EXPLORING FACTORS AFFECTING SMALLMOUTH BASS NEST SUCCESS AND REPRODUCTIVE BEHAVIOR

DISSERTATION

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By

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ABSTRACT

Herein, I describe research that explores factors affecting smallmouth bass

(*Micropterus dolomieu*) reproductive behavior and success. Smallmouth bass are a

model species to explore reproductive behavior because they invest large amounts of

energy in parental care, spawn multiple times, and exhibit indeterminate growth.

Smallmouth bass must balance current and future fitness when deciding how much care

to provide. Ultimately, reproductive success and behavior may influence recruitment.

By conducting a series of observational studies and manipulative experiments, I

examined how smallmouth bass reproductive success and behavior differed by

environment (Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada). In Lake

Erie, exotic nest predators (round goby, *Neogobius melanostomus*) consumed more than

800 smallmouth bass embryos from nests every time an angler caught and released the

nest-guarding male (Chapter 2). In addition, high round goby densities necessitated

vigorous nest defense by parents in Lake Erie, thus causing parents to expend twice the

energy on care than Lake Opeongo, where round gobies were absent (Chapter 3).

Smallmouth bass nest success in Lake Erie was negatively influenced by angling and

storms, but not by round goby consumption of offspring (Chapter 4). Simulations of

nest-guarding smallmouth bass, making decisions that maximized their expected lifetime

fitness, defended smaller broods in Lake Erie than in Lake Opeongo (Chapter 5). Mean adult survival rate, a function of age and care cost, was most important in determining optimal behavior (Chapter 5). By decreasing offspring survival and increasing cost of care, round goby caused optimal parents to abandon larger broods than when round gobies were absent (Chapter 5). Parental behavior, in turn, affected abandonment of offspring by simulated smallmouth bass populations; however, offspring production was not influenced by behavior (Chapter 6). Simulations of spawning smallmouth bass in lakes Erie and Opeongo demonstrated that the success of management strategies depended on parental behavior and the environmental conditions underlying optimal decisions (Chapter 6). While round gobies, as predators, may reduce smallmouth bass offspring production, round gobies, as prey, provided a new food source for young-of-the-year smallmouth bass, which are growing faster since the round goby arrived (Chapter 7).

DEDICATION

For my mother and father,

who encouraged and inspired me.

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PUBLICATIONS

Research Publication

1.   G. B. Steinhart, E. A. Marschall, and R. A. Stein. 2004. Round goby predation
on smallmouth bass offspring in nests during simulated catch-and-release angling.
Transactions of the American Fisheries Society 133: 121-131.

2.   G. B. Steinhart and W. A. Wurtsbaugh. 2003. Winter ecology of kokanee

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        American Fisheries Society 132: 1076-1088.

3.   G. B. Steinhart and W. A. Wurtsbaugh. 1999. Under-ice diel vertical migrations

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4.   C. Luecke, W. A. Wurtsbaugh, P. Budy, and G. B. Steinhart. 1996. Simulating

        production of Snake River sockeye salmon: Assessing lake management

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FIELDS OF STUDY

Major Field: Evolution, Ecology, and Organismal Biology

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CHAPTER 1

INTRODUCTION

All organisms must make crucial decisions, or trade-offs, about how to allocate

precious resources, such as time and energy (Stearns 1992). Because successful

reproduction is essential for passing along genes, individuals behaving so as to increase

their fitness compared to other individuals will pass on proportionally more genes and

should have a fitness advantage (Williams 1966). For example, female red deer (*Cerus*

elaphus) must decide between either nursing offspring or augmenting their own winter fat

stores to increase their own survival (Bell and Koufopanou 1986). Many neotropical

frogs call to attract mates, but this also attracts predatory bats; hence, mate-calling

frequency affects the probability of both survival and reproduction (Tuttle and Ryan

1981). Therefore, understanding the factors affecting reproductive success provides

insight into trade-offs and individual variation in reproductive behavior, improving our

knowledge of evolution and population dynamics.

Reproductive trade-offs have been studied in many species, with an emphasis on

trade-offs between offspring quantity and quality, and between current and future

reproduction. Initially, trade-offs were seen as a compromise between offspring quantity

versus quality (Lack 1947); that is, individuals must decide between producing many

poor-quality (i.e., low probability of survival) or few high-quality progeny. This idea

evolved into the concept of a trade-off between current and future reproduction (Williams

1966). Many birds alter their reproductive behavior as a result of placing values on

current and future reproductive possibilities. For example, nuthatches (*Sitta* spp.) with

low probabilities of reproducing in the future tend to react more strongly to nest predators

than to adult predators, but the reverse is true for nuthatches with long reproductive

futures (Ghalambor and Martin 2000). When species investing parental care have

uncertainty regarding the relatedness of their offspring, modeling simulations predict that

long-lived species are less likely to tolerate extrapair fertilizations (i.e., a reduction in

relatedness and fitness value of current brood) than short-lived species, presumably

because long-lived species will have more future reproductive opportunities (Mauck et al.

1999).

Fishes exhibit indeterminate growth, even gender change, and thus have the potential

for a wide variety of reproductive behaviors and strategies (Gross 1987; Gross 1996).

Many fishes provide parental care, which includes a cost to the parent due to energetic

costs of fanning (Coleman and Fischer 1991; Jones and Reynolds 1999), chasing

predators (Hinch and Collins 1991), and increased aggression (Chellappa and

Huntingford 1989; Unger 1983). In addition, parental care may limit foraging

opportunities (Hinch and Collins 1991), which exacerbates the costs of parental care and

can ultimately reduce parent survival (Sabat 1994). However, because parental care is

often plastic, fish make an ideal model for examining trade-offs in reproduction and

survival (Ridgway and Friesen 1992; Townshend and Wootton 1985). Nest-guarding bluegill (*Lepomis macrochirus*) decide how much energy to invest in parental care on the basis of the size of their current brood (i.e., current fitness) and past parental investments (i.e., investments that reduce future fitness; Coleman et al. 1985). Brood size not only affects parental behavior, but also may lead to additional extra-pair fertilizations, as females often select males with large broods (Forsgren et al. 1996; Jamieson 1995) because large broods are likely to receive better parental care (Coleman and Fischer 1991; Jonsson et al. 2002; but see Knapp and Warner 1991) and, ultimately, higher survival (Sargent 1988). Therefore, understanding trade-offs and mating systems should improve our understanding of parental behavior, reproductive dynamics, and recruitment in fishes.

Smallmouth bass (*Micropterus dolomieu*) is an ideal fish species for testing hypotheses about reproductive trade-offs. Male smallmouth bass guard their nests for up to 6 weeks (Friesen 1998), during which tremendous energy is expended on parental care, in the face of limited feeding opportunities (Gillooly and Baylis 1999; Mackereth et al. 1999). Brooding of this type represents an obvious cost, wherein survival and future reproduction must be balanced with the value of the current brood (Ridgway and Shuter 1994). While much is known about the ecology and biology of smallmouth bass, most work has been done in small, north-temperate, mesotrophic lakes. In contrast, Lake Erie (Ohio, USA) is more productive and, because of a very long fetch, is subjected to more intense storms than other more commonly studied smallmouth bass lakes. During the last 20 years, Lake Erie has undergone a series of changes, including reduction of nutrient inputs and introduction of numerous exotic species (Ludsin et al. 2001; Ricciardi and

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MacIsaac 2000), and an increase in smallmouth bass abundance. Smallmouth bass reproductive dynamics in Lake Erie are not well understood; however, as all reproduction in smallmouth bass occurs naturally in Lake Erie, adult abundance, reproductive success, and subsequent fishery performance, are linked to recruitment.

