Exploring Stunted Body Size: Where Have We Been, What Do We Know, and Where Do We Go?

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Abstract.—Although stunting is a fairly common phenomenon in fishes, confusion remains about underlying mechanisms and appropriate management strategies. Herein, I summarize current literature to provide a synthetic look at factors that can cause stunting and consider associated management strategies. First, I provide historical context by reviewing early literature, much of which is focused on density-dependent slow growth as the cause of stunting. A brief summary of more recent literature, however, suggests that stunting is often more complex than early investigations might indicate, and mechanisms such as early maturation and overexploitation of adults are considered. Because the bluegill *Lepomis macrochirus* is an extremely common reservoir species, a large body of literature related to its population size structure and associated management strategies is available. Therefore, I use bluegill as a model system to describe how various mechanisms might lead to stunting and indicate important considerations from a management standpoint. In the final section, I review management strategies and argue, among other things, that consistent language, clear identification of underlying mechanisms, and multifaceted management approaches are necessary for robust results when dealing with stunted populations.

Introduction

In the majority of fish species, the individual size of the population varies considerably in different lakes..... This is a matter of great economic significance. Populations consisting only of small individuals are most often of but slight value. Thus, an analysis of the reasons for these differences, as well as of the possibilities of obviating them, is undoubtedly called for. (Gunnar Alm 1946)

Body size is both a fundamental determinant of an organism's ecology (e.g., Werner and Gilliam 1984) and a primary response

variable for natural resource managers. For fishery biologists, maintaining a population of large, harvestable-size organisms is frequently the primary focus of management initiatives. Often, however, organisms exhibit strong intraspecific variation in growth rates, life history strategies, and, as a result, body size. As such, understanding population-specific mechanisms responsible for smaller-than-average individuals becomes necessary.

At one extreme of variation in body size is the phenomenon of stunting, a condition in which individuals in a population have a much smaller maximum size than conspecifics in other populations. This presents an interesting problem for theoretician and manager alike: why are individuals so much

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smaller, and what can be done to change that? Although fairly common in fish, stunting is still a poorly understood phenomenon and management strategies often fail to recover stunted populations (e.g., Beard et al. 1997). The goal of this paper is to help alleviate some of the confusion about stunting and to provide a framework for fishery managers dealing with stunted populations.

One impetus for this manuscript was to address the often imprecise language found in published literature. Improving our understanding of stunted populations will, in my opinion, require common language and consistent terminology. The terms "stunted growth," "stunted individuals," and "stunted population size structure," among others, appear interchangeably in the literature (e.g., Deedler 1951; Diana 1987; Amundsen and Klemetsen 1988). I believe that the focus should be on body size and population structure. Stunting is not always directly attributable to slow growth. Thus, "stunted growth" describes a mechanism whereby an individual can become stunted and, consequently, is only applicable to certain situations. Identifying a stunted population structure, on the other hand, reflects the current status of the population, regardless of how it came to be that way. As such, I suggest that stunting be defined at the population (versus individual) level: a stunted population is one in which the size structure of adults is significantly smaller than that of conspecifics in similar populations. Describing individuals with slow growth, therefore, would not necessarily indicate a stunted population but would provide useful information about predictions for size structure. Likewise, quantifying maturation schedule, resource availability, and adult mortality would also be beneficial, as variation in these life history parameters can also lead to stunting (e.g., Donald and Alger 1986; Diana 1987, 2004; Coble 1988). This

definition is similar to Diana (2004), with the exception that he places the emphasis on a significant decrease in growth rate (caused by mechanisms such as density-dependent slow growth, mortality, and inappropriate prey). There are many options for describing population size structure, including common metrics such as proportional stock density and relative stock density, catch per unit effort of fish over a certain size threshold, and mean total length of adults, all of which have been used effectively to describe stunted populations. These population-level metrics have the additional advantage of allowing broad comparisons across systems and, in some cases, species.

The specific objectives of this paper are to (1) synthesize current ideas and philosophy related to stunting, (2) focus attention on the variety of mechanisms that may be relevant to reservoir fisheries, and (3) suggest management strategies for addressing stunted populations. I emphasize reservoir species and systems when possible throughout the manuscript. However, the context of stunting and associated mechanisms is broader than just reservoir and small impoundment fisheries and, as such, I draw examples and include discussion from a wide variety of literature.

Historical Context

Density-dependent slow growth was the focus of much of the early research on stunting, particularly that on common reservoir species such as largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* in small impoundments. Classic research by Homer Swingle and colleagues, for example, focused on stocking rates and predator–prey interactions for bass and bluegills, emphasizing practices that would prevent overcrowding and stunting. The focus of this body of literature was almost

entirely on density-dependent mechanisms associated with stunting and strategies that could be employed to prevent production of these undesirable fish. Swingle (1946) suggested fertilization of small impoundments to produce algal blooms and reduce aquatic macrophytes as cover for juvenile bluegills, thereby increasing largemouth bass predation and alleviating density-dependent slow growth of the remaining bluegills. Swingle et al. (1953) suggested poisoning to prevent growth problems associated with overcrowding. In both cases, the theme was to restore balance in the fish community between predators (usually largemouth bass) and prey (usually bluegills) to prevent reduced growth rate.

Similar mechanisms were proposed by researchers in other systems. In particular, Gunner Alm studied extensively the causes of Eurasian perch *Perca fluviatilis* stunting through observation and experimentation in lakes and ponds. Again, the emphasis of this research was on the importance of density-dependent growth limitation (Alm 1946). Following years of study in a variety of systems, Alm concluded, "The growth of different fish populations is entirely or, at any rate, principally dependent on the environment, being above all a question of nourishment." Additional early (and even more recent) studies with Eurasian and yellow perch *P. flavescens* have reached the conclusion that stunted perch are the result of inadequate food supply (Alm 1946; Deedler 1951; Jansen and MacKay 1991).

