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Exploring Ecological Mechanisms Underlying Largemouth Bass Recruitment along Environmental Gradients

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Abstract.—Understanding how largemouth bass recruitment responds to population-, community-, or ecosystem-level processes often requires research conducted along environmental gradients spanning local (i.e., within a state) and geographic (i.e., across latitudes) scales. Comparing population-level patterns across systems revealed that the density of largemouth bass adults (above some minimum threshold) has little impact on recruitment strength. Whereas populations dominated by large adults may result in early hatched, rapidly growing, and ultimately more successful offspring in natural lakes, this phenomenon is not apparent in reservoirs. At the community level, prey assemblage character affects largemouth bass recruitment. In systems dominated by sunfish, a primary prey and a protracted spawner, growth of age-0 largemouth bass is largely regulated by the availability of late-hatched offspring. In systems dominated by gizzard shad, growth of age-0 largemouth bass is regulated by complex ecosystem-level interactions that vary along environmental gradients. Total phosphorus affects success of age-0 gizzard shad, thereby mediating its role as competitor or prey. Spring temperatures and water-level fluctuations further complicate these biotic interactions among age-0 fishes. Quantifying how early food-web interactions are driven by local responses to large-scale, watershed-level processes (which influence nutrients, water levels, etc.) will provide mechanistic insight into the recruitment dynamics of largemouth bass.

Introduction

The population dynamics of largemouth bass *Micropterus salmoides* have been the focus of both basic and applied research for more than 70 years. Over a much shorter time period investigators have worked to understand how this species affects ecosystems (Carpenter et al. 1987; Mittelbach et al. 1995). Typically, the research approach used to capture population dynamics and infer ecosystem effects must extend beyond the population level of organization because a host of interacting abiotic and biotic factors regulate population abundance and individual growth of fish (Noble 1975; Adams and DeAngelis 1987; Olson 1996; Garvey et al. 1998a). To unearth underlying mechanisms and generate robust predictions, largemouth bass population dynamics must be explored at the appropriate levels of organization (i.e., community, ecosystem, landscape) ranging across appropriate temporal and spatial scales (Lodge et al. 1998).

Our understanding of the factors influencing the population dynamics and community impact of largemouth bass largely has followed both the historical development of ecology and fisheries science (Kingsland 1991; Nielsen 1999). Tempting though it may be to suggest that a progressive

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change in focus from a single-species to an ecosystem level of organization has occurred, the transition has not been that simple. Ecologists long have recognized that biotic interactions are important in organizing the relative abundance and distribution of fishes (Forbes 1887; Swingle 1950). However, the search for a relatively simple, elegant solution to the management of fish populations led to the population-specific popularity of the concept of maximum sustained yield (MSY) for largemouth bass and other species in the latter half of the 20th century (Larkin 1978; Nielsen 1999). The concept of optimum sustained yield, and recognizing that complex biotic and abiotic interactions regulate populations, are relatively recent examples of a maturing approach to fisheries management (Stein et al. 1988; Nielsen 1999). In addition, during the past 25 years, recruitment (i.e., the successful transition from age-0 to age-1), a process long studied in marine systems (Bailey and Houde 1989; Chambers and Trippel 1997 for reviews), has received much attention in ecological studies exploring largemouth bass population dynamics (Aggus and Elliott 1975; Maceina and Isely 1986; Ludsin and DeVries 1997). Understanding mechanisms regulating recruitment is critical because year-class strength is set by this process.

Because largemouth bass often reside in fairly closed systems such as lakes or reservoirs, it is convenient to consider recruitment and population dynamics within a single body of water across multiple years as the appropriate organizational, spatial, and temporal combination. This approach generates useful information, particularly about inter-annual variation in population density, size structure, or habitat use. However, processes operating across systems at larger scales such as seasonal climate are important and may interact with system-specific characteristics to affect largemouth bass populations (Maceina and Bettoli 1998; Greene and Maceina 2000; Garvey et al. 2000). Particular patterns may only emerge when viewed across multiple systems within a region. Further, because largemouth bass is widely distributed (Mac-Crimmon and Robbins 1975; Table 1), systems may differ in fundamental ways (i.e., geologically, climatically) across regions, producing population responses that vary across broad environmental gradients (i.e., midwestern versus southeastern reservoirs). Understanding how systems are grouped along environmental gradients allows managers to categorize systems and implement strategies accordingly (Modde and Scalet 1985; Beamesderfer and North 1995; Bremigan and Stein 2001). Agencies often focus regulations and management strategies on a system-specific basis, which can be costly and time-consuming. By placing lakes or reservoirs into ecologically derived management categories using the gradient approach, limited agency resources may be applied most efficiently.

To provide important clues about how largemouth bass responds to the considerable environmental variation it experiences throughout its range (Table 1), the extensive literature for this species as well as others with similar life history characteristics should first be reviewed to generate hints about important environmental factors underlying differences and similarities among systems. A field survey should then be designed and conducted across the identified environmental gradient to bound the potential variability of the targeted response of largemouth bass (Peet 1991). If a field pattern emerges, causal mechanisms must be identified because several alternative processes may be responsible (Quinn and Dunham 1983). Plausible hypotheses should be refined, again allowing the literature to guide decisions. Realistic experiments bounding factors varying along the environmental gradient should be directed at mechanistic questions about largemouth bass population dynamics and subsequent effects (Lubchenco and Real 1991). Modeling exercises incorporating processes varying along the environmental gradient lend additional insight into underlying field patterns (Crowder et al. 1992; Brandt and Hartman 1993; Judson 1994; Marschall and Roche 1998), particularly when manipulative experiments are infeasible or prohibitively costly. Modeling results help to define potential responses (i.e., through sensitivity analyses), guiding the choice and design of experiments.

