given that larval duration is shorter for American eels than their European counterparts, this would imply that in Iceland eels should have longer larval durations compared to those recruiting to North America and shorter larval durations compared to those recruiting to Europe. However, time to recruitment, inferred from otolith structure and chemistry for eels arriving to Iceland, is considerably longer than time to recruitment calculated for eels at sites in both North America and Europe (Kuroki et al. 2008, see their Table 3). Likewise, drift times estimated by oceanic models suggest that larval eels would reach North America relatively quickly, but Iceland and Europe after similar durations (Kettle & Haines 2006, see their Fig. 2). Thus, rather than hybridization causing an intermediate phenotypic response in larval duration, it appears to be in a single direction (longer larval durations for both species); and instead of bringing resolution to the "eel problem", Iceland's eels add another layer of mystery.

After Chapter 6, a 2 page interlude "Recapitulation: Scaling Collective Movements from Fertilization to Speciation" very nicely distills Secor's earlier writing in a manner reminiscent of a similarly named section in Harden-Jones's *Fish Migration*. Chapter 7, "Resilience" is a strong note to end on. Secor clearly articulates how life-history, resiliency, and climate change are importantly interconnected for conservation and management of marine fisheries. He draws on a number of pertinent examples to underline his theoretical considerations on this topic, including the collapse of the Bluefin tuna fishery off the coast of Brazil and comparison between the vastly different response to management actions of Chesapeake Bay striped sea bass and North Atlantic cod. Aptly arguing for why to preserve species outside of locations where abundance is greatest, he revisits the importance of the "Storage" and "Portfolio" effects for building in resilience to fish populations (essentially, that diversity in age structure and diversity in spatial structure allow for populations to be resilient to environmental and anthropogenic perturbations).

In summary, Secor accomplishes what he set out to do, adding several useful new dimensions to the treatise by Harden-Jones. Indeed, the two books pair nicely. Each book brings different elements of fish migration to the forefront and should probably be read together. Given the legacy of *Fish Migration*, that final recommendation should be seen as a hearty endorsement for Secor's *Migration Ecology of Marine Fishes.*

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