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## PERSPECTIVE

## Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis

Roy A. Stein, Dennis R. DeVries, and John M. Dettmers

**Abstract:** The trophic cascade hypothesis currently being tested in north temperate systems may not apply to open-water communities in lower latitude U.S. reservoirs. These reservoir communities differ dramatically from northern lakes in that an open-water omnivore, gizzard shad (*Dorosoma cepedianum*), often occurs in abundance. Neither controlled by fish predators (owing to high fecundity and low vulnerability) nor by their zooplankton prey (following the midsummer zooplankton decline, gizzard shad consume detritus and phytoplankton), gizzard shad regulate community composition rather than being regulated by top-down or bottom-up forces. In experiments across a range of spatial scales (enclosures, 1–9 m<sup>2</sup>; ponds, 4–5 ha; and reservoirs, 50–100 ha), we evaluated the generality of the trophic cascade hypothesis by assessing its conceptual strength in reservoir food webs. We reviewed the role of gizzard shad in controlling zooplankton populations and hence recruitment of bluegill, *Lepomis macrochirus* (via exploitative competition for zooplankton), and largemouth bass, *Micropterus salmoides* (by reducing their bluegill prey). Reservoir fish communities, owing to the presence of gizzard shad, appear to be regulated more by complex weblike interactions among species than by the more chainlike interactions characteristic of the trophic cascade.

**Résumé :** L'hypothèse de la « cascade trophique », qu'on examine actuellement dans les systèmes des eaux tempérées du nord, pourrait ne pas s'appliquer aux communautés des eaux ouvertes des réservoirs, sous les basses latitudes, aux États-Unis. Dans ces réservoirs, la situation est remarquablement différente, car un omnivore des eaux ouvertes, l'alse à gésier (*Dorosoma cepedianum*), y abonde souvent. N'étant limitée ni par des poissons prédateurs (grâce à son taux élevé de fécondité et à sa faible vulnérabilité) ni par la disponibilité de ses proies zooplanctoniques (après la baisse du zooplancton au milieu de l'été, l'alse à gésier consomme des détritiques et du phytoplancton), cette alse régit la composition de la communauté au lieu d'être soumise à des forces s'exerçant de haut en bas ou de bas en haut de la chaîne. Dans des expériences menées à des échelles spatiales diverses (enclos, 1–9 m<sup>2</sup>; étangs, 4–5 ha; réservoirs, 50–100 ha), nous avons évalué la possibilité d'une application générale de l'hypothèse de la cascade trophique en mesurant sa force conceptuelle dans les réseaux trophiques des réservoirs. Nous avons examiné le rôle de l'alse à gésier dans la régulation des populations zooplanctoniques et donc dans le recrutement du crapet arlequin, *Lepomis macrochirus* (par compétition dans l'exploitation du zooplancton), et de l'achigan à grande bouche, *Micropterus salmoides* (par réduction du nombre des crapets arlequins qui leur servent de proies). Les communautés ichtyennes des réservoirs, à cause de la présence de l'alse à gésier, semblent davantage régies par un réseau d'interactions complexes entre espèces que par les interactions en chaîne caractéristiques de la cascade trophique.

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## Introduction

The trophic cascade hypothesis provides a conceptual framework for examining processes underlying community structure (i.e., species composition and relative abundance of species) in freshwater ecosystems. At the heart of this concept is the premise that community structure is determined by a series of chainlike interactions between adjacent trophic levels driven by strong interactors (Kitchell and Carpenter 1993). For example, predation by piscivorous fishes reduces planktivore abundance, allowing herbivorous zooplankton to increase; as zooplankton increases, phytoplankton abundance and primary productivity decline, regardless of nutrient availability ( Hairston et al. 1966; Carpenter et al. 1985; Carpenter and Kitchell 1988; Northcote 1988; for a similar perspective in stream communities, see Power 1990). Because control in this instance occurs from the top of the trophic pyramid, it is classified as top-down. In contrast, system structure can be regulated by nutrients (i.e., bottom-up control), as might be expected in eutrophic systems (see McQueen 1990; McQueen et al. 1986, 1989 for examples). However, it is likely that community regulation is not solely due to top-down or bottom-up forces (Hunter and Price 1992); instead, community composition derives from a combination of top-down (piscivore control) and bottom-up (nutrient control) forces (McQueen et al. 1986, 1989; Bartell et al. 1988; Jassby et al. 1990).

