Letter from the Desk of David Challinor
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This month's letter is about ichthyochory, a novel word for me. Learning it filled me with the delight we experience when we discover something new. Ichthyochory, I now understand, is the study of seed dispersal by fish, a subject unfamiliar to most of us. An intimately related subject—the ability of fish to adapt to and exploit changing water levels—is also addressed in this letter.

How do fish, which live underwater, manage to disperse seeds? The most visible seed-scattering agent is wind, which we commonly observe in the country or in our own back yards when we watch the winged seeds of dandelions, milkweed, aspen and other plant life fly by. Flowing water, birds, squirrels and other mammals up to and including rhinos also play important roles in dispersing seeds. My January 1992 letter described how the diets of the large Indian rhino are crucial for the germination and dissemination of the hard-coated seed of lowland Nepal's Trewia trees that frequently grow in clumps on old rhino communal dung middens. The role of fish as seed dispersers is obviously confined to those plants and trees that grow some or all of the time in water, but flooding often follows irregular cycles, and fish—like all other seed eaters—have evolved to adapt to and exploit changes in water level and other conditions of their aquatic habitats.

Although first reports of seed dispersal by fish appeared in a scientific journal almost a century ago, the subject has not been widely researched. It is only in the past few years that direct evidence of this behavior has been observed and described and, so far, all examples are from the New World. The Amazon Basin is an ideal site to study ichthyochory because its vast tracts of relatively undisturbed tropical forest are flooded annually during the wet season. Over many millennia, all sorts of unexpected aquatic animals have moved in to exploit the seasonal food resource that results from this cycle. For example, seeing a pair of pink-hued porpoises (*Inia geoffrensis*) foraging along a high forested bank of the Amazon, a thousand miles from the ocean, made a lifelong impression on me. These aquatic mammals are about six feet long with a toothed beak, a melon-shaped bulging forehead, and tiny eyes. The water is generally so muddy that their eyes must be almost useless for finding prey, so we assume they search for fish by echolocation, as do almost all their fellow creteceans. When the river is in full flood, they follow their fish prey as far as 50 miles from the main channel into the forest, and they have been found swimming placidly in water barely deep enough to cover them.

An important prey for these porpoises is a large and widespread group of boney Amazonian fish called characins (Characoidei), found in both South America and Africa.

There are 1,000 species in tropical America, but only about 200 in Africa. Among the characins that these dolphins eat are piranhas, but most of the basin's characins, especially in the genus *Mylens*, are fruit and seed eaters, not flesh eaters. Characins are just one example of seed-dispersing fish. Like other fish dependent on eating fruit, they have flat-topped teeth and strong jaws adapted to cracking seeds. (The flesh-eating piranhas in this family have sharp triangular incisors for biting.) When fruit falls into the water it is generally inaccessible to most forest birds and primates, and so fish become the principal seed dispersers for these fruit trees. Because fruiting is seasonal, most characins also eat insects, various invertebrates and even other fish.

Although we can watch birds or mammals eat, it is impossible to visually monitor seed consumption by individual fish. We know what fruits and seeds they consume by analyzing their stomach contents, but scientists can only speculate on other aspects of ichthyochory. For example, how far from the host tree will the foraging fish swim before excreting undigested (and thus generally viable) seed? Are there some fruit pits and seeds that can only germinate if they have passed through the gut of a fish? We know, for example, that the germination success of hard-coated mesquite beans is directly dependent on having its seed coat thinned or scarred by the stomach acids of browsing cows and horses. Other seeds sprout best when abraded by gizzard gravel in the crops of such large birds as turkeys or dodos. We still have much to learn about the relative importance of characins and catfish in disseminating seed and the effectiveness of gut passage in improving germination.

What we do know is that fish adapted to eat from the rich cornucopia of fruit in the flooded forest feed voraciously, accumulating fat, which later in the season helps bolster their reproductive systems and ensure prolific breeding. These new world forests are bountiful almost beyond imagination. Near Manaus, in the heart of the Amazon, fruit production is estimated at 10 to 30 metric tons per hectare per year, and some of these fruits, such as the seeds of the rubber tree (*Hevea brasiliensis*), have the highest energy concentration yet to be found for any seed.