Interestingly, however, Alm (1946) also considered a number of other mechanisms that could shape population size structure. In particular, he found some evidence for genetically based differences in capacity for growth and, perhaps more relevant to many reservoir fisheries in the United States, an influence of timing of maturation. In the latter case, he explored correlations between early maturity and reduced body size in certain populations and considered the energetic tradeoff between somatic growth and sexual maturation. That mechanism has received much recent attention, particularly in the context of stunted bluegill populations in U.S. reservoirs.

Other early investigations also discussed the implications of variation in timing of maturation among populations. Working with Eurasian perch, Deedler (1951) noted (as did Alm) the potential for fast-growing individuals to become stunted, which opposed the general "slow growth equals stunted body size" paradigm. Likewise, Geyer (1939) found good early growth rates of ultimately stunted cyprinids. In these cases, the primary issue was timing of maturity; good growth rates were noted, but maturation was early relative to conspecifics in other populations. These studies were important, if somewhat unusual, because they considered the population-level consequences of individual life history and energetic strategies and thereby introduced alternative explanations for stunted body size. The emerging theme was that stunted fish could result even from populations exhibiting high growth rates, making the phrase "stunted growth" somewhat paradoxical.

Despite these early considerations of sexual maturation, the prevailing wisdom was, and I think remains, that stunted body size is primarily a reflection of inadequate food resources. Further, following early characterizations of bluegills and perch by Alm, Swingle, Deedler, and others, numerous studies over the years have provided good evidence for density-dependent mechanisms associated with slow growth and stunting with fish such as rock bass *Ambloplites rupestris* (Beckman 1943), brook trout *Salvelinus fontinalis* (Donald and Alger 1989), and Arctic char *S. alpinus* (Amundsen and Klemetsen 1988) among others.

A Mechanistic Perspective

A number of mechanisms have been proposed to cause stunted body size, and though many suggest some variation on the resource-limitation theme, there are several other possibilities that deserve consideration. Rather than provide an exhaustive literature summary, in this section I highlight the breadth of mechanisms that have been suggested for lake and reservoir species. When considered together, these papers indicate the lack of consensus related to explanations for small body size and suggest that mechanisms may be species- and even population-specific.

Density Dependence and Resource Availability

When considering the issue of density-dependent growth and resource availability, it is important to distinguish between overcrowding, which assumes that the available prey is appropriate but not abundant, and the lack of appropriate prey. That is, an important distinction is prey quantity versus prey quality. Implicit in the early bluegill research focusing on overpopulation was that food resources were insufficient to support good growth due to overcrowding (e.g., Swingle et al. 1953; Ligler 1971). Alternatively, the quantity of available food might be far less important than the quality of food available, particularly for omnivorous species and those that undergo ontogenetic diet shifts. Heath and Roff (1996) indicated that lack of appropriate benthic food items caused stunting in yellow perch and discussed the concept of "trophic bottlenecks," whereby the absence (or limited availability) of certain prey items at a specific size can lead to stunting. Diana (1987) discussed the potential for lack of appropriate-sized prey to cause stunting in northern pikes *Esox lucius*. Donald and Ager (1986) attributed the stunting of certain lake trout *S. namaycush* to lack of

preferred amphipod and fish prey resources, and Bjøru and Sandlund (1995) discussed the implications of specific prey availability and habitat shifts to stunted populations of Arctic char. Even with extremely omnivorous species such as bluegill, issues of prey availability can be complex, and determining which prey types are most important can be difficult. For example, Werner and Hall (1988) and Mittelbach (1981), among others, suggested that foraging on zooplankton is the optimal strategy for bluegills. In contrast, El-Shamy (1978) suggested that benthic macroinvertebrates might be the important limiting resource. In sum, these studies suggest that it is important to understand whether high density or inappropriate food resources is causing stunted body size, as the management implications would be different for each.

A Question of Genes

Another possibility is that stunting is due to genetically based differences in capacity for growth among populations. Ample evidence for the heritability of growth rate comes from aquaculture and selective breeding studies, and a few investigations have found evidence for this mechanism in stunted populations. Jobling and Reinsnes (1986) suggested that there is a strong genetic component to the slow growth rate of stunted Arctic char. Murnyak et al. (1984) found that growth of stunted bluegills was not as good as growth of nonstunted bluegills when tested under similar conditions, and Mann and McCart (1981) implicated genetic mechanisms in stunted least cisco *Coregonus sardinella*. In contrast to these studies, however, the preponderance of the evidence suggests that stunting is the result of environmental rather than genetic variables. In a controlled-laboratory setting, growth of stunted and nonstunted yellow perch and pumpkinseeds *Lepomis gibbosus* was simi-

lar (Heath and Roff 1987). Amundsen and Klemetsen (1988) found no genetic basis for stunted body size in Arctic char. Finally, when Aday et al. (2003b) raised bluegills from stunted and nonstunted populations in a common environment, growth was similar, leading the authors to conclude that stunting in bluegills was primarily an environmental rather than genetic phenomenon. Belk (1995) also attributed differences in growth rates and timing of maturation among bluegill populations to environmental (in this case, mortality caused by predation) rather than genetic effects.

Harvest

It has been suggested that harvest rates can be high enough that the mean size of adults remaining in the population is significantly reduced. Coble (1988), for example, argued effectively that size-selective harvest of large bluegills combined with high production of offspring could lead to a stunted population. Goedde and Coble (1981) made a similar argument for populations of largemouth bass, pumpkinseeds, and yellow perch. A comparison of bluegill populations experiencing different fishing pressure indicated that high harvest rates of adult males resulted in smaller fish that matured earlier (Drake et al. 1997). This mechanism and these examples are important in the context of reservoir fisheries; all of the species above are important in reservoirs, and fishing pressure is often extremely high in these artificial systems.