The trophic cascade hypothesis has been explored in systems ranging from relatively small-scale enclosure-exclosure experiments (e.g., Bergquist and Carpenter 1986; Post and McQueen 1987; McQueen and Post 1988; Mazumder et al. 1988, 1990; Qin and Threlkeld 1990) to whole-lake manipulations (Henrikson et al. 1980; Shapiro and Wright 1984; Kitchell and Crowder 1986; Scavia et al. 1986; Carpenter et al. 1987; McQueen et al. 1989; Vanni et al. 1990). Whole-lake tests of this hypothesis, involving manipulation of piscivores (Kitchell and Crowder 1986; Scavia et al. 1986; Carpenter et al. 1987; McQueen et al. 1989) and planktivores (Henrikson et al. 1980; Shapiro and Wright 1984; Carpenter et al. 1987; Vanni et al. 1990), have been relatively successful in predicting qualitative changes in primary production resulting from changes in upper trophic levels, particularly when manipulations have been substantial and sustained (reviewed in Carpenter and Kitchell 1988; see also Kitchell and Carpenter 1987; McQueen 1990). However, whole-lake tests have been conducted in north temperate lakes (Lake Lilla Stockelidsvatten, Sweden, Henrikson et al. 1980; Round Lake, Minnesota, Shapiro and Wright 1984; Lake Michigan, Kitchell and Crowder 1986; Scavia et al. 1986; Peter, Paul, and Tuesday lakes, Michigan, Carpenter et al. 1987; Lake St. George, Ontario, McQueen et al. 1989; Lake Mendota, Wisconsin, Vanni et al. 1990); therefore, the extension of this hypothesis to reservoirs at lower latitudes, where adjacent trophic levels do not necessarily regulate one another, may be inappropriate.

Indeed, the trophic cascade hypothesis has been demonstrated to work in some systems, but not in others (Shapiro 1990; Carpenter and Kitchell 1992; DeMelo et al. 1992; Kitchell 1992). Under what conditions does this paradigm accurately predict the outcome of trophic interactions?

Specifically, researchers have pursued such questions as (i) is this phenomenon restricted to lakes of a particular trophic status (McQueen et al. 1989; Carney 1990), (ii) is it restricted to lakes and streams with depauperate communities (Strong 1992), (iii) is it restricted to systems with functionally significant linkages and (or) with few omnivores (Power 1992), (iv) is it restricted to systems that exhibit, from a variety of points of view, homogeneity (Hunter and Price 1992; Strong 1992), or (v) might it be limited in systems with deep-bodied, large planktivores (Hambright et al. 1991)? In this paper, we explore our ability to generalize the trophic cascade paradigm by applying concepts developed in north temperate lakes to lower latitude reservoirs.

## Reservoirs versus natural lakes

Reservoirs supported more fishing activity (40%) within the United States in 1980 than any other type of freshwater ecosystem (Fisher et al. 1986). Reservoir fishing translates to 5.4 billion U.S. dollars in expenditures, yet these systems are poorly understood and managed (Hall and Harris 1986). Geographically, most U.S. reservoirs are concentrated between 30 and 42°N latitude, in nonglaciated regions, whereas natural lakes typically occur north of 42°N in glaciated regions (Thornton 1990). Thus, U.S. reservoirs tend to be warmer and shallower with longer growing seasons than natural lakes. Owing to soils in the region, southern reservoirs typically have higher total dissolved and suspended solids than natural lakes (Thornton 1990). Because reservoirs typically are located in river valleys at the base of the drainage basin (Wetzel 1990), reservoirs have larger watershed to surface area ratios than lakes, leading to high, but irregularly pulsed, nutrient and sediment inputs. Reservoirs experience dramatic, irregular water-level fluctuations that derive from a combination of flood inflows, land-use practices unfavorable for water retention, and hydropower withdrawals. With higher turbidity and greater water-level fluctuations, fewer littoral macrophytes occur in reservoirs than in north temperate lakes (Wetzel 1990). As a consequence, most primary production in reservoirs typically derives from phytoplankton, rather than from macrophytes (Kimmel et al. 1990). These structural differences between reservoirs and lakes are confounded by longitudinal gradients in physical and chemical variables between upstream, lotic areas and downstream, lentic areas of reservoirs (Thornton 1990).