Although the aforementioned research approaches are not in themselves new, combining them to investigate effects across gradients extending beyond local scales should yield novel insight into ecological processes underlying the recruitment and population dynamics of largemouth bass. As such, we believe that investigators should embrace a multiplicity of research approaches and resource agencies should support efforts extending well beyond field surveys in single systems. Research projects exploring largemouth bass dynamics should be conducted across political boundaries with interagency cooperation. Causality, particularly in complex ecological systems, is an elusive quarry. Using only correlative field relation-

Table 1. Generalized characteristics of typical North American ecosystems along relevant environmental gradients in which largemouth bass resides. The productivity gradient reflects meso- to hypereutrophic. Morphometry is categorized as the proportion of surface area that is littoral zone.

Gradient	Pond	Midwestern (Ohio) reservoir	Southeastern reservoir	Northern lake
Discharge	Low	Variable	Variable	Low
Latitude	Across range	Middle	Low to middle	North
Productivity	Variable	Meso-Hyper	Meso-Hyper	Oligo-Eutro
Morphometry	All littoral	Low-littoral	Variable littoral	Moderate littoral
Exploitation	Variable	Very high	Medium	Medium
Fish Communities	Simple diverse	Moderately diverse	Moderately diverse	Moderately
Gizzard Shad Density	Low	Low-high	Low-moderate	Often absent
Macroinvertebrate Communities	Diverse	Simple	Moderately diverse	Very diverse
Surface Area	<50 ha	50–1,000 ha	50–10,000 ha	50–10,000 ha
Shoreline Length: Surface Area	Low	Low	High	Low
Depth	Shallow (1–5 m)	Shallow (1–15 m)	Intermediate (>15 m)	Often deep (>30 m)
Turbidity	Variable	High (inorganic)	High (algae plus inorganic) gradient within reservoir	Low but variable
Vegetation Density	Variable	Low	Low but variable	High but variable
Winter severity	Variable	Moderate	Low	High

ships across gradients without the supporting experimentation to manage largemouth bass and other species can lead to counterproductive or even deleterious results (see Anderson et al. 2001). In the sections to follow, we address largemouth bass recruitment at progressive levels of ecological organization. Within each organizational level, we explore mechanistically how dynamics change along environmental gradients, drawing on a multiplicity of research approaches in basic and applied ecology (Stein et al. 1996).

Ecological Mechanisms Underlying Largemouth Bass Recruitment

Overview

The 1975 Black Bass Symposium Proceedings (Clepper 1975) provide an ideal starting point for a discussion of our current understanding of ecological processes affecting largemouth bass recruitment and population dynamics across different organizational scales and environmental gradients. About one third of the proceedings in this volume proposed that stocking and/or regulations are important in the face of poor recruitment (Figure 1a). An additional 15 percent suggested that direct abiotic effects, such as water-level fluctuations, should influence the number of offspring produced either by affecting adult reproductive success or by enhancing habitat for offspring (Figure 1b). Size-dependent winter effects on age-0 largemouth bass also were recognized (Aggus and Elliott 1975; Figure 1b). Community interactions certainly were appreciated by many investigators, although specific processes were not explicitly explored (Figure 1c). Prey stocking and competitor removal were suggested as methods by which largemouth bass stocks might be enhanced (Figure 1c). The mechanisms by which abiotic factors influence community interactions and in turn, how the community might affect largemouth bass recruitment was mentioned using pond fertilization as an example (Figure 1d).

During the years following this publication, all of these concepts have been further explored and evaluated, particularly from the standpoint of improving angling opportunities. We argue herein that evaluating important recruitment mechanisms across environmental gradients yields useful information. Using the conceptual development in Figure 1 as our guide, we describe several approaches from both the literature and our experience in Ohio that demonstrate the process of: identifying the potentially important environmental gradient, and conducting research to confirm or refute the importance of ecological processes along the gradient. Searching for generalities and distinctions among the myriad systems in which largemouth bass reside (Table 1) enhances our basic understanding of underlying ecological processes and our ability to develop sound management practices.