Many biologists would argue that the size structure of a fish population exhibiting good growth rates but experiencing heavy adult mortality is not really stunted but simply truncated. However, I mention this mechanism for two reasons. One is semantic: is a population of fish with good growth potential stunted if the largest adults are removed? In at least some cases, I believe the answer is yes. This reiterates the previous discussion about common terminology. If the size structure of a particular population is reduced due to overharvest of the largest fish, that would indicate a stunted population even if the growth potential of remaining individuals is quite good (i.e., it is stunted because it is dominated by young, small fish). Although that may be quibbling over semantics, a more important consideration is that size-selective angling can induce life history changes that do indeed lead to classically stunted populations. Specifically, angling can alter mortality schedules, thereby influencing growth rate and timing of maturation. More discussion about these mechanisms is provided in subsequent sections.

Maturation

The early papers by Alm, Deedler, and others that acknowledged variation in timing of maturation among populations recognized a potential influence on size structure that has received considerable recent attention. It is well established that individuals must make energetic tradeoffs between allocations to somatic growth and reproduction (e.g., Williams 1966; Bell 1980), and these tradeoffs can be particularly significant in fish, which exhibit indeterminate growth (e.g., Roff 1984). Because of this energetic tradeoff, individuals that become sexually mature at a young age or small size may remain small relative to conspecifics that delay maturation. At the population level, this can lead to stunting, and I believe this mechanism, though identified in a number of investigations, is still underappreciated.

The association of stunting with slow growth and density-dependent resource limitation implies an ecological failure of the population to attain normal size. The decision to invest in reproduction at a small size, however, might instead reflect an adaptive strategy to maximize fitness in a particular environment (e.g., Jansen 1996; Aday et al.

2003b; Heibo et al. 2005). A number of investigations have implicated early maturation as a causal mechanism in stunted populations. When studying sexually precocious populations of barramundi *Lates calcarifer*, Davis (1984) noted, "These fish are maturing much earlier than normal barramundi and stunting becomes increasingly obvious as the fish grow older. It is likely that this stunting is due to the channelling of energy into gonadal growth at the expense of somatic growth at a relatively early age." Danylchuk and Fox (1994) found evidence for growth-maturation tradeoffs in pumpkinseeds and suggested that stunted populations can result from early investment in gonads. Studies with bluegills have reached similar conclusions and will be discussed later.

Perhaps the most difficult aspect of interpreting the influence of maturation schedules on adult body size is that timing of maturation is confounded with growth rate. This is further complicated by the realization that there is no consistent relationship between the two variables; certain studies have indicated that slow growth rate leads to early maturation, whereas other studies, even using the same species, have suggested the opposite. For example, Jansen (1996) found slow juvenile growth rate and early maturation in stunted yellow perch, which is consistent with other studies of the same species (e.g., Diana and Salz 1990). In contrast, a number of investigations have indicated similar juvenile growth rates between stunted and nonstunted yellow perch (e.g., Deedler 1951; Ridgway and Chapleau 1994). The same ambiguity applies across species, with evidence for a correlation between early maturity and slow growth rate (e.g., Alm 1959; Crivelli and Mestre 1988; Roff 1992) as well as normal or even rapid growth (e.g., Fox 1994; Justus and Fox 1994; Bertschy and Fox 1999; Haugen 2000). One note of caution in the interpretation of these results is that in some cases, comparisons are made among

individuals within populations and others are made among populations; because stunting is a population-level phenomenon (at least from a management perspective), I believe that the among-population comparisons are most relevant. In any event, despite the predictions of life history theory that fast growth leads to early maturation, there is certainly evidence to the contrary, and sorting out the relationship between growth and maturation in a given population, and the relative importance of each variable to adult body size, is necessary for developing appropriate management strategies.

Interacting Mechanisms

It should be clear at this point that it is common for several mechanisms to interact to influence population size structure. Because individual life history strategies are determined by energetic tradeoffs among major life processes, it is perhaps safe to say that stunting is most often the reflection of interacting mechanisms, in which alterations in growth, maturation, or mortality affect each other and, ultimately, adult body size.

Other Mechanisms and Summary

Although the previous mechanisms highlight the most frequently cited reasons for stunting, others have been proposed. Table 1 lists examples of investigations associated with stunting and illustrates the breadth of potential factors that can influence population size structure. For example, it has been suggested that species like bluegill that exhibit alternative life history strategies may become stunted due to an overproduction of cuckolders. However, Jennings et al. (1997) found no evidence that abundant cuckolders leads to stunted bluegill populations (Table 1). Clearly, given the variation in patterns across (and within) species and systems, managing stunted populations is not a one-

Table 1. Examples of mechanisms associated with stunting highlighting the breadth of published investigations. The table indicates the study, suggested mechanism, primary species studied, and a brief description of results. Note the different mechanisms even for the same species. See literature cited section for complete references.

Study[a]	Mechanism	Species	Study conclusions
Swingle and Smith (1950)	Density dependence	Bluegill	Overpopulation of bluegills led to stunting.
Deedler (1951)	Prey quality	European perch	Lack of fish prey for adults caused stunting.
Diana (1987)	Inappropriate-sized prey	Northern pike	Modeling suggested that lack of appropriate-sized prey can cause stunting.
Heath and Roff (1996)	Trophic bottleneck	Yellow perch, others	Limited prey availability at a specific life stage can cause stunting in yellow perch. Suggested similar effects for pumpkinseeds, rock bass, and brown bullheads *Ameiurus nebulosus*.
Murnyak et al. (1985)	Genetic	Bluegill	Growth of stunted bluegills not as good as nonstunted bluegills under similar conditions.
Jobling and Reinsnes (1986)	Genetic	Arctic charr	Suggested genetic component to slow growth of stunted char.
Coble (1988)	Harvest	Bluegill	High harvest rates coupled with overproduction of young leads to stunting.
Danylchuk and Fox (1994)	Early maturation	Pumpkinseed	Early, relatively high investment in gonads can lead to stunting due to growth-maturation tradeoffs.
Jennings et al. (1997)	Early maturation/ social influence	Bluegill	Removal of large male bluegills allowed smaller males to mature males to mature early and become stunted.
Drake et al. (1997)	Early maturation/ harvest	Bluegill	High harvest rates led to early maturity of males and smaller size structure.
Aday et al. (2006)	Early maturation/ resource availability	Bluegill	Study indicated sex-specific mechanisms may be associated with stunting. Male bluegills were responsive to resource availability and socially mediated maturation schedules. Females were only responsive to resource availability.
Diana and Salz (1990) (See Ridgway and Chapleau 1994)	Age-class convergence	Yellow perch	Slow growth, early maturity and led to stunting. Ridgway and Chapleau (1994) attribute this to convergence of older age-classes.