Reservoirs differ from natural lakes more fundamentally. North temperate lakes, where ecological research has concentrated, are 10 000 – 12 000 yr old and formed by Pleistocene glacial activity, whereas reservoirs typically are less than 60 yr old (Noble 1986; Thornton et al. 1990). Thus, biotic interactions among fish communities in north temperate lakes typically have been shaped by evolution (MacLean and Magnuson 1977), whereas those within reservoirs have not. Rather, reservoir fish communities are comprised of species with little history of co-occurrence (Noble 1986), resulting in unique, complex interactions without representation in well-studied natural lakes. Paleoecological records from lakes suggest long periods of trophic equilibrium; similar periods of stasis do not occur in reservoirs (Kimmel and Groeger 1986).

Species introductions characterize reservoirs. Assembled fish communities include predators such as largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion vitreum*), crappie (*Pomoxis* spp.), and channel catfish (*Ictalurus punctatus*). Prey species typically include bluegill (*Lepomis macrochirus*), other sunfishes (*Lepomis* spp.), golden shiners (*Notemigonus crysoleucas*), fathead minnows (*Pimephales promelas*), gizzard shad (*Dorosoma cepedianum*), and threadfin shad (*Dorosoma petenense*). Of these, gizzard and threadfin shad are most common, often accounting for 30% or more of all fish biomass within communities (Jenkins 1957, 1967; Grinstead et al. 1976; Timmons et al. 1978; Ploskey and Jenkins 1982; Johnson et al. 1988). These two species provide most prey for predators (Jenkins 1967; Timmons et al. 1978; Johnson et al. 1988) and typically have been those prey species most often introduced into reservoirs as additional prey for predatory sport fishes (DeVries and Stein 1990). Dominance of reservoir fish communities by gizzard shad is, in our view, the single most important difference between lakes and reservoirs with respect to the application of the trophic cascade hypothesis. To set the stage for our argument, we first describe how gizzard shad become dominant in reservoirs and then describe how this species (one not common to north temperate systems; Trautman 1981), from its position within the food web, acts to influence trophic levels above and below it.

### Gizzard shad success in reservoirs

The relatively small size of zooplankton in reservoirs compared with north temperate lakes may predispose reservoirs to successful recruitment of gizzard shad (Bremigan and Stein 1994). Larval gizzard shad have smaller mouth gapes than bluegill or walleye in spite of the fact that they all depend on plankton immediately post-hatching (Bremigan and Stein 1994; J.B. Mion, Aquatic Ecology Laboratory, Department of Zoology, The Ohio State University, Columbus, OH 43212-1194, unpublished data). In turn, larval gizzard shad prefer smaller zooplankton (0.5–0.7 mm) than bluegill (Bremigan and Stein 1994) and may grow faster on small rather than large zooplankton. After gizzard shad drive zooplankton to low densities by intense planktivory (DeVries and Stein 1992; Dettmers and Stein 1992), they switch to feed on benthic, detrital ooze of eutrophic reservoirs (Mundahl 1991), likely never succumbing to the consequences of zooplankton overgrazing. Hence, successful gizzard shad recruitment in reservoirs may be driven by the presence of small zooplankton, combined with abundant detritus rich in organic material.

Gizzard shad are preferred over sunfishes as prey (Lewis and Helms 1964; Aggus 1973), at times contributing >90% of the diets of largemouth bass (Johnson et al. 1988; Carline et al. 1987). Yet, owing to fast growth that permits young-of-the-year gizzard shad to exceed predator gape (Hambricht et al. 1991), only about 20% of gizzard shad mortality is due to predation by typical resident predators (Carline et al. 1984; Johnson et al. 1988).

Thus, neither resources (bottom-up forces) nor predators (top-down forces) control gizzard shad populations. What then prevents gizzard shad from completely dominating the fish community in reservoirs? We suggest the answer is

episodic winterkill of gizzard shad. Atypically long winters lead to subsequent gizzard shad mortality (Adams et al. 1982a) and may reset the fish community by reducing adult gizzard shad abundance and resultant interspecific competitive effects.