Fish eggs, embryos, and fry are subjected to many biotic and abiotic pressures, so only a small fraction of eggs ever survive to adulthood (Cushing 1968; Hjort 1914). Food availability and temperature are often linked to recruitment (Cushing 1968; Hjort 1914; Shuter and Post 1990). Smallmouth bass in Lake Erie, however, have one of the highest growth rates of any smallmouth bass population (Doan 1940; Hair 1979). Therefore, starvation and over-winter mortality (Garvey et al. 1998; Ludsin and DeVries 1997; Oliver et al. 1979) are not likely limiting recruitment of Lake Erie smallmouth bass. Changes in water clarity, macrophyte abundance, and substrate (owing to colonization by zebra mussels, *Dreissena polymorpha*) have altered habitat availability for nesting smallmouth bass and could affect their recruitment if nest habitat is limiting, but habitat limitation has not been reported for smallmouth bass (Ridgway et al. 1991). Within acceptable nesting habitats, reproductive success depends on the vulnerability of eggs to dislodgment by currents (Goff 1986; Lukas and Orth 1995; Popiel et al. 1996), the consumption of offspring by nest predators (Hinch and Collins 1991; Knotek and Orth 1998), and the amount of parental care provided by the guarding male smallmouth bass (Hurley 1975; Wiegmann and Baylis 1995). Predation also can limit offspring survival (Garvey and Stein 1998; Knotek and Orth 1998; Leggett and DeBlois 1994), but predator effects may be diluted by colonial nesting (Bietz 1981; Gross and MacMillan 1981), producing vast quantities of offspring, or by providing parental care (Sargent 1997).

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Male smallmouth bass care for their offspring by remaining near their nest and vigorously defending the nest from potential predators (Hinch and Collins 1991; Ongarato and Snucins 1993). However, humans can disrupt this evolved care by introducing exotic species or by interrupting parental care.

Herein, I describe how abiotic and biotic mechanisms affect reproductive behavior and nest success of smallmouth bass. I will contrast results from two very different systems: Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada. Lake Erie is a large lake, exposed to many storms, resulting in low overall nest success. In addition, high nest-predator densities and high angler effort targeting smallmouth bass result in both high offspring mortality during parental care and high adult mortality. Lake Opeongo is much smaller than Lake Erie (i.e., produces fewer large waves), has a relatively short and cold growing season, has low nest predator densities, and fishing regulations prohibit angling during the smallmouth bass spawning season.

I conducted a series of observational studies and manipulative experiments in both lakes, and described how smallmouth bass reproductive success and behavior vary in response to abiotic, biotic, and anthropogenic factors. In Chapter 2, I describe round goby (*Neogobius melanostomus*) consumption of smallmouth bass offspring from nests during simulated catch-and-release angling. In Chapter 3, I quantify male smallmouth bass nest-defense behavior and measure energetic cost of care in both Lake Erie and Lake Opeongo. I explore the factors (i.e., storms, angling, and nest predation) affecting smallmouth bass reproductive success in Lake Erie in Chapter 4. In Chapter 5, a dynamic programming model is used to examine how brood survival (Chapter 2), cost of care (Chapter 3), nest success (Chapter 4), adult survival, and angling affect optimal

smallmouth bass care decisions, including a comparison between optimal decisions in lakes Erie and Opeongo. In Chapter 6, I test the effectiveness of various angling restrictions on smallmouth bass offspring production, and explore how optimal and suboptimal behaviors affect offspring abandonment and production. Finally, in Chapter 7, I report how round goby provide a new prey source for young-of-the-year (YOY) smallmouth bass, resulting in increased YOY growth rate since the round goby invasion.

From a broad perspective, this study improves our knowledge of how organisms balance current and future fitness by adjusting reproductive behavior and, subsequently, how behavior and environment influence reproductive success. This study also identifies ecological mechanisms that limit smallmouth bass nest success. Ultimately, if recruitment is tied to nest success, these results will improve our understanding of smallmouth bass population dynamics and, thus, allow managers to better predict the effects of different angling regulations and to forecast possible impacts of anthropogenic environmental changes.

CHAPTER 2

ROUND GOBY PREDATION ON SMALLMOUTH BASS OFFSPRING IN NESTS DURING SIMULATED CATCH-AND-RELEASE ANGLING[1]

ABSTRACT

Round gobies (*Neogobius melanostomus*) first appeared in Lake Erie in 1993 and now occur in extremely high densities in some areas. As known nest predators, round gobies pose a threat to the progeny of nest-guarding smallmouth bass (*Micropterus dolomieu*). We evaluated the combined effects of round goby predation and catch-and-release angling via manipulative experiments during 1999-2001 in the Bass Islands, Lake Erie. We quantified how many smallmouth bass offspring were consumed by round gobies when nest-guarding smallmouth bass were present, when removed, and when recovering from angling-related stress. In 10 h of video observations, we only once saw round gobies consume smallmouth bass offspring while the nest was guarded. Upon removal of

nest-guarding smallmouth bass, round gobies quickly entered unguarded nests (4.3 round gobies/min for nests with unhatched embryos and 1.8 round gobies/min for nests with hatched embryos). During experimental catch-and-release angling, round gobies consumed an average of 2,000 unhatched embryos before the guarding male returned; post-return offspring losses were minimal (i.e., while the smallmouth bass recovered from angling stress). For an average smallmouth bass nest in the Bass Islands, round gobies could consume all offspring from an unguarded nest in about 15 min. Round gobies and anglers combined to reduce survival of smallmouth bass embryos, but we did not observe round gobies consuming free-swimming larvae or juveniles. During this study, most successful smallmouth bass nests contained embryos during only a short period: 6-20 June. If the number of smallmouth bass embryos surviving drives adult population size, managers should consider angling regulations that limit the deleterious effects of round gobies.

INTRODUCTION

Predation is an important cause of mortality during the early life stages of many fishes (Houde 1987). In fish, predator effects can be reduced by producing large numbers of offspring, by providing parental care, or by colonial nesting (Gross and MacMillan 1981; Sargent 1988). Because evolution of these reproductive strategies is tightly linked to the predator environment survival from egg to adult may be compromised should predation risk change (Foote and Brown 1998). In light of the rapid rate of global homogenization of aquatic communities (Rahel 2000), introduced species are changing the predator

environments in which fishes have evolved. For example, the Great Lakes have been invaded by more than 145 species, many of which have had profound ecological and economic impacts on the ecosystem (Mills et al. 1993; Ricciardi and MacIsaac 2000).

Ample evidence exists that recently introduced predators affect recruitment of fish species without parental care. As early-colonizers of lakes post-glaciation, lake trout (*Salvelinus namaycush*) evolved when few predators existed, so lake trout are less successful in lakes with diverse fish communities than in lakes with few species (Evans and Olver 1995). In the Great Lakes, a suite of exotic species has been blamed for lake trout restoration failures (Jones et al. 1995). For example, rusty crayfish (*Orconectes rusticus*) consume significant numbers of lake trout eggs in certain substrates (Horns and Magnuson 1981). Furthermore, predation by alewife (*Alosa pseudoharengus*) has caused poor and variable survival of young yellow perch (*Perca flavescens*) and bloater (*Coregonus hoyi*; Rice et al. 1987), while introduced rainbow smelt (*Osmerus mordax*) compromised recruitment success of lake whitefish (*C. clupeaformis*) and lake herring (*C. artedii*) by preying on their larvae (Loftus and Hulsman 1986).

Predators also affect reproductive success of species that provide parental care (Sargent 1988). In nest-guarding fishes, potential predators are vigorously chased from nests at substantial metabolic cost to the nest guarder (Hinch and Collins 1991). As predator density increases, so does chase frequency and energetic cost of parental care, which ultimately could lead to offspring mortality or nest abandonment. Nest-guarding fathead minnows (*Pimephales promelas*) experienced higher egg survival in the absence of crayfish predators than with crayfish (Sargent 1988). Nest success of pumpkinseed

(*Lepomis gibbosus*), a colonial nesting species with paternal-care, was lower in a lake with abundant predatory cyprinids than in a lake with few cyprinids (Popiel et al. 1996).