Table 1. Continued.

Study[a]	Mechanism	Species	Study conclusions
Jennings et al. (1997)	Cuckoldry	Bluegill	Study provided several potential mechanisms associated with stunting, including excess production of cuckolders. The frequency-dependent nature of bluegill reproductive strategies led the authors to suggest that this is an unlikely scenario.
Diana (1987)	Inappropriate thermal regime	Northern pike	Modeling suggested that extremely warm conditions could lead to conditions could lead to stunting in northern pike.

[a] Only one or two examples of each potential mechanism are shown in the table.

size-fits-all proposition. In addition, most of the considerations listed above emphasize individual- and population-level processes, whereas community-level interactions may also be important. Examples of this are particularly evident in bluegills.

Bluegill as a model system

The bluegill is one of the most sought-after sport species and often plays a primary role in reservoir fisheries (e.g., Drake et al. 1997). In addition to being important for anglers, they serve as prey items for apex predators such as largemouth bass and competitors with other planktivores. As a result, much research has been directed at understanding bluegill population structure and the factors that lead to variation in adult body size. Bluegills have also played an important role in research addressing fundamental ecological concepts such as optimal foraging (e.g., Mittelbach 1981), ontogenetic habitat shifts (e.g., Werner and Hall 1988), alternative reproductive strategies (e.g., Gross 1991), and socially mediated life histories (Jennings et al. 1997; Aday et al. 2006), among others. Because of unique aspects of bluegill life

histories (e.g., socially mediated reproductive strategies), some caution must be used when considering bluegill as a model for understanding stunting. However, virtually all of the mechanisms described previously have been identified as reasons for stunting in bluegill populations, and their ubiquitous distribution and high variability in adult body size provide a good opportunity for exploring the causes and consequences of stunted body size.

Following the studies by Swingle and colleagues, many investigations have focused on bluegill densities in reservoirs and small impoundments and emphasize the importance of density-dependent slow growth in stunted populations. Although growth rate is an important consideration in bluegill populations, variation in adult body size is often not simply a function of population density or resource availability. In a statewide assessment of size and age structure of Illinois bluegill populations, for example, adult body size was strongly correlated with age at maturation (Claussen et al. 1998); populations that were considered stunted generally matured earlier than those with normal size structures despite similar growth rates. Blue-

gill have extremely plastic life histories, and males in particular have the ability to modify their reproductive investment on a seasonal basis (e.g., Jennings et al. 1997; Aday et al. 2003b) In a series of experiments conducted at the Illinois Natural History Survey, researchers demonstrated that small, immature males modified their maturity schedules based on interactions with large, reproductively mature males. Jennings et al. (1997) showed that small parental males invested less in testes and nested less frequently in the presence of large males relative to their absence. Aday at al. (2003b) found similar results using individuals from one stunted and one nonstunted population raised in a common environment (experimental ponds) and verified that pattern in wild fish (Figure 1). The conclusion of these investigations is that male bluegills can become stunted due to early investment in reproduction at the expense of somatic growth. Further, they demonstrate that bluegills make strategic life history decisions based on the social structure of the population. Socially mediated life history decisions are not uncommon in fish and often involve male–male interactions (large males inhibit juvenile males; e.g., Borowsky 1978; Danylchuk and Tonn 2001). This aspect of bluegill life histories has important implications for understanding the influence of size-selective angling practices (see below).

It is important to reemphasize that the relationship between early maturation and stunted body size has been indicated for species other than just bluegills. Associations between early maturity and stunting have been shown for important lake and reservoir fish such as pumpkinseeds (e.g., Danlychuk and Fox 1994), yellow perch (e.g., Diana and Salz 1990; Jansen 1996), and northern pike (Diana 1983), indicating the necessity of considering this mechanism even outside the context of the socially mediated system exhibited by bluegills.

The previous studies indicate that both resource availability and socially mediated maturation schedules can independently shape adult body size. The next question is how these mechanisms might interact to influence the life histories of bluegills of both sexes (many bluegill studies focus only on males) and shape population size structure. To address that question, I conducted a pond experiment that varied both resource availability and the social structure of the population, quantifying growth and maturation of both sexes (Aday et al. 2006). Results of that experiment indicated that bluegills exhibit sex-specific life history strategies. Females were responsive only to resource availability, growing larger and investing more in reproduction (i.e., greater proportion of individuals with fully developed egg masses) when resources were abundant (Figure 2). Males responded both to variation in food resources and the social structure of the population; although juveniles grew larger when resources were more abundant, they still delayed maturation in the presence of large males (Figure 2). In addition, at the end of the experiment, juveniles of both sexes that became mature were significantly smaller than those that remained immature, further demonstrating the cost of maturation.