### Interactions between gizzard shad and zooplankton

Strictly planktivorous early in life, gizzard shad become omnivorous after reaching 25–35 mm total length (TL) and feed on zooplankton, phytoplankton, and detritus (Tiffany 1921; Dendy 1946; Kutkuhn 1957; Miller 1960; Pahl and Maurer 1962; Bodola 1966; Cramer and Marzolf 1970; Jester and Jensen 1972; Jude 1973; Mayhew 1977; Barger and Kilambi 1980; Drenner et al. 1986; Mundahl 1988). With these ontogenetic diet shifts, gizzard shad successively feed at different trophic levels (i.e., zooplankton and phytoplankton) (Tiffany 1921; Kutkuhn 1957; Miller 1960; Bodola 1966; Jester and Jensen 1972; Heindinger 1983; Todd and Willis 1985; Mundahl 1988; DeVries and Stein 1992). As omnivores, gizzard shad are not regulated by the primary consumers, i.e., zooplankton (even though they exert strong control over this level), unlike occupants of the intermediate level in north temperate systems (e.g., dace, *Phoxinus* spp., Carpenter et al. 1987; cisco, *Coregonus artedii*, Vanni et al. 1990).

As with other open-water planktivores (Brooks and Dodson 1965; Lazzaro 1987), gizzard shad can influence the abundance and species composition of zooplankton communities. When threadfin shad were stocked into a Kansas reservoir, large zooplankton were eliminated much earlier in the year than before shad stocking (Prophet 1982, 1985, 1988). Zooplankton density was negatively associated with threadfin shad abundance in two Arizona lakes (Ziebell et al. 1986) and elsewhere (Cramer and Marzolf 1970; Applegate and Mullan 1971; Cashman 1988; Kissick 1988).

Though most fishes spawn in spring and produce zooplanktivorous larvae, gizzard shad exceed the impact of these fishes, simply because of their extremely high fecundities (approaching 500 000 eggs/female, Bodola 1966; Wilder and Vondracek 1988; Parrish and Vondracek 1989), which can, in some years, translate into high larval fish densities (up to 86 fish/m<sup>3</sup>, DeVries and Stein 1992) that can exert strong predation pressure on zooplankton. Negative relationships have occurred between abundance of larval gizzard shad and crustacean zooplankton in two Ohio reservoirs. During 1986–1989 zooplankton abundance declined within 1–2 wk of peak larval gizzard shad abundance in Kokosing Lake, Ohio, and within 2 wk of peak larval threadfin shad abundance in Stonelick Lake, Ohio (DeVries et al. 1991; DeVries and Stein 1992). To determine if juvenile gizzard shad were responsible for these zooplankton declines, we conducted an in-lake enclosure experiment where young gizzard shad were either present or excluded. In enclosures with gizzard shad (at typical reservoir densities), zooplankton densities fell to zero within 2 wk; without gizzard shad, zooplankton densities remained above 500/L (DeVries and Stein 1992). These findings have been reinforced by a consumption model for young-of-the-year gizzard shad (Dettmers and Stein 1992).

Because gizzard shad suppress crustacean zooplankton, their presence in reservoirs will strongly influence recruitment (i.e., survival through critical early life stages) of fishes with obligate zooplanktivorous larvae. For example, bluegill larvae migrate from the littoral zone to the limnetic zone immediately after hatching, where they feed on zooplankton for 4–8 wk until reaching 20–25 mm TL, at which point they migrate back to the littoral zone (Faber 1967; Werner 1967, 1969; Amundrud et al. 1974; Keast 1980; Beard 1982; Werner and Hall 1988; DeVries et al. 1991). Larval crappie also make extensive use of open-water plankton (Mayhew 1977; Overman et al. 1980; Hanson and Qadri 1984; D.R. DeVries, M.T. Bremigan, and R.A. Stein, unpublished data). Thus, competitive interactions among gizzard shad and other limnetic larvae (such as bluegill and crappie) could dramatically influence growth, survival, and ultimate recruitment of these fishes.