A recent invader of the Great Lakes, the round goby (*Neogobius melanostomus*), was accidentally introduced via ship ballast water and has quickly spread throughout Lake Erie. After first appearing in the St. Clair River in 1990, round gobies were soon found in Lake Michigan and the eastern basin of Lake Erie (1993), Lake Huron (1994), Lake Superior (1995), and Lake Ontario (1997; Charlebois et al. 1997). A benthic fish that reaches 15 cm and can spawn multiple clutches per year (Charlebois et al. 1997), round goby can reach extremely high densities ($> 100/m^2$) in Lake Erie. Round gobies consume fish eggs and are ecologically similar to native benthic fishes [e.g., sculpin (*Cottus* spp.) and darters (*Ethostoma* spp.)], but are far more abundant than native benthic fish species (Chotkowski and Marsden 1999). This has raised concerns as to its potential to limit the reproductive success of indigenous fishes through predation on eggs, embryos, and larvae (Chotkowski and Marsden 1999; Janssen and Jude 2001).

Smallmouth bass (*Micropterus dolomieu*) nest on the lake bottom and, after courting and spawning with a female, the male cares for the developing offspring. Male parental care keeps nests free from debris, circulates water to provide oxygen, and protects offspring from predators (Hinch and Collins 1991). Although male smallmouth bass vigorously defend their offspring for up to 6 weeks (Ridgway 1988), some offspring are still eaten by predators (Clady 1975; Goff 1986; Knotek and Orth 1998) and predation causes many nest failures for nest-guarding smallmouth bass (Lukas and Orth 1995) and largemouth bass (*M. salmoides*; Swenson 2002). Smallmouth bass offspring may be particularly vulnerable to round goby predation because smallmouth bass often nest in

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rocky habitats where round gobies are common (Charlebois et al. 1997). Presumably, nest defense in smallmouth bass has evolved to increase offspring survival in the face of predators, but high round goby densities may overwhelm smallmouth bass and, combined with spring angling for adult smallmouth bass, could compromise juvenile smallmouth bass survival (Ridgway and Shuter 1997).

With removal of nest-guarding smallmouth bass by anglers, offspring are susceptible to predators (Kieffer et al. 1995; Philipp et al. 1997). Currently, angling for smallmouth bass during the spawning season is allowed in Ohio and New York waters of Lake Erie. In addition, seasonal closures in other regions do not necessarily protect nesting smallmouth bass during the entire parental care period (Kubacki et al. 2002). Even if anglers practice catch-and-release, nests are temporarily vulnerable to predation. In addition, recovery from angling requires several hours and may impair a male's ability to defend his nest (Kieffer et al. 1995; Cooke et al. 2000; Schreer et al. 2001). To assess the combined effects of round goby predation and angler removal of nest-guarding males on smallmouth bass offspring abundance, we conducted catch-and-release angling experiments in which we measured number of offspring consumed from guarded and unguarded smallmouth bass nests, time required for angled smallmouth bass to return to nests and number of offspring consumed during angling and after the angled fish returned to their nests. We also measured the timing and duration of spawning and parental care to determine when smallmouth bass nests may have been most vulnerable to the effects of angling and round goby predation.

METHODS

Study location

Nesting smallmouth bass were located around the Bass Islands, a belt of islands and reefs located in the western Basin of Lake Erie (41°40' N, 82°50' W). Smallmouth bass nests were typically found in water 2-4 m deep with a cobble substrate over a cohesive clay base. Round gobies were abundant in the habitats favored by spawning smallmouth bass (G. B. Steinhart, personal observation). Using SCUBA, we surveyed smallmouth bass nests during early May through June in Lake Erie, 1999-2001. Once located, nests used for predation experiments (1999 and 2000) were temporarily marked with a floating buoy while we observed and angled the nest-guarding male; these nests were not revisited. For the 2000 and 2001 angling experiments, nests were visited repeatedly, mapped, and marked with a numbered tile. On each visit, nest status (occupied or abandoned) and offspring developmental stage (unhatched embryos, hatched embryos, larvae, or juveniles) were recorded. Successful nests were defined as nests producing larvae (Ridgway et al. 1991).

Measuring round goby entry and offspring consumption rates

We used a remote underwater camera to record round goby predation while smallmouth bass guarded nests and to assess the rate of predator entry and consumption when smallmouth bass were removed via experimental catch-and-release angling. During preliminary work, we occasionally observed round gobies entering nests with

free-swimming larvae and even chasing larvae; however, we never observed a round goby consuming a larva. Consequently, we focused our efforts on videotaping nests with unhatched embryos (10 nests) or hatched embryos (17 nests). When a nest was located, divers placed a video camera mounted on a 0.5-m tripod within 0.5 m of the nest. Divers returned to the boat, waited 10 min, and began recording data on a combination TV/VCR connected to the video camera. We recorded nest-guarding behavior of smallmouth bass for 15 min before divers re-entered the water and angled the male smallmouth bass from the nest with a rod and reel and a single-hook plastic jig. Divers remained suspended above and to the side of the nest, careful not to disturb the substrate, and extended the rod to place the jig on the substrate within in the nest. Once the smallmouth bass was hooked, the diver passed the rod to a person in the support boat, who quickly reeled in the guarding male. Fish were weighed ($\pm$ 25 g) and measured ($\pm$ 1-mm total length [TL]) before release (mean angling plus processing time $\pm$ SE = 84 $\pm$ 8 s). Although the presence of the diver may have influenced smallmouth bass and round goby behavior, the divers were present only while installing the camera, angling, and during nest guarding, if applicable (see below).

We estimated the number of offspring consumed during experimental catch-and-release angling by measuring the entry and feeding rates of round gobies in unguarded smallmouth bass nests from videotaped observations. Round goby behavior (e.g., entering or exiting a nest, consuming an embryo) from the videotapes was recorded with Beast™ software, a program for real-time recording and analysis of behavioral data. We summed all round goby entries and exits at 3-s intervals, which provided the number of round gobies in the nest. In addition, we estimated the rate of offspring consumption by

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78 individual round gobies of various sizes (mean = 70 mm TL, range 42-136 mm) from

videotapes. Total length was estimated by measuring round gobies on the television

screen and correcting based on an object of known size (i.e., a ruler or a tile, also on the

screen). We assumed an offspring was consumed when a round goby tilted toward the

substrate and flared its gills to suck in an offspring. Observations of round goby

consumption lasted for the entire time the focal round goby was in the nest, and we

observed individuals at various times after a nest was left unguarded. Total number of

offspring consumed from an unguarded nest through time (s) was calculated as:

$$\# \, \text{Offspring consumed through time} \, T = \sum_{t=0}^{T} \left(\# \, \text{Round gobies}(t) \cdot \frac{\# \, \text{Offspring consumed}}{\text{Round goby} \cdot 3 \, \text{s}} \right) \quad (1)$$

where $t = 0, 3, 6, \ldots, T$. We measured round goby entry and consumption rates in both

nests containing unhatched embryos and nests with hatched embryos. For statistical

analyses, we included only those nests left unguarded for ≥ 5 min (6 nests with unhatched

embryos and 10 with hatched embryos). We used analysis of covariance (ANCOVA) to

test whether the mean number or entry rate of round gobies in an unguarded nest differed

between nests with offspring at different developmental stages. The model used

offspring stage (unhatched or hatched embryos) as a class variable and the time since the

guarding male was removed (0-300 s in 3-s intervals) as the covariate. We specifically

were interested in the interaction between offspring stage and time since removal to see if

there was a significant difference ($\alpha = 0.05$) in the rate of round goby entry.