Further emphasizing the importance of interacting mechanisms is the issue of harvest. In the case of bluegills, harvest can have a two-pronged effect: size-selective angling can remove the largest individuals from the population, thereby decreasing the average body size of remaining individuals (Coble 1988), and it can alter the social structure of the population, allowing smaller males to become mature earlier than they would in a population with abundant large males (Jennings et al. 1997; Aday et al. 2003b). Drake et al. (1997) provided evidence that angling pressure not only removed the largest bluegills, it also caused reduced size at maturity
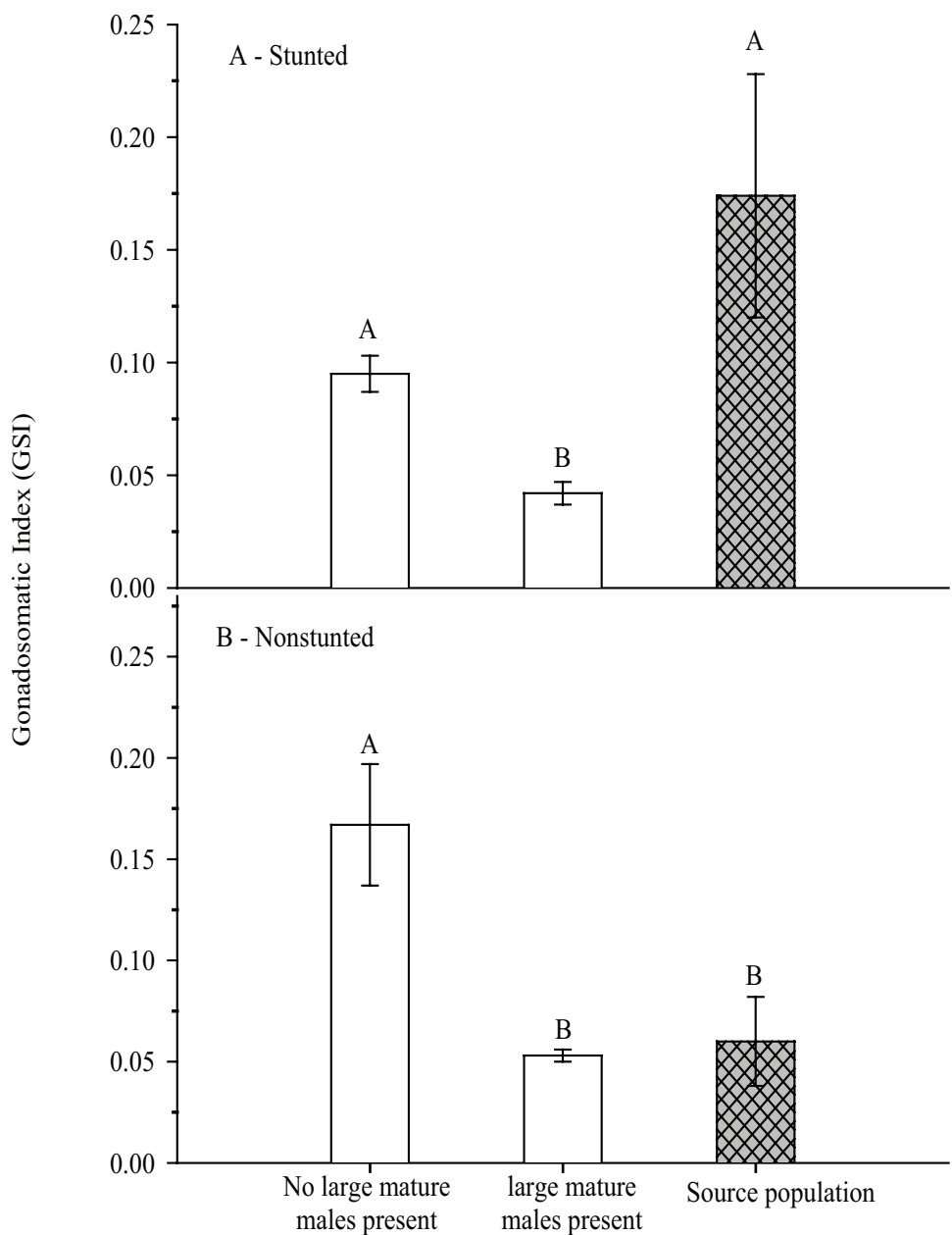
Figure 1. Mean gonadosomatic indices of juvenile males in the treatment ponds with and without large, mature males (open bars) and from their cohorts collected from the source populations at the end of the experiment (shaded bars). The top panel shows results for males collected from a stunted population and the bottom panel for males collected from a nonstunted population. Error bars are ± 1 standard error. Different letters over error bars represent significant differences between groups (analysis of variance [ANOVA]; $\alpha = 0.05$). From Aday et al. 2003b, reproduced by permission of the Ecological Society of America.
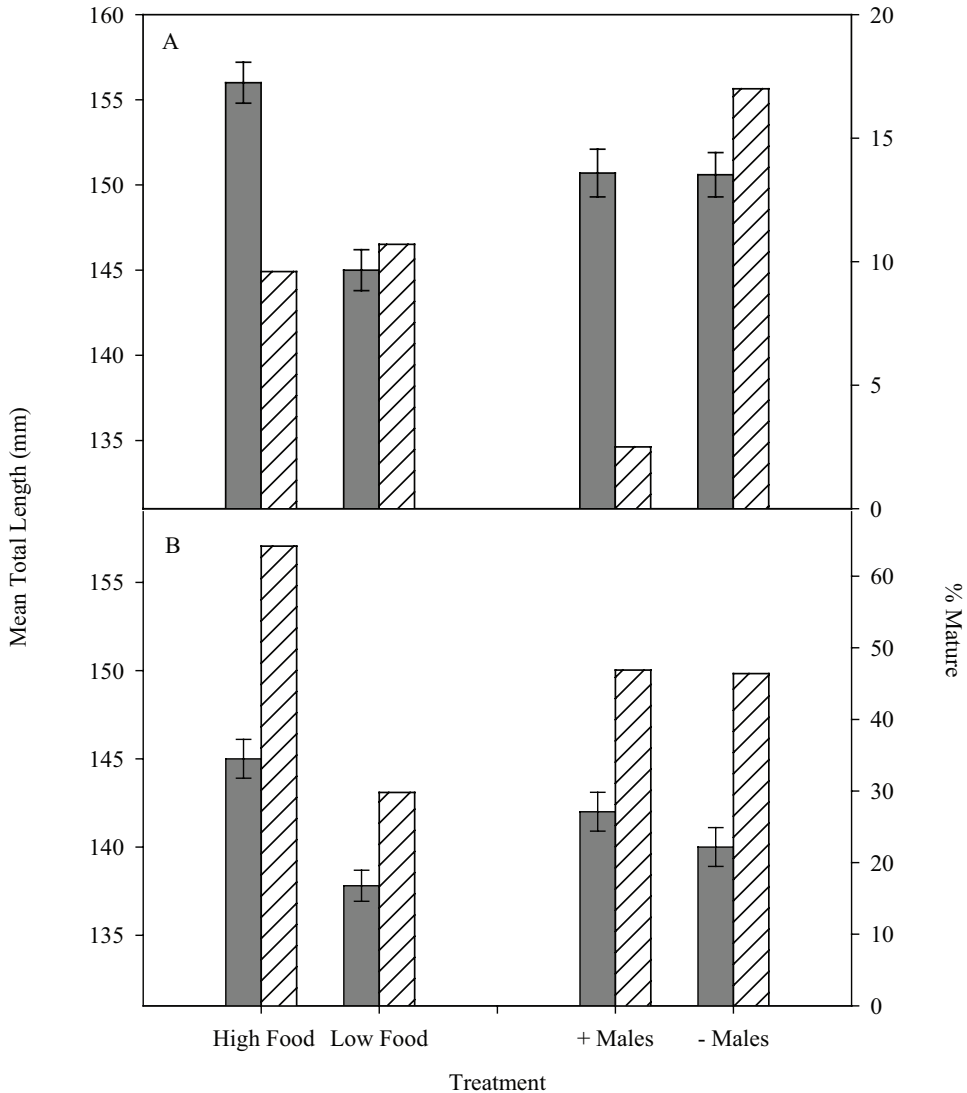
Figure 2. Mean total length (millimeters; left axis) and percent mature (right axis, hatched bars) of originally juvenile males (panel A) and females (panel B) in a pond experiment conducted to determine the influence of food resources and social interactions on bluegill life histories. Error bars (±1 standard error) are shown for total length. There were four ponds in each treatment (high food, low food, with and without large males). Full details can be found in Aday et al. 2006; original figure created from data in that publication.

