Preface to the special drift foraging issue of *Environmental Biology of Fishes*

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“Imagine a fish feeding in swift water.” With this statement in their landmark foraging model paper, Nicholas Hughes asked the reader to visualize how a drift-foraging fish captures its prey (Hughes and Dill 1990). It is a simple, elegant statement, but it captures the essence of stream fish ecology. A stream is defined, after all, as flowing water. Its inhabitants are the product of millennia of adaptations to the unique selective pressures created by this dynamic environment. Imagination is the key for many of us who have studied fish feeding in swift water. It was perhaps Nick’s greatest gift to us.

Foraging adaptations, in fact, have for many years led community ecologists to categorize stream fishes by their foraging guilds (e.g. Schlosser 1982). Clearly, stream fish fitness is largely determined by their ability to forage effectively in flowing water. Like all animals, the life histories of stream fishes have been finely tuned by natural selection to capitalize on spatial and temporal availability of prey resources. This truth is so transparent that it is surprising to realize just how under-appreciated it has become in stream fish ecology and management.

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A survey of the stream fish literature shows how much attention is paid to quantifying *where* fish make their living, versus how little attention is paid to quantifying *how* they do so. The study of physical habitat in streams has become a sub-discipline of its own, whereas the study of drift foraging has until very recently remained mostly in the realm of ecological theory. Were this a simple academic question it might not be so critical to bring this issue forward. But stream fish management, with its multitude of social and economic implications, has yet to come to grips with the fact that the distribution, growth, and abundance of fish probably depend as much (or more) on food as on space (Chapman 1966). Evolutionary theory, in fact, says as much. Darwin himself suggested that species are shaped more by interactions among themselves (e.g. predators and their prey) than they are by interacting with the physical environment. Animals must acquire resources to grow and reproduce, and those that are most successful enjoy the highest fitness. Thus, restoring natural flow regimes (e.g. Poff et al. 1997) to maintain fish habitat is only half the battle. Without a better mechanistic understanding of how food and space influence fish distribution, growth and abundance, we lack the tools to predict the outcome of habitat change, be it degradation or restoration. We still need an answer to the question that Nicholas posed in the opening lines of Hughes and Dill (1990):

“Why do fish chose one position over the multitude of others?”

With this special issue of *Environmental Biology of Fishes*, we highlight the fact that food and space are inextricably linked, and that a better understanding of

how fish acquire food is a prerequisite to a holistic approach to stream fish ecology and management.

We begin this special issue with historical overviews of the origins of drift foraging ecology from two international leaders in stream ecology, Kurt Fausch and Gary Grossman. It was part of Kurt's dissertation research that first brought net profitability to the forefront in stream fish research. Gary's lab, along with Hughes and Dill's (1990) work, first tested these models in field settings. Piccolo et al. review drift foraging models and their applications, focusing on theoretical developments stemming from the three landmark works noted above. In the second section six papers present new experimental work on drift-foraging related topics, including prey detection, social interactions, invertebrate prey, and the effects of parasitic mussels. The final section on applications of energetics-based habitat models is introduced by a comprehensive review by Rosenfeld et al., and it includes five papers highlighting some recent advanced applications on the effects of cover, prey and temperature, and habitat degradation. We end, fittingly, with Bret Harvey and Steve Railsback asking the question "Is drift feeding the whole story?"

This special issue is dedicated to Nicholas F. Hughes, whose work comprises perhaps the single greatest individual contribution to drift foraging theory and ecology. When Nick died in 2009, David Noakes asked me to write a piece highlighting Nick's contribution to ecology. This idea grew, not unlike a stream, first into symposia in Luecke, 2010 and in Seattle, 2011, then into a review paper on drift foraging, and finally into this special issue. Perhaps this is as it should be; Nick was certainly the most pure scientist we have ever known, and he firmly believed that the free exchange of scientific ideas, unfettered by self-interest, was central to scientific progress. I (JP) still have a copy of Sir Peter Medawar's "Pluto's Republic" that Nick gave me. In it, he had underlined a short passage that stated: "...the art of research... [is]...the art of making difficult problems soluble...". Nick's ecological legacy is a series of papers that attempt to solve the difficult problems of stream fish distribution, growth, and abundance, based upon sound ecological theory.

Nick's work on drift foraging began with his seminal paper with Larry Dill at Simon Fraser on individual fish foraging (Hughes and Dill 1990). He then extended this work to include dominance hierarchies (Hughes 1992a,b), spatial distribution in size-structure (Hughes and Reynolds 1994), whole stream distributions (Hughes 1998a), fish

movements (Hughes 1998b, 2000), and finally, production (Hayes et al. 2007). Hughes et al. (2003) remains the only explicit development and test of a drift-foraging model for stream fish. To better understand the costs and benefits of foraging, the foundation upon which all of the resulting theory builds, Nick and colleagues developed 3-D video technology to precisely measure fish swimming and foraging (Hughes and Kelly 1996a,b). Of course when we say "he" we include Nick's collaborators – he loved nothing more than constructive discussions about research. Their series of foraging-model based papers provide a template for how stream ecologists can link food and space at multiple scales.

Nick's ecological legacy extends well beyond drift feeding. I (JP) remember him showing me a life-size model of a king salmon that he was dragging behind a boat to better understand wave drag – further extending his work in applying sound, fitness-based theory to explain the pattern observed by Alaska Fish and Game biologists that bigger salmon migrate in the center of rivers. Nick's wave-drag hypothesis model (Hughes 2004) includes one of our favorite quotes:

"An extreme example of near-surface predator-prey interactions is provided by flying fish, Exocoetidae, which exploit ... physics...to the full by gliding above the water, where drag is vastly lower than for any predator pursuing them below the surface".

This truly remarkable way of looking at nature exemplifies Nick's contribution to ecology – throughout his research he sought to link the most rigorous of physical laws with fitness and hence natural selection, the most rigorous of natural laws. Nick's work remains a treasure chest of ideas that should help to guide ecologists in the aforementioned holistic approach to stream fish management.

Nick's passing left a gap that can't be filled in the lives of those who knew him, and in the field of ecology. But a Preface is a beginning, and we sincerely hope that this special issue will be just that; the start of new efforts to link food and space, the biological and physical aspects of stream ecosystems, to improve both our understanding and our management of flowing water. We also hope this special issue will help new readers to discover Nick's work, and some of the new directions in drift foraging ecology that are part of his legacy.

And from us some personal notes. We thank him for being a friend, always. For his gentle nature and his views on nature. We thank him most of all for his incredible insight into fish behaviour, and the joy he brought with every paper he presented at every meeting, and every one he published. Every year we share his papers with the latest class of students. Now they know how to look at fish because of what he told us.

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