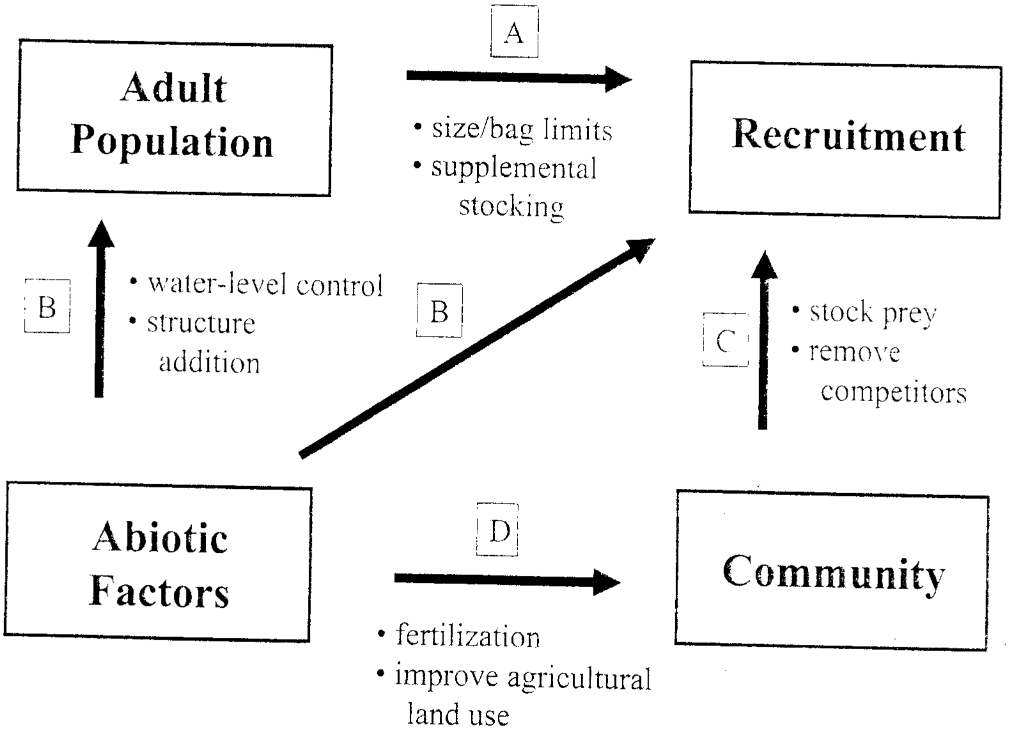

Figure 1. A general view of research approaches and management directed toward improving recruitment of largemouth bass. (A) A relationship between characteristics of the adult stock and the density of offspring may prompt managers to implement bag limits or stock additional age-0 largemouth bass, if adult densities are low. (B) Direct abiotic effects (i.e., uncontrolled water level fluctuations) on adult reproductive success or the growth and survival of offspring may be ameliorated by reducing water level fluctuations in spring. (C) Community characteristics such as the abundance of vulnerable prey will affect growth and potentially survival of age-0 largemouth bass. Supplemental stocking of prey fish or removal of competitors have been suggested to increase largemouth bass growth and survival. (D) The abiotic environment (i.e., productivity) affects the community and thereby largemouth bass recruitment. Historically, fertilizing unproductive systems to enhance prey has been one management option deriving from this knowledge. Watershed-level practices that reduce phosphorus in excessively productive systems (>100 μg/L) may enhance largemouth bass production.

Characteristics of the Adult Stock

Fisheries biologists and ecologists have long sought to quantify the relationship between characteristics of the adult stock of largemouth bass and other species and the number of offspring recruiting to reproductive age or harvestable size (Ricker 1954; Beverton and Holt 1957; Frank and Leggett 1994; Figure 1A). Since the adult stock can sometimes be influenced directly by harvest strategy, a strong stock-recruit relationship would permit management of population production through harvest regulation, a tool that is both available to managers and acceptable to anglers. If adult stock strongly determined recruitment, it would greatly simplify a variety of predictions (Hilborn et al. 1995). Managers could identify how population dynamics of largemouth bass vary across a gradient of adult characteristics (or across environmental factors that affect adults), developing management strategies accordingly.

While it is true that insufficient eggs will be produced to generate a strong year-class when adult densities are low (Hilborn and Walters 1992), it is more typical that excess eggs and larvae are produced to replace the spawning stock. With such high fecundity, other factors may act independently of the adult stock to determine recruitment, thereby resulting in no relationship between stock and recruit densities. In ponds, the number of adult largemouth bass and the density of offspring were unrelated (Reynolds and Babb 1978). During spring 1995–1997, we explored stock-recruit issues by surveying age-0 largemouth bass using inshore blocknets and electrofishing in 10 Ohio reservoirs (Garvey et al. 1998b; E. Lewis, Ohio Division of Wildlife, District 2, Findlay, Ohio, unpublished data). Densities of age-0 largemouth bass were unrelated to the number of adults that were estimated from electrofishing CPE and converted to total densities using CPE-density regressions (range 5–70 adults/ha; Hall 1986; Garvey et al. 1998b; E. Lewis, unpublished data). Abundance of adult largemouth bass did not influence number of offspring, suggesting that other abiotic or biotic mechanisms set cohort strength following spawning.

Body size of adults may indirectly affect recruitment. If large adults spawn earlier in spring than small ones and early hatch dates facilitate growth of offspring, recruitment should improve. In a pond experiment, Goodgame and Miranda (1993) demonstrated that larger adults spawned earlier, producing earlier hatch dates for age-0 largemouth bass. Similarly, large smallmouth bass spawn before their smaller counterparts in northern lakes (Ridgway et al. 1991; Baylis et al. 1993; Wiegmann et al. 1997). To explore how size structure of adults affects hatch dates and ultimately growth of offspring in Ohio reservoirs (mean adult total length 250–330 mm), our research group quantified age-0 largemouth bass size and abundance using the blocknetting and electrofishing effort (described above). No field pattern emerged, leading us to conclude that unknown factors present at the whole-reservoir scale, but not in ponds or natural lakes, masked any effect of adult size structure on hatch date (Garvey et al. 1998b; E. Lewis, unpublished data). In Ohio, management strategies directed across systems to protect large spawners probably will not hasten spawning and enhance age-0 largemouth bass growth. Because we did not detect a field pattern along a gradient of adult size, mechanistic experiments to further examine the effects of adult body size were an unproductive use of resources in our view. We have redirected our research effort toward uncovering other plausible mechanisms underlying the recruitment of largemouth bass in Ohio reservoirs. Even so, investigators might learn much from determining what environmental characteristics render adult size important in some systems (i.e., natural lakes and ponds) but not in others (i.e., small Ohio reservoirs; Table 1).

Adult Reproductive Success

Spawning effort and success of adults may vary among lakes or reservoirs as a function of a gradient of human-induced effects. For example, how disruption of spawning translates to recruitment success at the population scale is unclear given the lack of a strong stock–recruitment relationship (see previous section). However, if reproductive responses of adult largemouth bass do affect the total production of offspring (Figure 1B), direct removal of adults from nests by anglers bodes poorly for survival of eggs and larvae because these life stages would likely be removed by predators (Philipp et al. 1997). Hence, largemouth bass recruitment success may vary across a gradient of fishing pressure during spring spawning.

System-wide environmental characteristics (i.e., habitat quality) or perturbations (i.e., uncontrolled water level fluctuations) may categorically affect spawning success and thereby production of offspring across reservoirs. High precipitation during spring spawning of largemouth bass may yield positive or negative effects. If high but stable water levels occur and are regulated as in some large southeastern reservoirs, age-0 largemouth bass use inundated vegetation for refuge and foraging, thereby enjoying improved growth and survival (Maceina and Stimpert 1998; Sammons et al. 1999). However, when water levels are largely unregulated and vary during spring as they are in relatively small midwestern reservoirs, densities of age-0 largemouth bass decline (Kohler et al. 1993; Garvey et al. 2000), perhaps due to a variety of mechanisms including adult nest abandonment (Heidinger 1975), stranding of juveniles, or reduced littoral development (reduced vegetation for refuge and forage). In Ohio reservoirs, water levels fluctuate more in systems with watersheds that are large relative to reservoir surface area, suggesting that age-0 production should be low in systems with relatively large drainage areas (Garvey et al. 2000). During wet years, largemouth bass density varies inversely with watershed area in these unregulated systems. When managing largemouth bass in reservoir ecosystems, it is clear that direct effects on reproduction vary along many identified (see above) and yet unidentified environmental gradients spanning location (i.e., southeastern versus midwestern) and time (i.e., wet versus dry years).