and age at maturity for both males and females. Beard and Essington (2000) modeled the effects of harvest and life history processes on bluegills and found that harvest had more influence on population size structure than did reduced size at maturity. However, they found that harvest combined with reduction in size at maturity significantly influenced recovery time (i.e., the recovery rate of exploited populations was much longer when changes in size at maturity were included in the simulations).

Again, the interacting effects of harvest mortality and other aspects of life history are not limited to just bluegills. Ricker (1981) discussed the relationship between harvest and maturation schedules for a number of salmonids. Goedde and Coble (1981) discussed harvest-induced changes in size structure, age structure, and life span, among other factors, for pumpkinseeds, largemouth bass, and northern pike. Indeed, the influence of harvest and its interacting effects on individual life histories is becoming an increasing concern in the face of declining global fish stocks (e.g., Conover and Munch 2002). Because of the large influence harvest-induced mortality can have on population size structure, this mechanism should at least be considered when evaluating any stunted sport fish population.

In combination, research on bluegills highlights all of the major mechanisms associated with stunting, as well as various interactions among them. The fact that similar mechanisms are found in association with stunted body size in other common sport fish indicates that though bluegill may have fairly unique life histories, they still serve as a good model for understanding stunting in lakes and reservoirs. Further, bluegill research provides an opportunity to expand consideration beyond individual- and population-level processes, as a number of investigations have addressed the potential for other biotic and abiotic interactions to influence size structure. For example, complex interactions with other planktivores can apparently have a significant influence on adult body size. Aday et al. (2003a) showed that bluegills exhibited significantly smaller body size in reservoir populations with gizzard shad *Dorosoma cepedianum*, and Porath and Hurley (2005) found similar results in borrow pits and gravel mine ponds. Interestingly, the abundance of important food resources appeared to be similar among the reservoir populations, and direct competition was ruled out as a mechanism for the reduction in body size. Rather, it appeared that indirect interactions (e.g., increased turbidity when gizzard shad were present, perhaps reducing bluegill foraging ability; reduced predation on juvenile bluegills by largemouth bass in systems with gizzard shad) were more important. Tomcko and Pierce (2001, 2005) examined the relative importance of internal versus external processes shaping bluegill population size structure and demonstrated that variables like lake morphometry, secchi depth, lake area, and temperature can be important. Paukert et al. (2002) found a correlation between quality bluegill populations and emergent vegetation. These studies provide support for considering community- and ecosystem-level processes when attempting to understand and address the cause of stunting in bluegill populations, and it seems likely that similar processes would be important to other species.

Management Implications

Results of the previously described studies make the management implications fairly self-evident. However, there are several important points that should be reiterated in this section to emphasize the variety of strategies that might be used to deal with stunted reservoir species. One important prerequisite is the use of common, consistent language. Next is focusing on identifying the mechanism underlying the stunted population, and finally is the development of multifaceted management strategies aimed at recovering and sustaining a nonstunted size structure.