### Effects of gizzard shad on phytoplankton

The trophic cascade hypothesis applied to reservoirs predicts that in the presence of gizzard shad, crustacean zooplankton abundance should be reduced and, as a consequence, phytoplankton abundance should increase. However, in addition to their direct effects on zooplankton, gizzard shad can directly and indirectly influence phytoplankton communities. Adult gizzard shad can reduce large phytoplankton >60  $\mu\text{m}$  (e.g., *Ceratium* spp.; Drenner et al. 1984) and permit small forms (1–4  $\mu\text{m}$ ) to increase by enhancing the turnover rate of small algae via nutrient recycling (Threlkeld and Drenner 1987; Lazzaro et al. 1992), with the size of phytoplankton removed being inversely related to fish size (Drenner et al. 1984; Mummert and Drenner 1986). In our gizzard shad enclosure–exclosure experiment (described above), we found that edible phytoplankton (primarily *Cryptomonas* spp.) declined in enclosures with gizzard shad relative to fishless enclosures (DeVries and Stein 1992). These data, combined with diet data identifying phytoplankton in gizzard shad diets (Kutkuhn 1957; Miller 1960; Bodola 1966; Baker and Schmitz 1971; Heidinger 1983; Drenner et al. 1984; Todd and Willis 1985; Mundahl 1988), suggest that gizzard shad directly influence phytoplankton, complicating predictions from the trophic cascade hypothesis. In addition, nutrient uptake may increase through the summer (Kitchell et al. 1975; Johnson et al. 1988; D.R. DeVries and R.A. Stein, unpublished data), as young-of-the-year gizzard shad grow.

To summarize, gizzard shad are not controlled by zooplankton abundance (i.e., bottom-up control does not appear to operate). Rather, gizzard shad modify community composition of both zooplankton (directly via predation) and phytoplankton (indirectly through zooplankton and directly via herbivory and nutrient uptake) communities.

### Complex effects of gizzard shad on fish communities

Gizzard shad can influence reservoir communities in a complex fashion, mediated through several trophic levels. First, because annual variation in the density and spawning time of gizzard shad is substantial, their vulnerability to

predators may vary across years. When gizzard shad spawn late, their young-of-the-year are vulnerable to young-of-the-year largemouth bass for much of the summer (see Johnson et al. 1988 for a discussion of this phenomenon in Ohio reservoirs). However, when gizzard shad spawn early, they grow beyond the morphological capability of young-of-the-year largemouth bass to consume them (see general review in Adams and DeAngelis 1987). As a result, growth of young-of-the-year largemouth bass declines, for they are forced to consume less preferred foods. Thus, the size of young-of-the-year largemouth bass at the end of the summer growing season varies greatly as a result of these size-structured interactions. This variability in young-of-the-year size has dramatic implications for largemouth bass recruitment; small bass have been postulated to die at a disproportionately higher rate during winter than large individuals (Aggus and Elliott 1975; Shelton et al. 1979; Timmons et al. 1980; Adams et al. 1982a; Gutreuter and Anderson 1985), likely because of depletion of lipid reserves in smaller fish (Saiki and Tash 1978; Oliver et al. 1979; Adams et al. 1982b; Ludsins 1994). Hence, gizzard shad may well control recruitment success of largemouth bass in reservoirs by influencing size of young-of-the-year largemouth bass and ultimately their overwinter survival. Reduced recruitment of largemouth bass can further enhance the ability of gizzard shad to succeed, leading to their domination of the system.

Both gizzard shad and bluegill have limnetic zooplanktivorous larvae, but gizzard shad typically spawn 1–3 wk before bluegill; thus, larval gizzard shad precede larval bluegill in the limnetic zone. Because young-of-the-year gizzard shad can drive zooplankton to low levels, we hypothesize that reduced zooplankton abundance deprives bluegill of zooplankton, reducing bluegill recruitment. In fact, in Kokosing Lake, Ohio, abundance of larval gizzard shad is inversely related to abundance of littoral young-of-the-year bluegill (DeVries and Stein 1992).

Normally, if bluegill survive and grow in the limnetic zone, they migrate inshore at about 20 mm (Werner 1967; Werner and Hall 1988), where they serve as prey for young-of-the-year largemouth bass. If gizzard shad reduce survival of limnetic larval bluegill such that few bluegill migrate to the littoral zone, then prey available to young-of-the-year largemouth bass (which remain in the littoral zone as young-of-the-year) is reduced and bass growth declines. Data collected from two lakes in Ohio, before and after introduction of threadfin shad, provide insight into this perspective (note that as larvae and juveniles <30 mm TL, threadfin shad and gizzard shad are both obligate zooplanktivores). After being stocked into both lakes, threadfin shad had little impact on the zooplankton in Clark Lake, whereas in Stonelick Lake, threadfin shad eliminated the zooplankton at a time when larval bluegill required it as a food source. Hence, in Clark Lake, we observed what we would consider an excellent environment for growth and survival of larval bluegill, whereas in Stonelick Lake less than ideal conditions existed. If bluegill larvae recruiting to the littoral zone are important to young-of-the-year largemouth bass, then we expect higher bass growth (post-threadfin shad) in Clark than in Stonelick lake. This is precisely what happened. Largemouth

**Table 1.** Predicted year-class strength of bluegill and largemouth bass in Ohio reservoirs as dictated by gizzard shad abundance, zooplankton productivity, and relative spawning time of gizzard shad and bluegill.