Abiotic Variability

Abiotic is a broad term and as expected, abiotic characteristics such as turbidity, structure, and temperature can affect the growth and survival of age-0 largemouth bass across systems (Figure 1b). Turbidity influences the foraging success and predation risk of largemouth bass by modifying their reactive distances and those of their prey (Crowl 1989). Physical structure provided by vegetation influences the foraging success of fish; intermediate densities of vegetation may provide adequate refuge for prey while still allowing largemouth bass to forage successfully (Crowder and Cooper 1982). High vegetation abundance reduces foraging opportunities for largemouth bass (Garvey et al. 1998a) because their prey effectively use the refuge (Savino and Stein 1989; Hayse and Wissing 1996). Although an absence of vegetation increases predation risk for largemouth bass and may cause prey depletion, several investigators suggest that age-0 largemouth bass may fare well when vegetation density is reduced (Bettoli et al. 1992; Hayse and Wissing 1996; Olson et al. 1998; Pothoven and Vondracek 1999), although it is not clear that this effect is sustainable through time. It is important to note that an important problem with many whole-system vegetation manipulation studies is a lack of power (i.e., replication across systems) to detect responses (Carpenter et al. 1995). In addition to stem density, the physical structure (i.e., as affected by species composition, growth form, architecture, and spatial heterogeneity of macrophyte assemblages) should affect largemouth bass foraging success and refuge from predation (Lillie and Budd 1992; Dibble and Harrel 1997; Valley and Bremigan in press). Although age-0 largemouth bass mortality as a function of predation has historically been viewed as important during summer, the presence of structural refuges from predators may be important during winter as well (Miranda and Pugh 1997).

One of the most important abiotic factors influencing all aspects of the biology of fishes is water temperature (Love 1980). Seasonal temperatures differ dramatically across the range of largemouth bass. As such, the length of the growing season declines with increasing latitude, ultimately reducing first-year growth (Shuter et al. 1980). Within a latitude, temperatures also may differ among systems depending on their size and depth, with similar consequences for growth and potentially survival of age-0 largemouth bass.

Body Size and Winter

Conventional wisdom has long held that high, size-dependent mortality of age-0 largemouth bass and congeners occurs during winter (Oliver et al. 1979; Gutreuter and Anderson 1985). Thus, cohort strength is typically linked to the extent of first year growth and fall size. Energy depletion in age-0 largemouth bass has historically been held as the primary cause of size-selective overwinter mortality (Gutreuter and Anderson 1985). For many species, both field patterns and experimental evidence support the view that small size is detrimental (i.e., Post and Evans 1989). Thus, environmental factors affecting the extent of first year growth among systems can influence patterns of winter survival and cohort strength. This field pattern appears to hold for largemouth bass in Ohio reservoirs. In fall 1994, we sampled age-0 largemouth bass in two Ohio reservoirs, Knox Lake and Pleasant Hill Reservoir (Garvey et al. 1998c). Our sampling in spring 1995 revealed that small individuals in both systems experienced higher mortality during winter than large ones. However, the relative proportion of small largemouth bass dying differed between systems (Garvey et al. 1998c), suggesting that the role of size on recruitment may indeed vary. Because winter temperatures did not differ substantially between these reservoirs, other factors apparently contributed to differences in size-dependent mortality.

If size-dependent energy depletion is the primary mechanism governing juvenile largemouth bass overwinter survival, several management strategies can be implemented as a function of variable body size among systems. Age-0 largemouth bass will continue consuming prey at greater than or equal to 6°C (Garvey et al. 1998c; Fullerton et al. 2000). As such, management actions that increase food availability in systems with small individuals during fall through spring might offset loss of fat reserves. Drawdown of reservoirs to concentrate prey in reservoirs could increase food availability (but see below). Efforts to increase first-summer growth, and thus size during winter, also will reduce the probability of winter starvation. If increased adult size leads to earlier spawning and hatching (Goodgame and Miranda 1993) and large fall size of age-0 offspring is linked to an early hatch date (Phillips et al. 1995; Sammons et al. 1999), then protecting large spawners might increase winter survival in some systems. Strong, consistent relationships among body size, energy depletion, and mortality might allow managers to develop management criteria based on a critical threshold length of age-0 largemouth bass by fall (Gutreuter and Anderson 1985). If a cohort does not reach this critical size, supplemental stocking of large hatchery-reared largemouth bass might be used to enhance year-class strength in systems producing predominately small individuals (Lawson and Davies 1977; Buynak and Mitchell 1999; Heidinger 1999), although the contribution of this tactic to population dynamics should be assessed.

Was energy depletion really the sole mechanism responsible for patterns of size-selective mortality in our two Ohio reservoirs? A lack of a temperature effect on size-selective mortality between reservoirs and discrepancies in the literature suggest another mechanism which apparently varied along some unidentified environmental gradient (Garvey et al. 1998c). Experiments provide mechanistic insight. During winters 1994–1995 and 1995–1996, 0.4 ha pond experiments were conducted in Ohio to determine how size affects overwinter survival of age-0 largemouth bass (Garvey et al. 1998c). All individuals were marked to tease apart the impacts of mortality and growth on shifts in size distributions during winter. In contrast to our reservoirs, size-selective winter mortality in ponds was slight. Significant reductions in small age-0 largemouth bass only occurred in ponds in which large, potentially cannibalistic conspecifics occurred (Garvey et al. 1998c). Outdoor pool experiments conducted during that same winter revealed that food availability did not affect overwinter survival of small and large largemouth bass (Garvey et al. 1998c). Combining all lines of evidence suggests that patterns of overwinter mortality in Ohio reservoirs are driven, at least in part, by predation rather than solely by size-dependent energy depletion. Other recent studies conducted in mid- and low-latitude systems support the view that size-selective predation, perhaps in concert with energy depletion, may regulate overwinter survival of small age-0 largemouth bass (Miranda and Hubbard 1994).