Mechanism-Specific Strategies

The first step in any management strategy is to identify the cause of stunting. Although it seems obvious, the default approach commonly used is to deal with perceived slow

growth due to overcrowding. Perhaps this is due to the influence of early studies on density dependence in common reservoir species. Regardless, the literature is replete with examples of the failure of this strategy to achieve satisfactory or lasting results, and the multiple mechanisms that can lead to stunting must be considered. Adult size structure should be viewed as a continuum, where individuals end on that continuum will depend on life history strategies related to growth, maturation, and mortality. In many cases, the growth potential of individuals in a population may be quite good, but size structure is limited, for example, by overharvest of adults or early maturation of juveniles. Knowledge of a few key variables, including size at age, age at maturation, and harvest pressure, should allow determination of the underlying cause of stunting in a particular population. In addition, quantifying the ratio of adult-to-juvenile growth can be useful. This metric can be calculated using body mass and gonad mass of individuals and can be used to measure the potential gain in fecundity to juveniles by delaying maturation (see specific methodology in Fox 1994). Rather than actual growth rate, this may be the metric that most influences life history strategies such as timing of maturation (e.g., Hutchings 1993; Fox 1994), which also influence size structure. In combination, knowledge of these metrics should help delineate the range of potential strategies that might be appropriate in a specific system.

When encountering a stunted population, the first consideration must be whether the system is fundamentally unsuited for producing large adults of the target species. Both Porath and Hurley (2005) and Tomcko and Pierce (2001) point out the importance of understanding water body characteristics and their influence on potential bluegill management strategies, and that argument should be applicable to any reservoir species.

If biotic (e.g., high abundance of competitors) or abiotic (e.g., extremely low productivity, inappropriate thermal regime) factors prevent the accumulation of large adults, management efforts should be directed elsewhere (Figure 3). For example, Fox (1994) found that populations of pumpkinseed experiencing highly unstable environments due to risk of overwinter mortality matured earlier and invested more in gonads than pumpkinseeds in stable environments. This could be particularly important in reservoirs that often experience fluctuating water levels. Although there is no way to address this from a management perspective, that information might prevent costly attempts to fix a potentially solutionless problem.

If there are no obvious barriers to producing quality size structure, the first step would be to construct a complete size and age structure description for the population. If slow growth appears to be occurring at a specific life stage, a number of management strategies are available. In this case, an important determination would be whether the problem is one of food quality or food quantity (Figure 3). Slow growth of juveniles might warrant supplemental feeding (in the case of small impoundments where that might be practical; e.g., Berger 1982), physically reducing their density, or increasing predation pressure by stocking and/or regulating the harvest of predators. Water drawdowns might also be useful in increasing vulnerability of juveniles to predators (see review in Ploskey 1986). Unusually slow growth of adults might suggest the existence of a trophic bottleneck, particularly in species that undergo ontogenetic diet shifts, and management strategies would need to address the particular life stage that is affected. For example, stocking prey fish in a system with stunted piscivorous adults might be necessary. In larger systems this would likely not be feasible, and management ef-
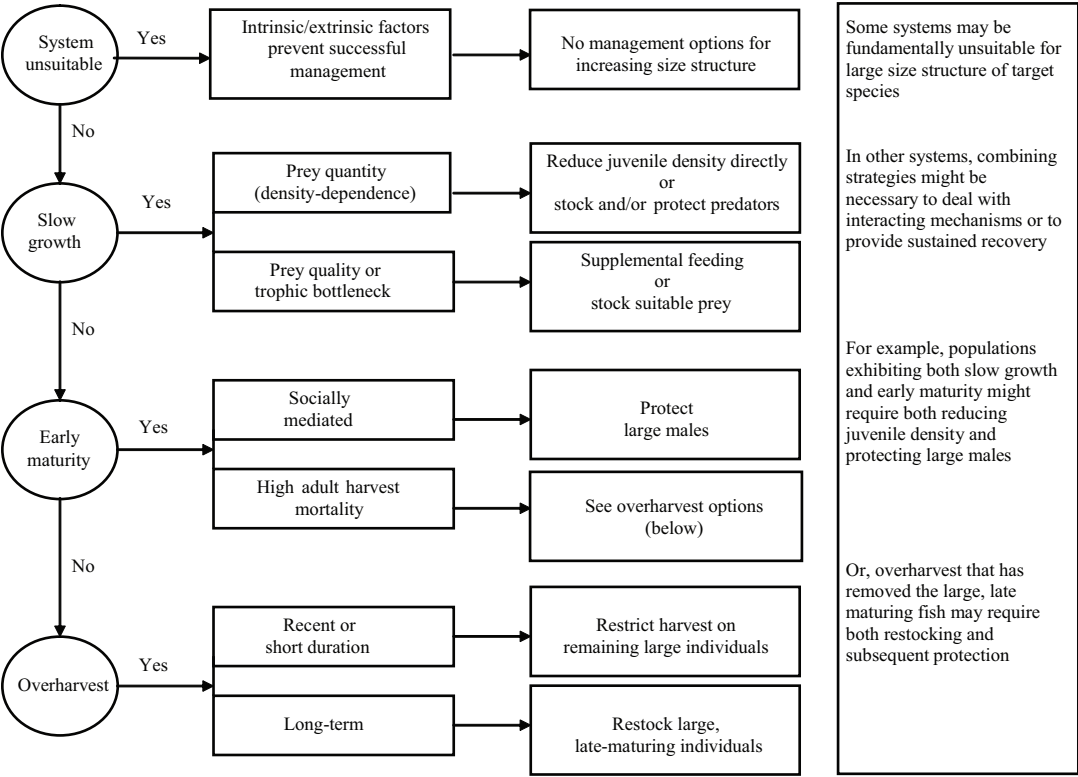
Figure 3. A flow diagram indicating important mechanisms associated with stunting, issues associated with each mechanism, potential management strategies for each, and examples of multifaceted management approaches. Progression is from top to bottom, left to right. The first step is to determine whether stunting is a function of the system being fundamentally unsuitable (e.g., high natural mortality of adults, lack of appropriate prey species, and high abundance of competitors) for production of large adults. If the system is suitable, mechanisms such as slow growth, early maturation, and overharvest can be considered, and options for each (including multi-faceted approaches) are listed.

forts aimed at alleviating stunting might be abandoned.