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Effect of holding time on smallmouth bass return time

To quantify the time smallmouth bass required to return to their nests after release and to determine if holding time affected return time, we held angled smallmouth bass for different lengths of time before release. In 1999, fish were either immediately released (18 fish) or held for 6 min before release (12 fish). In 2000, treatments were immediate release, 2, 6, and 12-min hold periods before release (6 fish for each treatment), with treatment systematically assigned. Hold time was in addition to angling and handling times (84 ± 8 s, as described earlier). Fish were held in a cooler filled with lake water before release into the lake. Return time was recorded when the guarding male appeared on the TV/VCR at the nest and resumed parental care. We used an analysis of variance (ANOVA) model to test if treatment (hold time) or male TL (mean, range = 364 mm, 270-468 mm; 2 fish were not measured, leaving a sample size of 52) affected return time.

Changes in nest size and embryo density during and following catch-and-release angling

To more directly estimate the effects of round goby predation, we measured smallmouth bass nest area before and after catch-and-release angling of the nest-guarding male. Because angling causes physiological stress that can last for several hours, parental care may be compromised during this post-angling recovery period, so we designed treatments to separate offspring losses during angling from losses during post-angling recovery. In 2000 and 2001, smallmouth bass nests were assigned to one of three treatments: 1) control (no angling); 2) angling-without-predation, where nests were

guarded by a SCUBA diver until the male returned (i.e., only post-angling offspring losses); and 3) angling-with-predation, where nests were exposed to predators (i.e., offspring losses during and post-angling). Angling methods were as previously described, except that all smallmouth bass were jaw tagged before release (mean angling plus processing time $\pm$ SE = 146 $\pm$ 11 s). Tagging ensured proper identification because smallmouth bass sometimes used nests abandoned by other smallmouth bass (G. B. Steinhart, personal observation).

For each nest, we traced the perimeter occupied by broods before angling and on the next visit, an average of 4 d later (range 1-8 d). Nest tracings (34 nests) were made on a clear acrylic sheet and nest area was quantified using a digitizing tablet with SigmaScan™ software. We used ANCOVA to test whether change in brood area was affected by treatment. The number of days between tracings served as a covariate. To determine if brood losses occurred during angling or during post-angling recovery of the nest-guarding male, we used least significant difference tests (LSD with Tukey-Kramer correction for multiple comparisons) to compare change in brood area between control and angling-without-predation or angling-with-predation treatments, along with a comparison between both angling treatments. In addition, we estimated embryo density before and after angling with photographs of nests containing unhatched embryos (46 nests before angling and 21 nests after angling). Nests with offspring that had hatched were not used because offspring both blended into the background and wiggled into interstial spaces. Unhatched embryo densities were estimated from digitized photographs, enhanced with Optimas™ image analysis software, by averaging the number of unhatched embryos counted in six randomly selected 4-cm^2 areas within the

brood (~ 5% of brood area). A similar method, but using SCUBA diver unhatched

embryo counts, produced results comparable to counting all unhatched embryos in the

nest or in nest photographs (Raffetto et al. 1990). We used ANOVA to test whether

embryo density differed among angling treatments. We also tested for angling treatment

effect on initial (before angling) density to ensure that there had been no bias in nest

selection for treatment assignment.

RESULTS

Round goby entry rate into smallmouth bass nests

Round gobies were the primary predator on smallmouth bass offspring (> 99% of

predators observed). On two occasions, logperch (*Percina caproides*) entered unguarded

nests; in one case, a rock bass (*Ambloplites rupestris*) ate unhatched embryos from an

unguarded nest (nest not included in analyses). In 10 h of video observations, only once

did a round goby eat offspring from a guarded smallmouth bass nest. For unguarded

nests, the average time to first entry by round goby was 78 s (range: $2 - 288$ s), with

many round gobies following. During the first 5 min after bass removal, round gobies

entered nests with unhatched embryos more rapidly (4.3 round gobies/min) than they

entered nests with hatched embryos (1.8 round gobies/min; offspring stage x time since

removal interaction; $F_{1,198} = 702.7$, $p < 0.0001$; Figure 1).   As a result, within 5 min after

the guarding smallmouth bass was removed, nests with unhatched embryos contained an

average of 20 round gobies (range = 9-34; Figure 1) and nests with hatched embryos had

9 round gobies (range = 0-18). From 5 to 15 min, the mean density of round gobies (17 per nest with unhatched embryos, and 12 per nest with hatched embryos) was relatively stable at > 200 round gobies/m^2.

Round goby consumption rate

After entering nests containing unhatched or hatched embryos, each round goby ate an average of one offspring every 3.5 s (± 2.2 SD) for the duration of its visit. During an average visit (mean ± SD = 69.2 ± 59.1 s), a round goby consumed 18.0 offspring (± 21.6 SD). Using average consumption rate and number of round gobies in an unguarded nest, round gobies consumed an estimated 1,000 unhatched embryos or 400 hatched embryos during the average time a male was absent following catch-and-release angling (Figure 1; ~ 5 min, See Results: Effect of holding time). Offspring consumption rate by all round gobies in the nest was higher in nests with unhatched embryos (2.8 unhatched embryo/s) than in nests with hatched embryos (1.0 hatched embryo/s) during the first 5 min after the guarding male was removed. An estimated 3,800 unhatched embryos or 2,400 hatched embryos were consumed within 15 min while male smallmouth bass were held off their nests (Figure 1). Given this rate of consumption, an average smallmouth bass brood in Lake Erie (mean ± SE = 4,600 ± 360 unhatched embryos) would be entirely consumed by round gobies in approximately 17 min, assuming that consumption rate remains constant.

Effect of holding time on smallmouth bass return time

Male smallmouth bass exhibited highly variable return times to their nests (Figure 2). Return time was unaffected by either time held after capture ($F_{3,47} = 0.3$, $p = 0.82$), or TL ($F_{1,47} = 1.5$, $p = 0.22$). With no consistent pattern for return times, we generated a probability distribution of the return times for angled smallmouth bass using all return times measured during 1999-2000 (84 males, mean $\pm$ SE $= 188 \pm 31$ s). To these return times, we added 2 min for angling and handling to calculate total time a male may be absent from his nest. Our mean angling plus handling time was 1.4 min, but typical anglers may take longer to release a fish if they use multi-hook lures (longer time to unhook fish), weigh, measure, and photograph the catch. We converted the distribution of absence times to the predicted number of unhatched or hatched embryos consumed (Figure 3). A 0.5 probability exists that at least 1,100 unhatched embryos or 500 hatched embryos would be consumed, and a 0.25 probability that at least 2,400 unhatched embryos or 1,200 hatched embryos would be consumed during catch-and-release angling. The expected, or average, number of offspring consumed by round gobies was 1,600 unhatched embryos or 800 hatched embryos during a single catch-and-release angling of a nest-guarding smallmouth bass. Thus, about 35% of the offspring in an average Lake Erie smallmouth bass nest were lost during typical catch-and-release angling.

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Changes in nest size and embryo density during and following catch-and-release angling

Angling treatment affected the change in area occupied by unhatched embryos ($F_{2,30}$ = 4.41, p = 0.021), but the number of days (1-4 d) between tracings ($F_{1,30}$ = 2.46, p = 0.13) did not; consequently, we assumed that offspring losses occurred during or immediately after catch-and-release angling, not during the days between tracings (Figure 4). Nests exposed to predation during angling lost an average of 222 cm^2, or 34%, of the area occupied by unhatched embryos, which was greater than the average loss of 14 cm^2 from nests guarded during angling (LSD, t = 2.81, p = 0.023). Nests not subjected to angling (control nests) lost an average of 70 cm^2, which was no different than losses from nests guarded during angling (LSD, t = 0.82, p = 0.69) or unguarded, angled nests (LSD, t = 2.31, p = 0.069). Embryos were typically in a single layer and embryo density (measured from photographs) did not differ between treatments before angling ($F_{2,44}$ = 0.25, p = 0.78) or after angling ($F_{2,19}$ = 0.96, p = 0.40). Therefore, we calculated mean unhatched embryo density for all nests (mean ± SE = 8.6 ± 0.4 eggs/cm) and multiplied it by change in nest area for each treatment. From these estimates, control nests lost a mean of 600 unhatched embryos and nests guarded during angling lost a mean of 200 unhatched embryos (Figure 4), representing 4-13% of the embryos in an average smallmouth bass nest in Lake Erie. When nests were left unguarded during catch-and-release angling, however, they lost an average of 2,000 (43%) of the unhatched embryos in an average nest.