If predation affects recruitment of age-0 largemouth bass in Ohio and other mid- and low-latitude locales, management strategies other than those that counterbalance winter energy depletion should be implemented across a gradient of potential predation pressure during fall through spring. Reservoir drawdown to enhance foraging opportunities for small age-0 largemouth bass also would increase their susceptibility to either cool-water active predators (i.e., walleye *Stizostedion vitreum*) or cannibalistic conspecifics. Hence, this technique may exacerbate, rather than ameliorate, winter mortality. The practice of stocking piscivorous species such as saugeye (*S. vitreum* × *S. canadense*) which likely forage actively during cool months (Donovan et al. 1997) may further contribute to losses of small age-0 largemouth bass, which is a warmwater species that may not be well-adapted for avoiding coolwater predators. If recruitment strength indeed varies among systems as a function of interactions between largemouth bass size structure and predation intensity, ecologists and managers may craft predictive models to forecast cohort strength by gathering current information about refuge availability, the predator assemblage, and age-0 largemouth bass size structure. If predation risk is low or refuges are abundant during fall through spring, strong recruitment may occur even given small fall sizes, thereby saving managers the cost of supplemental stocking or manipulating forage to enhance cohort strength.

Patterns of size-selective overwinter mortality also may differ along a latitudinal gradient for age-0 largemouth bass. Energy depletion during extended cold temperatures may well be the mechanism ultimately limiting the northern range of largemouth bass as it does for smallmouth bass (Shuter et al. 1980; Shuter and Post 1990; Fullerton et al. 2000). However, starving individuals at northern latitudes likely reduce metabolic rates to offset the cost of fasting during long winters (Wright et al. 1999). If this physiological adjustment is unaccounted, investigators will overestimate winter energy depletion and mortality during long, cold winters near the northern range limit. In southern and middle latitudes, in which winters often are milder, energy depletion and predation may interact to regulate recruitment of largemouth bass (Ludsin and DeVries 1997; Garvey et al. 1998c). As such, management in northern systems may primarily involve an understanding of how energy depletion affects survival, whereas management in southern systems also may require an appreciation of the impact of resident predators.

Complex Community Interactions

Competition: A gradient of abiotic effects may not adequately explain differences in recruitment of largemouth bass among systems. Complex interactions between largemouth bass and other species across several environmental gradients may regulate their recruitment. Although predatory and competitive interactions regulate growth and ultimately survival of many species (Figure 1c; Hairston et al. 1960; Paine 1966), these interactions have only been explicitly explored for largemouth bass in the past few decades (Gilliam 1982; Turner and Mittelbach 1990; Olson et al. 1995). Following a brief zooplanktivorous larval stage, juvenile largemouth bass become insectivorous (Keast and Eadie 1985; Garvey et al. 1998a). Experimental work suggests that competitive interactions with bluegill *Lepomis macrochirus* during the juvenile stage compromise a later switch to piscivory, limiting first-year growth (Olson et al. 1995). To our knowledge, this interaction has not been verified in systems larger than small lakes. Intraspecific competition at high population densities also can negatively affect growth, if prey are limited (Garvey et al. 2000). Thus, largemouth bass recruitment may vary among systems as a function of inter- and intraspecific competitive interactions.

Piscivorous switch: Differences in prey assemblage composition and density among systems also may generate differences in largemouth bass success. Research conducted across multiple scales clearly demonstrates that piscivory increases energetic intake and thereby the growth of age-0 largemouth bass through its range (north, Olson 1996; middle, Garvey et al. 1998a; south, Phillips et al. 1995, Ludsin and DeVries 1997). Modeling, experiments, and field data confirm that slight differences in relative sizes of largemouth bass (which are gape limited) and their prey drive patterns of growth (Adams and DeAngelis 1987; Wright 1993; Garvey and Stein 1998a). The recognition that piscivory is important suggests that prey stocking may improve largemouth bass growth and recruitment. However, the impact of stocking programs of prey such as threadfin and gizzard shad *Dorosoma* spp. has been met with mixed success (DeVries and Stein 1990), in part due to complex, unexpected food web interactions. Exploring dynamics across a gradient of prey availability may be more complex than once thought.

Food web interactions: Because prey composition does not necessarily generate predicted responses, a food web approach is necessary to uncover underlying mechanisms. We provide an example of such an approach in highly productive (> 100 μg total phosphorus/L) Ohio reservoirs. In these systems, a potential prey species indirectly affects the first-year growth and recruitment of largemouth bass (Stein et al. 1995). Age-0 gizzard shad *D. cepedianum* reach very high densities (> 80/m^3; Dettmers and Stein 1992; DeVries and Stein 1992; Garvey and Stein 1998a; Bremigan and Stein 2001) and can deplete zooplankton density upon reaching juvenile sizes (> 25 mm total length, Dettmers and Stein 1992). Field surveys and multiscale experiments strongly suggest that reductions in zooplankton negatively affect the growth and potentially the survival of age-0 bluegill in these systems (Garvey and Stein 1998a; but see Welker et al. 1994; Figure 2). Because age-0 bluegill often remain at vulnerable sizes through summer, whereas gizzard shad rapidly grow beyond susceptibility, the competitive outcome favoring gizzard shad can reduce largemouth bass piscivory and growth (DeVries et al. 1991; Garvey et al. 1998a; Garvey and Stein 1998a; Figure 2). During rare years when spring precipitation is regionally low (<15% of years in Ohio), age-0 gizzard shad may remain vulnerable for an extended time and contribute to rapid growth of age-0 largemouth bass (Garvey et al. 2000). Causal mechanisms underlying this field pattern in Ohio have not been isolated, although the impact of spring water-level fluctuations and temperature on species-specific patterns of spawning might be important. Identifying how the impact of gizzard shad as a competitor and prey species varies among systems and years in Ohio and other regions is crucial for predicting its impact on the recruitment of largemouth bass.