Stunting due to early maturation would require a different management approach, one that depends on the cause of early maturity (Figure 3). In socially mediated systems such as bluegill, in which maturation of small males is influenced by the presence of large males (e.g., Jennings et al. 1997; Danylchuk and Tonn 2001; Aday et al. 2003b), management strategies would be needed that specifically protect the large males. If harvest has been extensive, stocking of large males might be an option (Beard et al. 1997). Mortality schedules can also be important. Life history theory predicts that individuals subjected to high adult mortality rates will mature early (e.g., Roff 1984; Kozlowski 1991), and changes in mortality may have a greater influence on timing of maturation than growth rate (see discussion in Fox 1994). Measuring size-specific predation, for example, would be useful in determining whether high adult mortality is causing ear-

ly maturation and, therefore, reduced body size. Another important consideration might be system stability, as described above.

One of the major sources of mortality for sport species is harvest, and this factor can clearly influence population size structure. The difficult issue with harvest is the potential cascading effect it can have on a population. If individuals are otherwise growing and maturing as expected, high harvest of adults that is simply cropping the largest individuals can be dealt with quite easily through harvest regulations, and resulting population recovery might be expected to be successful and long-lasting (e.g., Schneider and Lockwood 2002). However, if size-selective harvest induces life history changes (as described in previous sections), recovering stunted populations will likely be significantly more difficult (e.g., Beard et al. 1997; Beard and Essington 2000; Figure 3). This can become more difficult still when prolonged harvest causes genetic changes within populations. Numerous studies have indicated that size-selective harvest can reduce genetic variation and alter genotype frequencies in favor of slower growth and earlier maturation (e.g., Ricker 1981; Trippel 1995; Conover and Munch 2002), which might further diminish the probability of a population recovering from overexploitation (Hutchings 2000). Situations such as this may require restocking adults from populations with adults that grew rapidly and delayed maturation.

Interacting Mechanisms and Multifaceted Management

If a single mechanism is responsible for stunting in a population, management options should be, if not easy, at least fairly straightforward. Often, however, growth, maturation, and harvest are linked, and it can become difficult to determine which is the actual cause of stunted body size and which is an effect. Growth rates and maturation schedules, for

example, are often coupled in individuals, and interactions between these factors can make cause-and-effect relationships in stunted populations difficult to determine. The basic question here is "do fish become stunted and therefore mature early or do fish mature early and therefore become stunted?" In the case of the former, slow growth would be implied prior to maturation, and management strategies would need to address the reasons for slow growth. In the latter case, early maturity (followed, presumably, by slower growth due to energetic tradeoffs) would be the causal mechanism, and management strategies would need to address that. To whatever extent possible, separating the influence of slow growth versus early maturation is necessary for effective management. However, the relatively common occurrence of populations exhibiting both slow growth and early maturation makes it difficult to predict whether strategies aimed at delaying maturation or improving growth rate will be met with greater success. Ylikarjula et al. (1999) addressed interactions between growth and maturation in stunted populations and suggested that although resource limitation is the most common cause of stunting, interactions between growth rate and maturation schedules influence the persistence of stunted populations. In other words, changes in maturation schedules and their subsequent influence on growth rate may intensify or alleviate stunting. This reiterates the complexity of dealing with stunted populations in which interacting mechanisms are to blame.

As indicated in previous sections, mortality due to harvest pressure also interacts with growth rates and maturation schedules to ultimately influence size structure, and the common nature of these interacting mechanisms argues for a multifaceted approach to managing stunted populations. In general, published literature supports this conclu-

sion; one-dimensional management strategies have often been met with less success than those that address multiple mechanisms (e.g., Coble 1988; Schneider and Lockwood 2002). Dealing with both slow growth and early maturation in bluegills, for example, might require both reducing juvenile density and protecting large males (Figure 3). Schneider and Lockwood (2002) found that management strategies aimed at both reducing the density of small bluegills and protecting large ones worked better than just dealing with density-dependent growth. Coble (1988) suggested managers should focus on four factors when dealing with stunted bluegills, recruitment of young of year, size-selective angling, slow growth, and natural mortality. Although these examples are specific to bluegills, evidence suggests that this multifaceted approach should be appropriate for other common reservoir species (e.g., Diana 1987; Coble 1988). Further, identifying the complexities of interacting mechanisms, even in the absence of an easy management solution, is useful in establishing predictions for recovery and, therefore, expectations for anglers and managers alike.

Conclusions

Perhaps the take-home message is that there is no silver bullet for dealing with stunted populations of reservoir species; even a limited literature review reveals equivocal results of management strategies involving the same species in different systems. This reflects the variety of mechanisms that can cause stunting in populations and the complexities that are often associated with correlations among them. Despite frequent focus on resource limitation in stunted populations, it is clear that the generally plastic life histories of fish and their adaptive responses to growth rate, maturation schedules, and harvest often makes managing stunted pop-

ulations more complex than just dealing with density dependence. The key is to identify the mechanism or mechanisms underlying stunted body size and deal directly with the source or sources of the problem (Figure 3).

The good news regarding this plasticity is that individuals are not generally genetically predisposed to stunting, and their malleable life histories provide a range of options for improving population size structure; in many cases, stunting should be a tractable problem. Despite the species- and even system-specific nature of stunting, three steps should be broadly applicable and useful as we enhance our understanding of this relatively common phenomenon. First, common language focusing on average body size at the population level (rather than "stunted growth") will aid communication as we distinguish mechanisms (growth rate, maturation schedule, mortality) from consequences (stunting). Second, identifying the source of stunting and potential interactions among mechanisms will address the root of the problem and provide important information for managers in similar systems (Figure 3). Third, multifaceted management strategies will often provide more robust results than single-dimensional approaches and should offer the greatest opportunity for successful, long-lasting recovery.

Acknowledgments

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