Timing of smallmouth bass spawning

Smallmouth bass began spawning in early May, and continued guarding broods until early July, in 2000-2001 (Figure 5). Nests where the guarding male was not angled and were active in May ultimately failed, primarily due to storms (Chapter 4). Nests that were ultimately successful were occupied in June and July. Over 3 years of this study, most of the successful nests contained non-mobile embryos primarily during a two-week period, from 6-20 June.

DISCUSSION

Despite the high density of round gobies in Lake Erie, smallmouth bass were able to defend their offspring from potential predators, except when nest-guarding males were removed from nests by angling. During our experiments, round gobies consumed 20-50% of the offspring in a smallmouth bass nest during catch-and-release angling. Survival from egg deposition to maturity is often very low for smallmouth bass (Clady 1975) and only a few nests may produce the majority of juveniles surviving until fall (Gross and Kapuscinski 1997). Even a small increase in episodic predation can further reduce recruitment to adulthood (Houde 1989) and, when the nest predator is a recent and hyper-abundant invader, mortality via nest predation may be significant.

We estimated that round gobies could consume an entire smallmouth bass brood in little more than 15 min, a result of high densities and gregarious nature of round gobies. Our estimates, however, assumed a constant consumption rate (1 offspring/3.5 s). Often,

predation rate is modeled as a declining function due to predator satiation and because reduced prey abundance increases search times. Our estimate of round goby consumption was calculated from entire round goby visits: from the time an individual entered to when it left a nest. Therefore, time spent searching for prey, interacting with other round gobies, and changes in appetite owing to satiation were accounted for in our estimate of consumption rate. In our observations, round gobies were constantly entering and exiting nests, thus there were new (i.e., not satiated) round gobies entering the nest at various times. In this situation, long search times are unlikely as smallmouth bass embryos are non-mobile and confined within small nests (mean brood area $\pm$ SD = 0.05 $\pm$ 0.02 m^2). Even if we have overestimated round goby consumption rate, non-mobile offspring, confined to a small area and exposed to high predator densities, are extremely vulnerable to predation.

In fact, our data could underestimate the actual number of offspring consumed because we quickly reeled the smallmouth bass to the boat and released it near its nest after a short holding time. In practice, fish are occasionally played to exhaustion, which increases return time (up to 4 times as long; Kieffer et al. 1995). In addition, fish are often held out of water for longer than in our experiments, especially when hooks are deeply imbedded or the catch is measured or photographed. Holding a smallmouth bass out of the water for just 1 min increases return times two to threefold (Philipp et al. 1997). Further, as angling or handling times increase, the angler's boat may move farther from the nest, which also increases return time (Philipp et al. 1997). In extreme cases (e.g., fishing tournaments), smallmouth bass may be held for several hours or transported several km before release, almost assuring total nest destruction. In addition, angled

smallmouth bass experience significant physiological stress that requires several hours of recovery, especially when they are played to near exhaustion (Schreer et al. 2001). In fact, locomotory behavior of nest-guarding male largemouth bass can be impaired for more than 24 h (Cooke et al. 2000). During this recovery period, parental care could be compromised. However, because neither smallmouth bass nest area nor egg number declined for nests guarded by SCUBA divers during angling (i.e., angling without predation treatment), nest predation was not apparent during post-angling recovery of the guarding male.

Even though we quantified the impact of round gobies on individual smallmouth bass nests, we did not directly measure their effect on total number of juveniles that survived to fall or beyond. In fishes, recruitment of larvae to juveniles, and juveniles to adults, is highly variable and can be related to both environmental factors and predation (Houde 1987; Houde 1989). Frequently, mortality during early life stages, including egg predation by benthic predators, can determine recruitment success (Rice et al. 1987; Bouwes and Luecke 1997; Foote and Brown 1998). Although there are few data on smallmouth bass, for largemouth bass, the number of offspring produced from nests may drive adult abundance (Summerfelt 1975; Fuhr et al. 2002). Thus, the combination of round gobies and anglers, which reduce the number of offspring in a brood, may ultimately influence cohort success.

Clearly, there are many factors that can affect smallmouth bass recruitment success, and the question of what controls recruitment success is still under debate. What is evident, however, is that smallmouth bass were adapted to a particular environment in Lake Erie and, since the introduction of the round goby, predation risk has changed in

Lake Erie. Although we observed many nest failures associated with strong winds, storms have always affected Lake Erie, whereas round gobies have arrived only recently. Furthermore, in Ohio waters of Lake Erie, angling has long been allowed during smallmouth spawning, but a 10-fold increase in angler effort targeting smallmouth bass since 1985 (Lichtkoppler and Hushak 2001), coupled with the invasion by round gobies, could increase mortality of smallmouth bass (Philipp et al. 1997; Ridgway and Shuter 1997).

Given that smallmouth bass repeatedly spawn in the same location and aggressively defend their nests, anglers easily target them during the parental-care period (Ridgway 1988; Ridgway et al. 1991). Male vulnerability, coupled with nest-predation by introduced species, brings into question the practice of spring angling for smallmouth bass. At a minimum, anglers should be encouraged to shorten playing and handling times of nest-guarding males (Philipp et al. 1997; Cooke et al. 2000); however, additional protections may be needed. Managers use a variety of fishing regulations, including closed seasons, length limits, creel limits, and sanctuaries to protect species vulnerable to over-harvest (Fox 1975). Closed seasons often are used to protect spawning fishes, but must coincide with critical spawning periods (Kubacki et al. 2002). In Lake Erie, smallmouth bass nested during early May through early July; even so, successful nests did not occur until June (Figure 5). Further, round gobies consumed few free-swimming offspring; consequently, angling restrictions will be most beneficial when successful nests contain embryos. But, compliance with closed seasons is often poor (Kubacki et al. 2002). Illegal or incidental catch-and release often occurs (Sztramko 1985; Philipp et al. 1997), thereby making data comparisons before and after regulation changes difficult.

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Indeed, an estimated 63% of anglers in four systems in Ontario fished for smallmouth and/or largemouth bass during the closed season (Philipp et al. 1997). Even if observed, results suggest that closed seasons do not necessarily improve smallmouth bass recruitment. In eastern Lake Erie, moving from a closed to open season during smallmouth bass nesting in New York waters produced no change in smallmouth bass relative abundance (Einhouse et al. 2002).

An alternative tool, more common in marine than in freshwater systems, is establishing sanctuaries and no-take reserves (Murray et al. 1999). Marine reserves can prevent collapse and enhance speedy recovery of over-fished stocks; indeed, fish biomass rapidly increases after their establishment (Roberts et al. 2001). The establishment of a sanctuary in Long Point Bay, Lake Erie, resulted in increased catch-per-unit-effort of smallmouth bass: a consequence of either lowered pre-season harvest or greater recruitment stemming from reduced interference with nesting males (Sztramko 1985). Voluntary sanctuaries observed during the smallmouth bass spawning in Ontario led to reduced angling pressure and higher nest success inside the sanctuaries compared to outside (Suski et al. 2002). In addition, when a northern Wisconsin lake was closed to fishing year-round, largemouth bass nest success increased and nest predation decreased; however, these effects may have resulted from a combination of reduced angling during spawning and changes in population size-structure (Swenson 2002).

In Lake Erie, the effects of angling and round goby predation during the spawning season on smallmouth bass cohort survival are unknown, but must be recognized as a new source of mortality. As such, round goby predation may compromise recruitment success. In the past, substantial proof of damage has been required before limiting a

fishery, but with the current rate of species introductions (Rahel 2000; Ricciardi and

MacIsaac 2000), managers should allow for some uncertainty when making decisions

(Murray et al. 1999). At a minimum, future efforts should include assessing exploitation

rates of nesting smallmouth bass and encouraging anglers to promptly and carefully

release their catch.