Abiotic Effects on Food Web Interactions

The small, highly productive Ohio reservoirs in which much historical work exploring gizzard shad effects was conducted (see above; Stein et al. 1995) comprise a small subset of the systems in which largemouth bass reside (Table 1). Although impor-

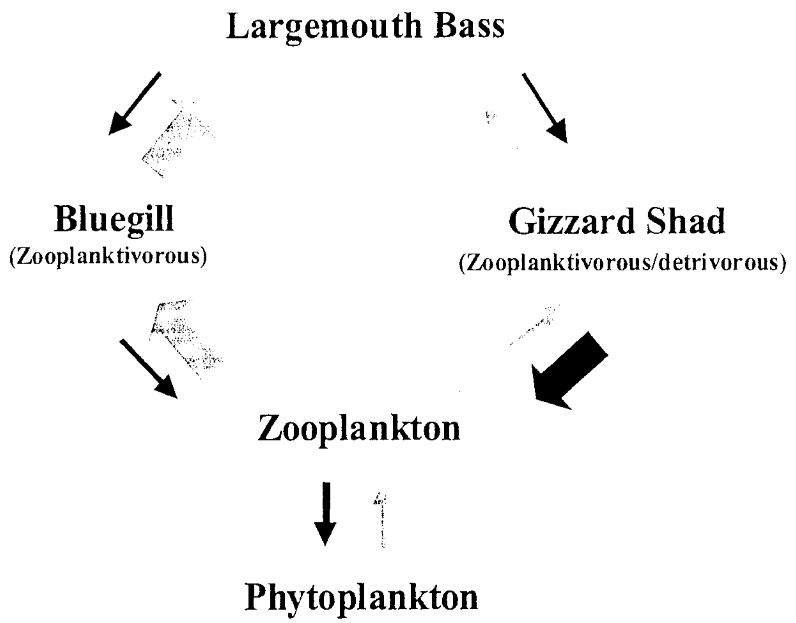

Figure 2. Conceptual pelagic food web structure of a small (<100 ha), hypereutrophic (>100 µg TP/L) midwestern reservoir. Black arrows represent the importance of consumption by a predator to the abundance of the prey population. Gray arrows represent the potential importance of the prey to the predator population. These relative strength of these interactions are greatly modified by variation in abiotic characteristics including seasonal temperature, precipitation, and productivity.

tant mechanisms have been identified and tested in these reservoirs, surveys conducted through time and across gradients both within and among reservoirs in Ohio suggest that the direct and indirect effects of gizzard shad on the community and ultimately on largemouth bass vary (Figure 1d). The potential role of gizzard shad in reservoirs also appears to differ geographically, in which processes in Ohio are not detected in some southeastern reservoirs (Allen et al. 1999; Jackson and Noble 2000; Table 1). Abiotic characteristics that vary among these systems include spring warming, summer temperature, turbidity, lake morphometry, and productivity (i.e., total phosphorous loading). These characteristics should influence food web interactions, with implications for early first-year growth and survival of largemouth bass (Table 1).

Patterns of spawning of bluegill, gizzard shad, and largemouth bass throughout their range of overlap may be affected differentially by several variable abiotic factors that vary annually among systems including temperature (Claussen 1991) and water level fluctuations (Michaletz 1997). These effects likely interact with adult body size to further influence spawning duration and intensity in some systems, although adult size did not appear to be important for largemouth bass in Ohio. Differential timing of overlap of larvae as a function of these complex factors should influence competitive interactions for zooplankton and availability for largemouth bass predators, as it does for other taxa in other systems (Lawler and Morin 1993; Tupper and Boutilier 1995; Hodge and Mitchell 1996).

Abiotic effects on larval interactions: In the small, highly productive Ohio reservoirs in which we predict a negative effect of gizzard shad, early larval appearance may allow age-0 bluegill to persist, albeit at low densities, when zooplankton densities are subsequently driven to low abundances by gizzard shad. Experiments conducted in small, replicate mesocosms (1 m^3) revealed that differential timing of appearance of gizzard shad and bluegill larvae affects their competitive interactions (Garvey and Stein 1998a) and availability to age-0 largemouth bass. When appearing early relative to bluegill, gizzard shad grow rapidly, reach sizes at which they reduce zooplankton, and reduce growth of bluegill (Garvey and Stein 1998a). Interestingly, when larval bluegill and gizzard shad appear simultaneously, gizzard shad have little impact on bluegill, regardless of their density (Garvey and

Stein 1998a). Thus, only when bluegill appear before or simultaneous with gizzard shad during spring should bluegill grow and potentially survive to later life stages. During some years, abiotic conditions favorable to the relatively early spawning of bluegill may favor strong cohort production in the face of high gizzard shad densities (Garvey and Stein 1998a). Early spring warming may well be the mechanism enhancing early bluegill spawning, although this has not been explicitly tested. Age-0 largemouth bass should be more likely to switch to piscivory and grow rapidly during years when bluegill larvae appear relatively early. However, the tradeoff here is that early hatched bluegill might grow sufficiently rapidly to reduce their vulnerability to predation by most gape-limited, age-0 largemouth bass (Garvey et al. 1998a).

Management that alters competitive interactions between bluegill and gizzard shad may affect the availability of these prey fish to age-0 largemouth bass. However, regulating abiotic conditions that reduce early competitive interactions is improbable, particularly if spring warming is the ultimate regulatory mechanism. Biotic factors such as adult bluegill size might facilitate early spring spawning, thereby increasing the production of age-0 bluegill. If adult bluegill size affects the timing and duration of spawning in bluegill in Ohio reservoirs, we could enhance largemouth bass production by managing the size structure of the adult bluegill. Only by understanding mechanisms underlying the relative timing of hatching and appearance of age-0 gizzard shad and bluegill across systems in Ohio and other regions will we begin to develop sound predictions for the growth and potentially overwinter survival of age-0 largemouth bass.

Productivity Effects: Our work suggests that spring conditions affect fish interactions and ultimately largemouth bass success among years, at least within highly productive reservoirs. Productivity (as affected primarily by total phosphorous) both among and within reservoirs appears to alter the growth and abundance of age-0 gizzard shad and therefore the relative effects of this species on largemouth bass and other species (DiCenzo et al. 1996; Bremigan and Stein 1999; Bremigan and Stein 2001). The realization that the impact of gizzard shad may change in complex ways along productivity gradients is both daunting and intriguing, opening many possible scenarios for management.

