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Foraging Theory and Piscivorous Fish: Are Forage Fish Just Big Zooplankton?

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Abstract.–Insights into the dynamics of fish growth can be gained by using foraging theory to link bioenergetics models of fish and their prey. These links are critical for modeling fish daily ration and growth, prey mortality, selection among prey, and competition among predators. However, the foraging theory that is relatively well developed for planktivores does not always apply to piscivores without important modifications. Visual encounter is often limited by visual acuity for most planktivores, but probably limited by prey contrast for piscivores, so that piscivore reactive distance is much less dependent on prey size. Whereas handling time per prey may limit the capture rate for some planktivores, it is irrelevant for most piscivores, which eat relatively small numbers of large prey and are more likely to have daily ration limited by rates of digestion or prey encounter. Time for gastric evacuation or digestion should not be a part of handling time, because search can occur simultaneously with digestion. If handling time is not important for piscivores, then Holling's Type-1 functional response may be more appropriate than the Type-2. An alternate form of the functional response is presented for predators that feed on prey of uniform size and stop foraging each day when some maximum number of prey are ingested. This functional response has a negatively accelerated rise to an asymptote, similar to the Type-2 functional response, but based on a very different mechanism. Simulations with a bioenergetics model show that the variance in daily growth among individuals is likely to be greater for piscivores, which feed on a small number of large prey, than for planktivores, which feed on a large number of small prey.

The trophic linkages between fish and their prey are critical to understanding and modeling fish daily ration and growth, prey mortality, selection among prey, and competition among predators. Bioenergetics models are useful for studying the factors influencing fish growth and food consumption, and much has been learned by using single-species bioenergetics models. In typical applications, the seasonal pattern of fish growth (or consumption) is specified and the corresponding pattern of consumption (or growth) is computed; prey dynamics are not explicitly included in such calculations, but appear indirectly in the specification of diet composition (Kitchell et al. 1977; Rice et al. 1983; Hewett and Stewart 1989; Stewart and Ibarra 1991). Further insights into the dynamics of fish growth can be gained by using foraging theory to explicitly link bioenergetics-based models of fish to models of their prey (Adams and DeAngelis 1987; Trebitz 1991; Madenjian and Carpenter 1991). However, the foraging theory that is relatively well developed for