Figure 1. Number of round gobies in nests and number of offspring consumed since

male smallmouth bass removal from nests containing unhatched or hatched

embryos in the Bass Islands of Lake Erie during 1999 and 2000. Top panel:

number of nests observed. Middle panel: mean and 95% confidence intervals

of the number of round gobies in a nest. Bottom panel: mean and 95%

confidence intervals of the number of offspring consumed by round gobies.
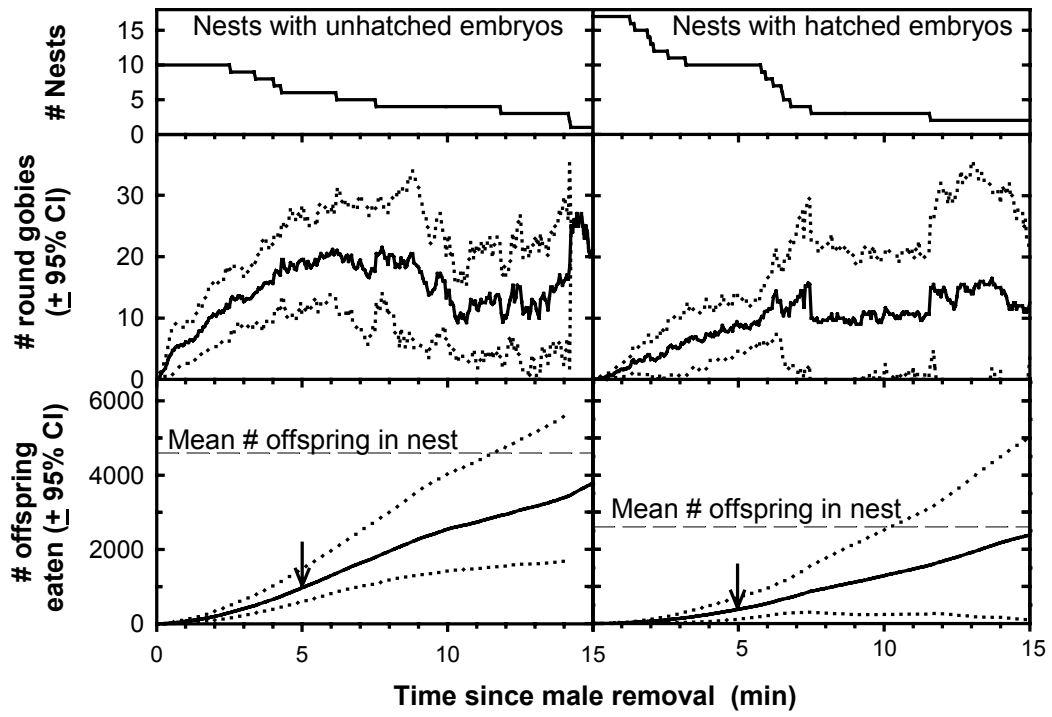
Figure 1.

Figure 2.   Average time taken by nest-guarding smallmouth bass to return to their

nests after catch-and-release angling during May through June 1999-2000 in the Bass

Islands, Lake Erie. Time held after capture refers to how long a smallmouth bass was

held in a cooler in lake water before release.
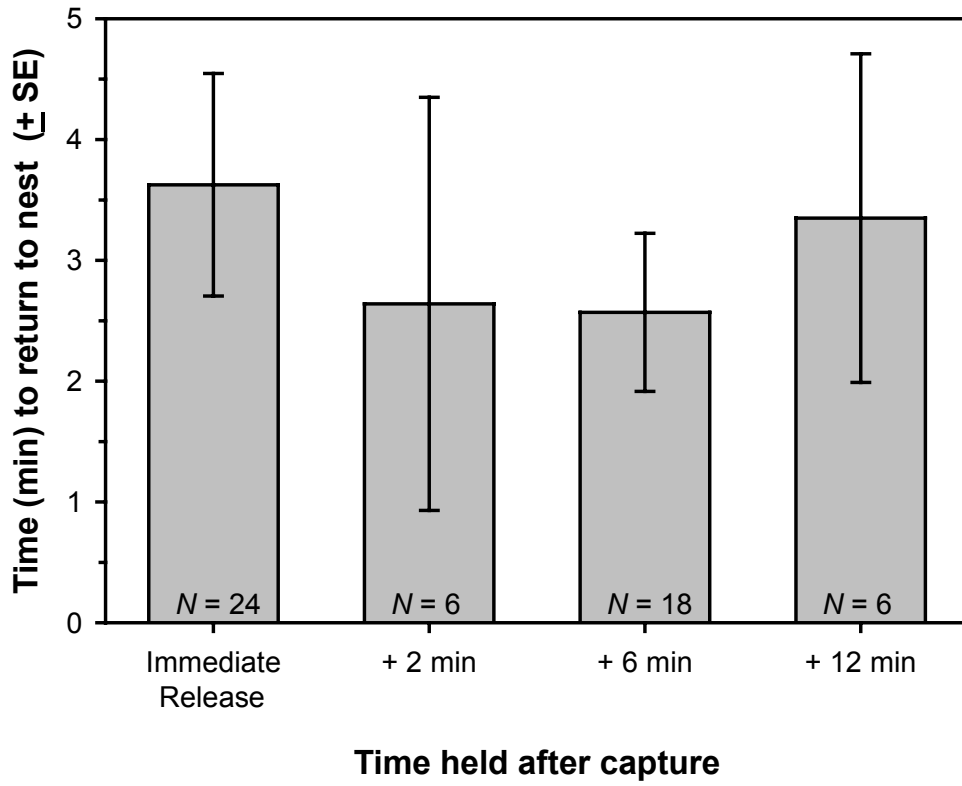
Figure 2.

Figure 3.   Probability of the average number of offspring consumed by round gobies

from smallmouth bass nests during a typical catch-and-release angling event in the Bass

Islands, Lake Erie. Probabilities were based on the frequency distribution of return times

for 84 male smallmouth bass, including a 2-min angling and handling time before release

during May through June 1999-2001. Asterisks indicate the minimum number of

offspring consumed from nests for which the male smallmouth bass did not return during

our post-release observation period (15 min).
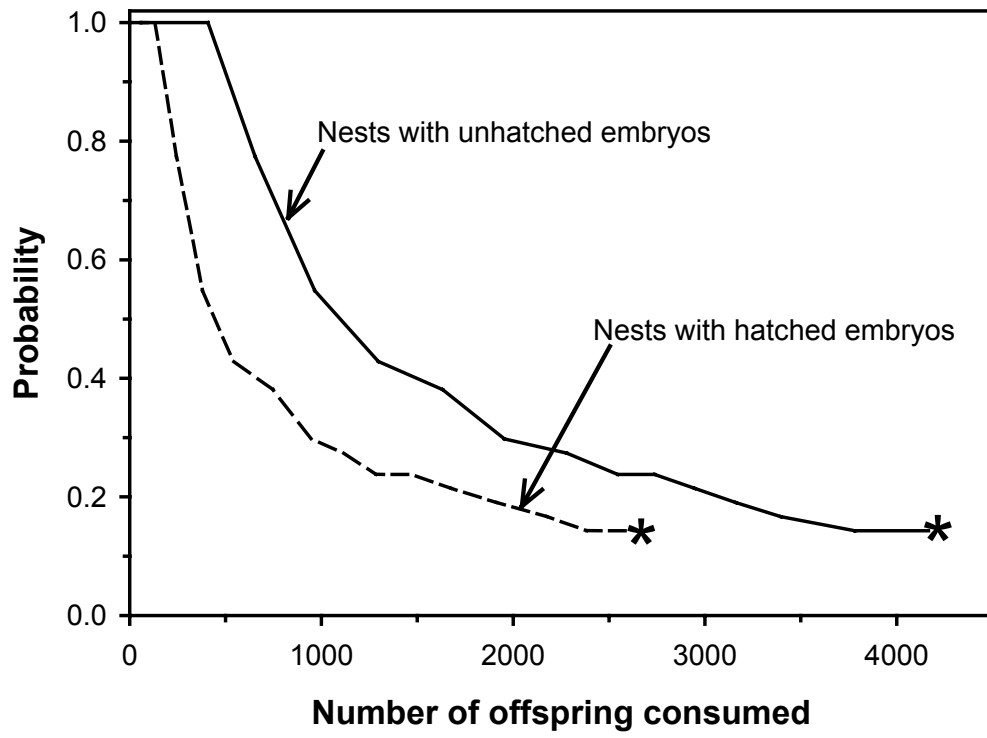
Figure 3.