High densities of gizzard shad in highly productive reservoirs arise as a function of combined high egg densities plus high larval survival (Bremigan and Stein 1999, 2001). Resulting juvenile gizzard shad densities are high, and should lead to reductions in individual growth. However, they can switch to abundant detrital resources and grow rapidly (Mundahl 1991; Stein et al. 1995; Yako et al. 1996), typically remaining vulnerable to age-0 largemouth bass for only a short time (Hambright et al. 1991; Garvey and Stein 1998b). These responses of gizzard shad to high phosphorous concentrations lead to the complex food web interactions described earlier (Figure 2).

Gizzard shad impact on food webs and ultimately largemouth bass may differ markedly as productivity declines both in Ohio reservoirs (Bremigan and Stein 2001) and likely in other systems (DiCenzo et al. 1996; Michaletz 1999). In eutrophic Ohio reservoirs (i.e., at an intermediate point along the productivity gradient), hatch and survival are relatively high, but juvenile growth rates are reduced by intraspecific competition (Bremigan and Stein 1999). With slower growth, age-0 gizzard shad remain vulnerable to largemouth bass longer. Thus, first-year growth and potentially recruitment of largemouth bass may be facilitated by the presence of gizzard shad. In mesotrophic reservoirs, hatch and survival of age-0 gizzard shad may be low, but resulting juveniles grow quickly (Bremigan and Stein 1999). In these systems, we predict that other prey fishes will be released from competitive interactions with gizzard shad and serve as important piscine prey for largemouth bass. Surveys of growth of adult largemouth bass and other sport fish demonstrate that adult growth declines with declining productivity (Ney 1996). However, recruitment strength may increase. The impact of productivity on largemouth bass success is complex and depends on unique responses of different life stages.

Predatory Control in a Food Web Context: Control of gizzard shad by abundant stocked predators such as hybrid striped bass has been suggested as a possible management tool for largemouth bass and other species (Dettmers et al. 1996). This concept is predicated on the trophic cascade hypothesis, which predicts that consumer effects cascade down through food chains to affect lower, nonadjacent trophic levels (Carpenter et al. 1985 1987). Piscivores remove planktivorous fish. Released from planktivory, herbivorous zooplankters increase and graze phytoplankton to low densities. Following this logic, if hybrid striped bass reduce gizzard shad densities in reservoirs, zooplankton abundances should increase, thereby facilitating the growth and survival of other zooplanktivorous prey fish for predators such as age-0 largemouth bass. Because littoral largemouth bass and pelagic hybrid striped bass probably do not overlap spatially, we expect little direct interaction between them. Pond experiments revealed that hybrid striped bass can reduce gizzard shad densities, allowing zooplankton to increase to levels that support bluegill recruitment (Dettmers et al. 1996). However, field experiments, surveys, and modeling suggest that control of hybrid striped bass in reservoirs is limited to a subset of reservoirs in which: stocking densities of hybrid striped bass are high; gizzard shad densities are low (< 25 larvae/m^3); and zooplankton productivity is high (Dettmers et al. 1996; Dettmers and Stein 1996). Only about five percent of Ohio reservoirs reflect this combination of characteristics (Dettmers et al. 1998), greatly limiting this management tactic in this region. If the efficacy of this technique varies geographically due to some unidentified difference, it may be adopted elsewhere.

Watershed Management Approach: As we begin to isolate the complex ecological mechanisms leading to patterns of largemouth bass abundance along productivity gradients, we must consider effects that occur at the watershed-scale. Reducing input of nutrients to highly eutrophic reservoirs should favor species such as bluegill and largemouth bass in Ohio reservoirs. Indeed, total phosphorous in Ohio reservoirs increases with the percent agriculture area in the watershed (W. Renwick, Miami University, Oxford, Ohio and P. Soranno, Michigan State University, unpublished data). Other systems may receive significant nutrients from urban runoff or wastewater treatment. Reducing phosphorous loading will involve changes in land-use patterns, either through conversion of farmland to woodlands or improved agricultural practices. Immediate responses of largemouth bass and the fish community should not be expected. Watershed-level nutrient changes may lag substantially. And nutrients trapped in sediment may continue to be resuspended by detritivory for years following reductions in phosphorous loading (Vanni 1995; Schaus et al. 1997).

Conclusions and Future Directions

In our view, management strategies for a single species such as largemouth bass can only be produced with an emphasis on strong research—a defining characteristic of contemporary fisheries management (Nielsen 1999). As we have demonstrated for largemouth bass, the road map for fisheries research is a varied one, and may or may not involve a single-species, community, or ecosystem approach (Figure 1), although we must often look across environmental gradients at relatively local (i.e., within Ohio) and geographic (i.e., North America) scales to generate ecological understanding (Table 1).

Management Recommendations

Management recommendations can derive from our ecological work, especially as we consider how these recommendations might fall along ecological gradients (Figure 3). From a population perspective, our work and that of others suggest that the number of offspring produced likely will vary little with adult density, except when adults are quite scarce (Figure 3a). Thus, adult populations should be protected at some acceptable minimum threshold density through harvest regulations. Although a high proportion of large adults in Ohio reservoirs does not appear to shift hatch dates earlier, this mechanism may operate in other systems such as natural lakes and small impoundments (Figure 3b). Managers may benefit by protecting large spawners to potentially enhance early spawning and greater growth of offspring. A community-level, food web approach demonstrates that the densities of gizzard shad (>10 larvae/m^3) that typically occur in high productivity reservoirs can reduce densities of other prey fish, notably bluegill (Figure 3c). As such, stocking of aggressive predators such as hybrid striped bass hypothetically may reduce their deleterious effects on zooplankton and other zooplanktivorous fish, although this approach appears to be restricted to reservoirs in which an unlikely combination of low gizzard shad density and high zooplankton productivity occurs (Dettmers et al. 1998; Figure 3c). From an ecosystem perspective, working with agencies to maintain stable water levels during spring should enhance largemouth bass reproductive success (Figure 3d). Patterns of spring warming as affected by latitude and depth likely affect relative timing of appearance of larval fish. Managers may expect bluegill to fare better during warm springs (Figure 3e). Finally, research conducted across productivity gradients suggests that reduced phosphorus loading may reduce the deleterious effects of gizzard shad, necessitating a watershed-level management approach (Figure 3f).

