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Comment: Vertical Migration of Bloaters

TeWinkel and Fleischer (1999) described the diet of diel vertically migrating bloaters *Coregonus hoyi* in Lake Michigan and concluded that their data did not support a hypothesis advanced by Eshenroder and Burnham-Curtis (1999) to account for the vertical migration of deepwater ciscoes *Coregonus* spp. We believe that TeWinkel and Fleischer (1999) seriously misstated our hypothesis. In this comment, we (1) quote what we hypothesized regarding deepwater cisco migration, (2) explain what we think led TeWinkel and Fleischer (1999) to misinterpret our hypothesis, and (3) suggest an alternative approach for testing our hypothesis.

Our Hypothesis on Vertical Migration

Eshenroder and Burnham-Curtis (1999) hypothesized that the deepwater ciscoes of the Great Lakes, a species flock containing the bloater and five other species (Smith and Todd 1984), evolved to feed on *Mysis relicta,* an ecological dominant in the deep waters of the Great Lakes. We inferred that planktivorus (shallow water) ciscoes "colonizing the benthic waters of the Great Lakes were selected for reduced specific gravity because the amount of buoyancy regulation provided by their swim bladders inhibited their ability to feed on *Mysis relicta,* an important prey species that vertically migrates at night." In our paper, there are 10 instances where we connect cisco vertical migration and planktivory on *Mysis.* The context for all of these connections is that planktivory, as a selection pressure, shaped the evolution of deepwater ciscoes.

So, where does the problem arise? TeWinkel and Fleischer (1999) stated in their introduction that our hypothesis proposed that diel vertical migrations (of fish) are driven by *Mysis* migration and that deepwater ciscoes vertically migrate to continuously feed on *Mysis.* In their discussion, they further state that we hypothesized that "bloater vertical migration and feeding is linked solely to *Mysis.*" On the contrary, our hypothesis refers to causal mechanisms that contributed to the evolution and maintenance of diversity among the deepwater ciscoes. The evolution of a behavior in response to a selection pressure does not mean that the behavior is obligate. We do not state in our paper that deepwater ciscoes only migrate to feed on *Mysis.* In fact, we state that planktivory on *Mysis* may be enhanced when both organisms are migrating.

Why a Misunderstanding

We speculate that TeWinkel and Fleischer (1999) misstated our hypothesis because they did not distinguish between proximate and ultimate causes for the observed behavior of bloaters. Mayr (1982) differentiates between "ultimate causes responsible for the evolution of a given genetic program and proximate causes responsible, so to speak, for the release of the stored genetic information in response to current environmental stimuli." TeWinkel and Fleischer (1999) found that bloaters fed on *Daphnia* in the water column and on *Mysis* and *Diporeia* (another macroinvertebrate) on the lake bottom and concluded that our hypothesis was not supported. Our hypothesis, however, is clearly about ultimate causes: the selection pressures that led to the evolution of the deepwater ciscoes. We did not state that vertical migration and feeding on *Mysis* are the only (proximate) reasons for bloater vertical migration. In fact, we cited Wells and Beeton (1963) and were aware that Lake Michigan bloaters fed on alternative prey, including cladocerans. For us to state that a planktivore can only feed on a single prey item at any one time would have been adventurous indeed.

Alternative Approach

Is our hypothesis on the ultimate causes of bloater vertical migration impervious to testing because it relates to long-ago events? No, one can test for plausibility by comparing fitness consequences of alternative adaptations (phenotypes) in the present (see Reeve and Sherman 1993). Envision one bloater phenotype that does not vertically migrate and feeds on *Mysis* during the day and an alternative phenotype that migrates and has access to *Mysis* and other prey both day and night. The fitness consequences for each phenotype would be growth estimated from a bioenergetic model such as that of Rudstam et al. (1994). Our hypothesis would be in jeopardy if estimated growth of bloaters without access to vertically migrating *Mysis* was even nominal. Especially revealing would be estimated growth of bloaters from deeper water. The bloater is, as we noted in our paper, the smallest-bodied and shallowest-dwelling member of its spe-

cies flock (in Lake Michigan), and does feed more on *Mysis* at the deep end of its depth distribution (Wells and Beeton 1963). Our hypothesis, however, dealt with adaptations of deepwater ciscoes not just adaptations of bloaters. To effectively test the hypothesis, therefore, the fitness consequences should mimic deep-water patterns of prey abundance and predator reactive distance.

This approach would require seasonal data on bloater diets and a method to separate prey items consumed on the bottom both day and night from items consumed in mid-water at night. TeWinkel and Fleischer (1999) made progress on delineating how migration affects consumption. They sampled during a 10–12-d period in mid-August for 2 years, and found that bloaters had significantly fewer empty stomachs when their vertical-depth distribution paralleled that of a night-migrating invertebrate like *Mysis*. They also reported that bloaters taken in mid-water had significantly more intact prey items. This finding supports one rationale for our hypothesis: planktivory on *Mysis* may be enhanced when *Mysis* are migrating. TeWinkel and Fleischer (1999) also found a dietary dominance of *Mysis* in 1996 and of *Daphnia* in 1995. They did not, however, discuss the implications of 91% pelagic food (*Daphnia*) in 1995. If bloaters can thrive without migration, as suggested by TeWinkel and Fleischer (1999), why didn't nonmigratory bloaters contain more prey?

In summary, we are concerned that our hypothesis on the evolution of deepwater ciscoes in Eshenroder and Burnham-Curtis (1999) was seriously misstated by TeWinkel and Fleischer (1999). This hypothesis dealt with ultimate causes of observable behavior whereas TeWinkel and Fleischer (1999) focused on proximate causes. We show why their approach was not a good test of our hypothesis and provide an alternative test scenario.

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