Figure 4.   Change in nest area, after an average of 4 d between sampling, for smallmouth bass nests assigned to experimental treatments in Lake Erie, 2000-2001. Treatments were defined as follows: control (no angling); angling-without-predation (angling with nests guarded by a SCUBA diver); and angling-with-predation (angling with nests exposed to predators).
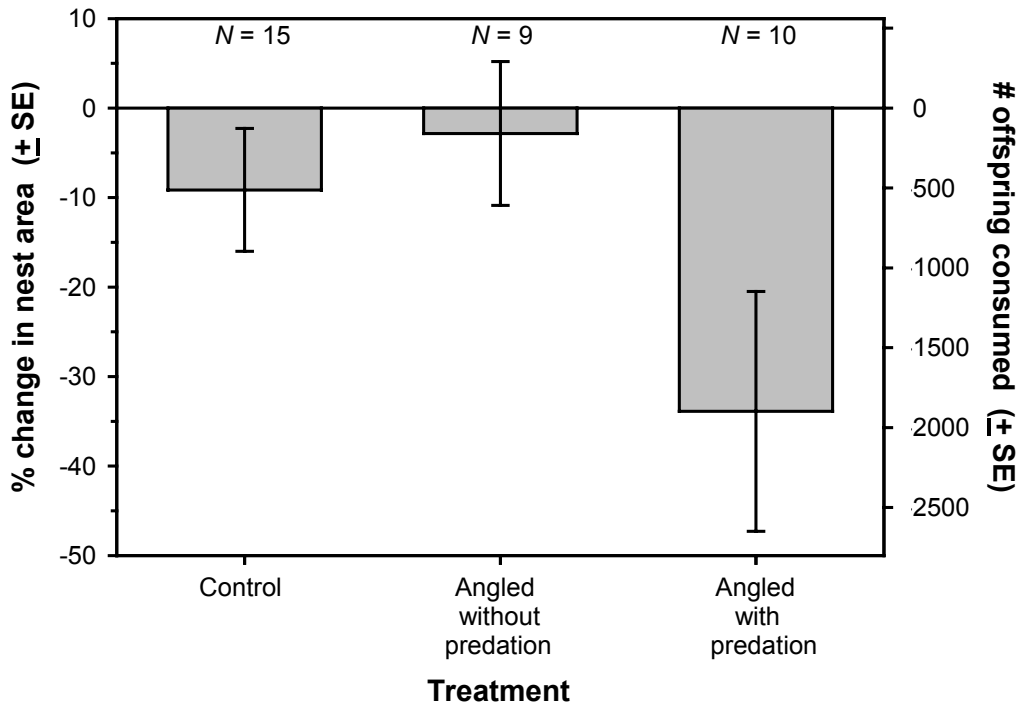
Figure 4.

Figure 5.   Number of guarded smallmouth bass nests (141 nests) present each day

during 6 May – 9 July at our sample sites in the Bass Islands, Lake Erie, 2000-2001.

Lines reveal the number of guarded nests on each day for nests that ultimately failed (i.e.,

never produced free-swimming larvae) or were ultimately successful. Data for successful

nests were split into when nests contained non-mobile embryos (i.e., vulnerable to round

goby predation) and when nests contained less vulnerable, free-swimming larvae or

juveniles. We did not remove guarding males from nests depicted in the graph, but they

were susceptible to local anglers.

Figure 5.

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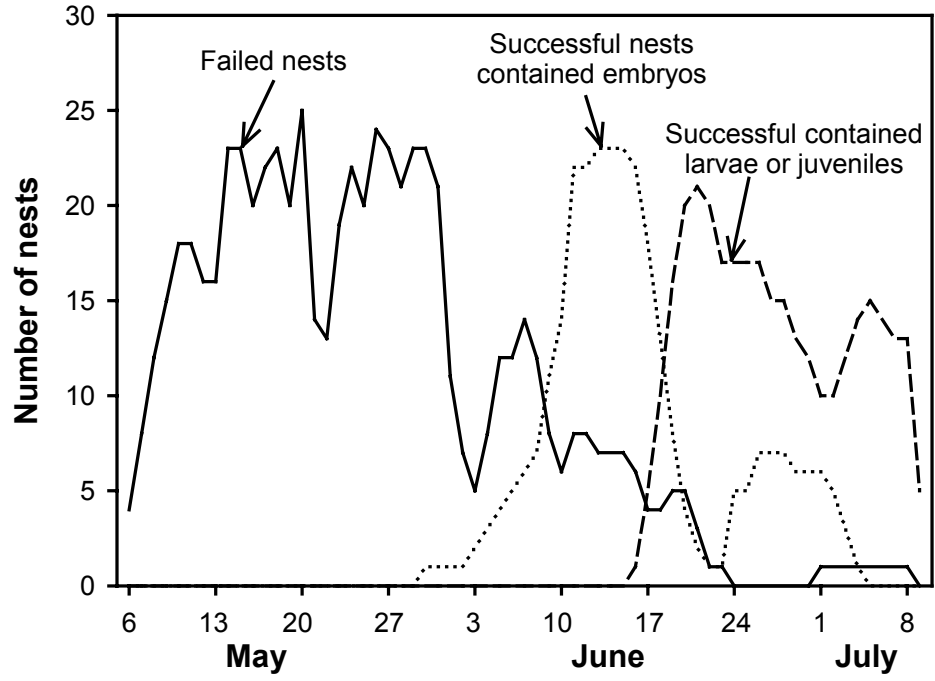
CHAPTER 3

PARENTAL CARE COST FOR A NEST-GUARDING FISH INCREASES IN RESPONSE TO A HYPER-ABUNDANT PREDATOR

ABSTRACT

Whereas parental care increases the likelihood that current offspring will survive to reproduce, providing care is costly, reducing parental growth and survival and, thereby, compromising future reproductive success. To determine if an exotic benthic predator might be affecting parental care and, ultimately, nest abandonment by nest-guarding smallmouth bass (*Micropterus dolomieu*), we compared nest-guarding behavior and the associated energy expenditures in two systems, one with a hyper-abundant recently introduced predator, the round goby (*Neogobious melanostomus*). In Lake Erie, USA, smallmouth bass vigorously defended their nests from benthic round gobies. In Lake Opeongo, Canada, smallmouth bass were exposed to fewer and predominantly open-water predators and were less active in their nest defense. From SCUBA and video observations, we documented that nest-guarding smallmouth bass chased predators (99%

of which were round gobies) nine times more frequently in Lake Erie than in Lake Opeongo, resulting in a significant decline in weight and energetic content of guarding males in Lake Erie, but no change in Lake Opeongo males. Bioenergetic simulations revealed that parental care increased smallmouth bass standard metabolic rate by more than 300% in Lake Erie, but only by 28% in Lake Opeongo. As energy reserves declined, males in both lakes consumed more prey and spent more time foraging away from their nests. Because nest-guarding smallmouth bass consumed few prey, increased parental care costs due to presence of round gobies could contribute to nest abandonment if smallmouth bass approach critically low energy reserves, as well as limit future growth, reproduction, and survival.