Gizzard shad abundance	Zooplankton productivity	Scenario I	Scenario II
		Bluegill and largemouth bass year-class strength Excellent —————> Poor	Bluegill and largemouth bass year-class strength Excellent —————> Poor
Absent	High	████████████████████	████████████████████
Low	High	████████████████████	████████████████████
High	High	████████████████████	████████████████████
Absent	Low	████████████████████	████████████████████
Low	Low	████████████████████	████████████████████
High	Low	████████████████████	████████████████████

Note: Under scenario I, young-of-the-year gizzard shad appear in the limnetic zone before bluegill, whereas under scenario II gizzard shad appear in the limnetic zone after bluegill.

bass growth was not depressed in Clark Lake in the post-threadfin shad year, though we did not document fish in largemouth bass diets. However, in Stonelick Lake, largemouth bass growth was depressed substantially in the post-versus pre-threadfin shad year (DeVries et al. 1991). Herein, we have compared between years and lakes for both threadfin and gizzard shad across different predator densities. Consequently, the scenario of shad controlling zooplankton abundance, eventual bluegill recruitment to the littoral zone, and diet and growth of young-of-the-year largemouth bass is likely, but certainly not the whole story (witness Clark Lake).

### Testing food-web regulation by gizzard shad

If our hypothesized interactions are correct, then we expect differential year-class success of bluegill and largemouth bass in reservoirs with differing gizzard shad density and zooplankton productivities (Table 1). Without gizzard shad, bluegill and largemouth bass should experience variable year-class success. If larval gizzard shad occur in the limnetic zone before larval bluegill, then bluegill and hence largemouth bass should exhibit intermediate to poor year-class strength, regardless of gizzard shad abundance and zooplankton productivity. If young-of-the-year gizzard shad appear in the limnetic zone after larval bluegill, then bluegill and bass should exhibit excellent to poor (with high zooplankton productivity) or intermediate to poor (with low zooplankton productivity; Table 1) year-class strength. Even if larval gizzard shad occur in the limnetic zone after larval bluegill, the presence of larval shad will overlap with bluegill larvae, thereby at least partially reducing bluegill recruitment success. As is perhaps obvious, we predict that gizzard shad absence is a necessary, but not sufficient, condition for excellent recruitment of bluegill and largemouth bass. However, when this keystone species is present, the opportunity for successful recruitment of sport fishes is greatly limited.

These predictions can be tested explicitly by randomly sampling adult bluegill and largemouth bass from reservoirs

for which we have historical information, including temporal patterns of larval fish abundance and zooplankton productivity. By aging individuals of these two species, we can determine the occurrence and relative frequency of strong and weak year-classes, permitting us to judge the validity of these predictions (Table 1).

### Exploring generality across systems

As Hunter and Price (1992) suggest, species at any trophic level can drive community dynamics. With gizzard shad, we have an excellent example of a species within the food web influencing not only trophic levels below it, but also above it. Clearly, eutrophic reservoirs that support gizzard shad differ from those aquatic systems described by Oksanen et al. (1981), where, as productivity increases, the food web shifts from three to four trophic levels. In their model, piscivores increase in abundance as productivity increases from very low levels (Persson et al. 1992). In reservoirs, though, piscivores occur at low abundance and do not exert strong top-down effects. Thus, a pattern best characterized by a three-level food chain develops, with planktivores and producers limited by resources, and zooplankton strongly suppressed by planktivores.

Why do the systems described by Persson et al. (1992) support more piscivores with increasing nutrients, whereas eutrophic reservoirs do not support high densities of piscivores? In reservoirs, gizzard shad can persist at high densities even with reduced zooplankton resources. Such persistence of gizzard shad, in the face of seemingly limited resources, strengthens their top-down effects and differs from the predictions of Oksanen et al. (1981), where consumer effects are limited by low prey abundance. Power (1992) characterizes such a food chain shift as a spillover because gizzard shad exerts even greater top-down effects on zooplankton by virtue of its capacity to use alternative food resources, yet can continue to consume zooplankton.