Extending the Gradient Approach—Watersheds

One major goal in ecology is to generalize across systems. Currently, though we appreciate some pattern, we are unable to understand all systems, thereby leading us to conclude that "all systems are unique." We believe this is an unproductive path, for we, and especially agencies, do not have the resources to study every lake. Hence, explaining common patterns in groups of lakes through ecologically oriented, mechanistic work will allow us to make management progress. Where we fail with our generalities or predictions offers new opportunities for research and paradigm adjustment.

Ideally, common systems with similar food web interactions may be identified along appropriate environmental gradients. Management options for component species (i.e., largemouth bass) of interest may then be derived. This is a challenging task, but information for systems and species as widely studied as reservoirs and largemouth bass, respectively, appears to be growing exponentially. The task at hand is to synthesize across the current knowledge base, identify the important

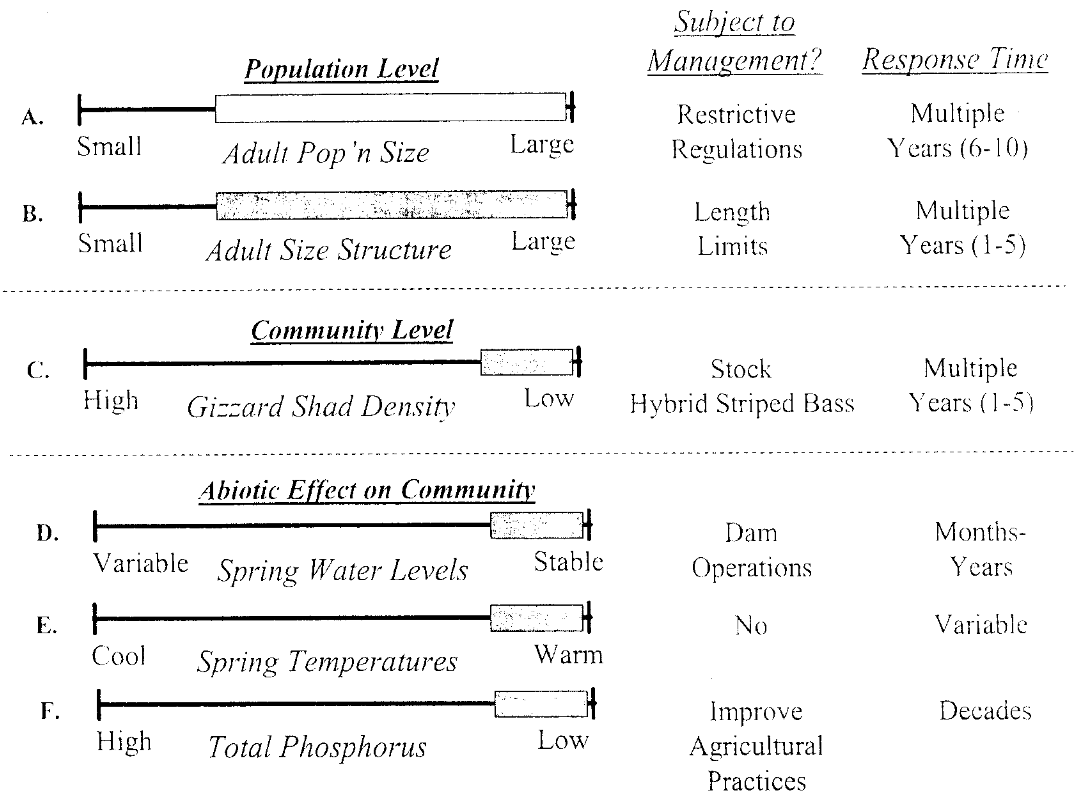

Figure 3. Potential management options at the population, community, and ecosystem levels for improving largemouth bass growth and production along environmental gradients. Response times vary among options. Areas along each gradient with a shaded box are conditions under which management should improve largemouth bass density and first-year growth. (A) Systems in which adult density are above some minimum threshold potentially produce high densities of age-0 largemouth bass. Restrictive harvest regulations will maintain adult densities above this threshold and perhaps improve reproductive output. (B) A large proportion of large-bodied, adult spawners enhances early hatching and rapid growth of offspring in some systems. Length limits should be used to protect large adults if this process is important. (C) In productive systems in which densities are intermediate or low (<25 gizzard shad/m^3), negative competitive effects may be reduced by stocking species such as hybrid striped bass. (D) Water level fluctuations during largemouth bass spawning may reduce the density of offspring produced. Maintaining reservoirs at stable, elevated water levels during spring may enhance production and growth of age-0 largemouth bass. (E) In highly productive reservoirs, warm spring temperatures may encourage early spawning of bluegill, thereby reducing their competitive interactions with gizzard shad and increasing their densities for piscivorous age-0 largemouth bass. No management option currently exists, although these interactions should vary latitudinally with seasonal temperature. (F) Reductions in phosphorus loading as a function of improved land use should reduce gizzard shad densities and their negative competitive effects.

gradients, and design and implement research to fill in the relevant gaps. In small, highly productive, mid-latitude reservoirs in the U.S., we understand much about food web interactions and thereby have gained confidence in our management recommendations for largemouth bass. The next step is to understand processes acting at lower levels of productivity.

Large-scale factors such as productivity, water-level variability, and discharge likely operate at the scale of the watershed. If this holds true, then the grouping of systems for the management of largemouth bass and other species may well be organized at this level. To determine if implementing management for largemouth bass is appropriate at the watershed scale, we must adopt a requisite interdisciplinary approach (Wesche and Isaak 1999), touted by many and, in reality, attempted by few. Mechanisms underlying largemouth bass recruitment and population dynamics are certainly complex. However, by exploring mechanisms across gradients spanning regional and geographic scales, generalities do emerge, providing useful ecological and management insight.

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