The ways in which fish exploit and adapt to changing water levels have been studied not only in the Amazon basin but also around the Tonle Sap, Cambodia's largest lake (100 miles x 15 miles), which is connected to the Mekong River by a tributary. The Mekong is still the world's largest undammed river. Located in the heart of Southeast Asia's monsoon belt, the Mekong at flood fills the Tonle Sap with its tributary flowing west. During the dry season, the lake shrinks to a fraction of its extent when flooded, and the surviving fish are concentrated in what relatively shallow water is left. When the monsoon fills the lake, the surviving fish fan out to gorge on earthworms and other soil invertebrates—and perhaps plant seeds as well—that had heretofore been on dry land and inaccessible to them. As the fish population explodes, the fishermen reap their annual harvest, just as they have been doing for millennia. When the dry season returns, the tributary reverses its flow and most of the lake drains eastward back into the Mekong. I cite this example to illustrate how adaptable fish are in exploiting a new food source, which in turn supports a crucial local fishery.

A human threat to this natural and efficient cycle is ever present. In the early 1970's, the U.S. government made a huge and ill-advised effort to design a mainstream dam on the Mekong just upstream from Vientiane, the capital of Laos (where the river is the boundary between Laos and Thailand). With financing for our trip from U.S.AID, my colleagues and I found that storing such a gigantic volume of water behind the dam during the wet season would not only flood out Thailand's best cotton producing area, but would also eliminate the seasonal flows in and out of Tonle Sap and thereby threaten the lucrative and long-sustainable fishery there. This planned mainstream Pa Mong dam has yet to be built, although periodically, development advocates still push for its construction.

In addition to dispersing seeds, the fish of the world keep surprising us with their extraordinary ability to develop survival strategies when water runs low or disappears. A striking example is the mangrove killifish (*Kryptolebias marmoratus*). These fish inhabit the mangrove forests of the New World's east coast, where they normally live in shallow puddles of water that surround the mangrove's stilted roots. The puddles, however, often dry up, forcing the fish to live elsewhere. After a painstaking search, scientists found them lined up head to tail in the beetle grub galleries of rotting logs scattered among the stilt roots of the drying substrate. Crammed in these tunnels, the fish have had to temper their normal aggressive territorial behavior in order to survive. Even more amazing, they cope with having to live out of water by adjusting their gills to close tightly in order to retain water and nutrients. Furthermore, they are able, by adding new proteins to their epidermis, to excrete nitrogen waste directly through their skin. When enough water returns to float the log in which they have taken refuge, the whole amazing process reverses and they swim out as regular fish again. If the floating log should wash ashore elsewhere, these killifish can reproduce asexually and thus easily start a new colony; the refugees do not even have to have a male among them.

The strategies used by fish to adapt to changing conditions are intriguing. Some fish burrow deep in the mud bottoms of evaporating lakes and, curling up in a ball, reduce their metabolism enough to enable them to survive until the lake refills. Mudskippers, which I have watched at low tide in the mangrove swamps of the Seychelles, have bulging eyes on the top of their heads and stiff leg-like pectoral fins to propel them in the open air over the muddy substrate. Since the common red mangrove's (*Rhizophera mangel*) seed germinates while still attached to the tree, the fish play no role to my knowledge in their dissemination. The seedling root is carrot-pointed and when ripe, drops like a dart. At low tide it plants itself in the mud; at high tide it floats until—carried by currents—it can embed in another suitable site in a distant atoll.

Fish and trees! I had never made much of a connection between them, and now I discover that they can be mutually dependent. Trees supply food for fish; fish become agents of propagation by dispersing these seeds. Surprises like this are what make the natural world such a treasure trove. The excitement of learning so many new things, even at my age, is one of the reasons I am inspired to share this pleasure with you, the readers of these letters.

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P.S. An excellent article on ichthyochory for those interested is: S.B. Correa, Winemiller, K.O, López-Fernández, H. and Galetti, M. (2007) "Evolutionary Perspectives on Seed consumption and Dispersal by Fishes." *BioScience* 57(9): 748-756.

The source for the mangrove killifish example is E. Dolgin, "The fish that love to live in trees" *New Scientist*. 20 October 2007, p.20.