A trophic level may not be functionally significant if it does not influence the abundance of the trophic level immediately below it (Power 1992). In our view, gizzard shad effectively neutralize the potential piscivore effect

of largemouth bass via size-structured interactions among largemouth bass, bluegill, and gizzard shad as we have described. Similar food web studies in Sweden indicate that piscivore abundance declines in more productive lakes because young-of-the-year piscivores cannot successfully compete for zooplankton resources with the resident planktivore (roach, *Rutilus rutilus*; Persson et al. 1991). Similarly, largemouth bass are not sufficiently abundant to consume many gizzard shad because of the recruitment bottleneck described above, and we may consider piscivores a functionally nonsignificant trophic level in reservoirs. Thus, we conclude that reservoir food webs are more properly described as three-level chains because the piscivore level is not functional because of reduced piscivore recruitment and the increased effect of gizzard shad on zooplankton as a result of its omnivory.

Though we have focussed on the response of one type of system to one species of fish, regulation of the type that emanates from the middle of the food web occurs not just in reservoirs containing gizzard shad, but also in those ecosystems where species within the food web enjoy both a predatory refuge (via size, habitat structure, spatial separation, etc.) and an opportunistic foraging mode. Interestingly, invaders (whether human-assisted or natural) often possess these characteristics for they establish themselves in the face of predatory pressure and typically are opportunistic in their reliance on resources.

The rusty crayfish (*Orconectes rusticus*), a species that has successfully invaded northern Wisconsin lakes (Capelli 1982) and Ohio streams (Mather and Stein 1993), is relatively invulnerable to predatory fishes (Garvey et al. 1994) and has a broad generalist diet (Hill et al. 1993; Lodge et al. 1994). They exert dramatic impacts on both upper and lower trophic levels of north temperate aquatic ecosystems, indicating that from their position from within the food web, they regulate the benthic community (Lodge et al. 1994).

Another example derives from deep, oligotrophic lakes, where freshwater opossum shrimp, *Mysis* spp., may regulate community structure via their position in the middle of the food web. As with gizzard shad, *Mysis* spp. can alter zooplankton taxonomic composition and abundance (Lasenby et al. 1986; Spencer et al. 1991). Because *Mysis* spp. can feed on phytoplankton and zooplankton (Grossnickle 1982), they are not limited by zooplankton availability. Further, because early life stages of the primary piscivores in these systems (kokanee salmon, *Oncorhynchus nerka*) rely on zooplankton, *Mysis* spp. can negatively affect their eventual predators through exploitative competition. Because *Mysis* spp. vertically migrate (Beeton 1960; Spencer et al. 1991), they are often spatially segregated from their visually feeding predators during the day. Thus, in a scenario similar to that of gizzard shad in reservoirs, *Mysis* spp. influence zooplankton abundance via tactile feeding in the upper water column at night, yet enjoy relative immunity from predation in their daytime deep-water refuge.

## Conclusions

Our expectation is that through time, reservoirs should move toward one of two steady states, relative to fish community structure. Where gizzard shad are abundant, systems should

experience a decline in sport fishes, such as bluegill and largemouth bass, as gizzard shad, through the ecological interactions described above, come to dominance. By exploitatively outcompeting bluegill, gizzard shad also compromise largemouth bass recruitment, reducing predatory pressure on themselves and enhancing their eventual rise to dominance. Under these conditions, gizzard shad in lower latitude reservoirs regulate the community in a weblike fashion, rather than in the chainlike fashion more characteristic of the trophic cascade hypothesis (sensu Power 1992). In reservoir systems without gizzard shad at least occasional strong year-classes of sport fishes will be produced with resultant high-quality angling.

Even though not directly applicable to our systems, the trophic cascade hypothesis has provided an important organizing paradigm. Through comparison, we discovered that a prolific, rapidly growing planktivore with a size refuge and omnivorous diet compromised the strong, chainlike linkages required for a trophic cascade. By exploring mechanistic explanations for food-web structure in reservoirs, as compared with north temperate lakes, we grow to appreciate the diversity of natural systems while simultaneously improving our ability to understand, predict, and manage their complexity.

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