INTRODUCTION

Many organisms provide parental care for their offspring because, as investment in parental care increases, so does the probability that offspring survive (Sargent 1988). Providing care is energetically costly and, therefore, parents must decide how much care to provide by balancing the conflicting energetic demands of their offspring (current reproduction) and maintenance of their own energetic condition for future reproduction (Sargent 1997). Providing care reduces energy reserves (Horak et al. 1999), reducing survival (Sabat 1994), increasing time to next reproduction (Smith and Wootton 1994), and reducing future fecundity (Balshine-Earn 1995; Jones and Reynolds 1999). Therefore, understanding parental-care costs and parental behavior in response to brood value and parental condition is essential for our knowledge of reproductive systems.

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Energetic cost of parental care varies greatly and depends on abiotic and biotic factors. When conditions demand more care (e.g., ambient temperature requires incubating or oxygenation of offspring), parents expend more energy caring for their brood than when conditions are favorable (Coleman and Fischer 1991; Jones and Reynolds 1999; Skolbekken and Utne-Palm 2001). In addition, parents must increase nest-defense behaviors when nest predators are abundant (Ghalambor and Martin 2002; Popiel et al. 1996), or risk losing offspring. Increased parental aggression depletes energy reserves (Chellappa and Huntingford 1989) and, ultimately, may lead to brood abandonment if a parent falls below a low-condition threshold (Horak et al. 1999). Although some studies have compared parental behavior across different environments (Ghalambor and Martin 2000; Ghalambor and Martin 2002; Townshend and Wootton 1985), few studies have evaluated how *in situ* environmental conditions affect the energetic cost of parental care.

We sought to assess parental behavior and parental care costs in a nest-guarding fish, the smallmouth bass (*Micropterus dolomieu*), in two populations, one population exposed to a hyper-abundant nest predator. Male smallmouth bass provide sole parental care for their offspring, constantly circulating water over their offspring and defending their brood from predators (Ridgway 1988; Ridgway and Shuter 1994). Providing care is costly with the metabolic rate of nest-guarding smallmouth bass up to 50% higher than non-guarding individuals (Hinch and Collins 1991). Parental-care costs are amplified because males rarely leave their brood to forage and foraging range is reduced (Mackereth et al. 1999). As a result, male smallmouth bass lose energy during nesting (Gillooly and Baylis 1999; Mackereth et al. 1999).

We measured the cost of parental care for smallmouth bass facing different risks of nest-predation. In Lake Erie, Ohio, USA, smallmouth bass faced a high risk of nest predation from a recent invader and hyper-abundant nest predator, the round goby (*Neogobious melanostomus*), while in Lake Opeongo, Ontario, Canada, smallmouth bass experienced much lower predation risk. We hypothesized that male smallmouth bass that faced high nest-predation risk would exhibit more aggressive and defensive behaviors while guarding their offspring than would males exposed to low nest-predation risk. Further, aggressive males (i.e., those facing high nest-predator densities) should expend more energy than less aggressive males. Males may, however, compensate for energy expended on care by foraging more frequently.   We hypothesized that male smallmouth bass may ameliorate the cost of brood defense against round goby by consuming this abundant fish. Whereas increased consumption may compensate for some costs of parental care (Ridgway and Shuter 1994), foraging also reduces time spent on parental care (Townshend and Wootton 1985); thus, offspring may be more vulnerable to predators while the parent forages.

METHODS

Study species and sites

Smallmouth bass is one of many fish species that provide care for their offspring. In spring, as water temperatures approach 15ºC, male smallmouth bass clear an area for a nest over cobble. After the female deposits her eggs, the male remains to guard developing offspring as the young pass through several developmental stages. As

embryos, smallmouth bass are non-mobile and, therefore, extremely vulnerable to nest predators. During this stage, the male not only chases potential predators, but also fans the nest to provide oxygen and clear the nest of debris. Even after the offspring develop into free-swimming larvae and juveniles, the male continues to protect his brood 24 h a day for as long as 6 weeks. Care increases energetic costs (Gillooly and Baylis 1999; Mackereth *et al.* 1999) by raising metabolic rate and reducing feeding opportunities (Hinch and Collins 1991; Ridgway and Shuter 1994). Herein, we considered parental behavior at three stages of offspring development (i.e., unhatched embryos, hatched embryos, and free-swimming juveniles) and used these stages as surrogate measures of the time a parent has guarded his brood when evaluating parental behavior and energetic content.

We observed and sampled nesting smallmouth bass in Lake Erie, USA, and in Lake Opeongo, Canada. In mesotrophic Lake Erie, we surveyed smallmouth bass using SCUBA in the Bass Islands, located in the western basin of Lake Erie (41° 40' N, 82° 50' W) during May and June 1999-2000. Their nests typically occurred in water 2-4 m deep over cobble with a cohesive clay base, where round gobies also were abundant (Steinhart *et al.* 2004). In oligotrophic Lake Opeongo (45° 42' N, 78° 22' W, Algonquin Park, Ontario), we observed nesting smallmouth bass via snorkeling during June 2001. Smallmouth bass nests were most common at 1-2 m depth on cobble. Round gobies were not present in Lake Opeongo during this research.

Nest-guarding behavior

In both lakes, when divers or snorkelers located a smallmouth bass nest, we recorded offspring developmental stage and used an underwater, black and white video camera connected to a combination TV/VCR to record smallmouth bass behavior. After the camera, mounted on a 0.5-m tripod, was placed within 0.5 m of the nest, we waited 10 min before recording at least 15 min of smallmouth bass nest-guarding behavior. Once nests contained free-swimming young, the offspring and attending parent often would swim beyond the camera's view; hence, we analyzed parental behavior only for nests containing unhatched (i.e., fertilized eggs) and hatched embryos.

We analyzed videotaped parental behavior using Beast™ software, a program for real-time recording and analysis of behavioral data (G. Losey, University of Hawaii). All video recordings were pre-viewed to assign behaviors (by agreement between two observers) to one of two categories: "chase" or "leave." For 15 min of nest defense, we recorded the timing and duration of these behaviors in real-time using Beast™. Behaviors were defined as follows:

Chase: Guarding male rapidly departed from or returned to the nest with quick, powerful tail beats. Additional behaviors indicative of a chase included: 1) sudden orientation to a potential threat, 2) jawing, yawning, or fin displays, common when nest-guarding males are threatened (Ridgway 1988), or 3) swimming toward a threatening organism visible to the camera.

Leave: The guarding male slowly swam from the nest without any visual display of aggression.

We assumed that chases were aggressive behaviors directed toward potential nest predators, but the function of leaves was unclear. We summed total time spent away from the nest during chases and leaves, then calculated percent time away from the nest. We used general linear models to examine how independent variables, male total length, lake, offspring stage, and the lake-by-offspring stage interaction, affected frequency of chases and leaves and the percent time away from the nest. Because predators were not always in camera view, we recorded chase orientation to provide insight into what predator (i.e., benthic or water column) was chased. We recorded the direction of each chase as up (long body axis >10º above horizon), down (long body axis <10º below horizon), or horizontal (10º below horizon < long body axis < 10º above horizon), and compared chase orientation between the lakes with a Chi-square test ($\alpha = 0.05$ in all analyses).

Parent condition and energy density

We measured condition and energy density of male smallmouth bass early in parental care, when males were guarding unhatched embryos, and late in care, when males were guarding free-swimming juveniles. In Lake Erie, SCUBA divers used a rod and reel or a landing net to remove nest-guarding males. In Lake Opeongo, males were angled from nests from shore or a boat. In both lakes, males were selected haphazardly, captured,

euthanized in a mixture of MS-222 and lake water, placed on ice, then frozen at -10ºC within 1 h of capture.

After thawing, we weighed (± 0.01 g, wet weight, WW) and measured (± 1 mm total length, TL) each fish and removed its digestive tract. Tract contents were removed and stored in 95% EtOH. We separated testes from other viscera, setting both aside for energy density measurements. To test if a small tissue sample could accurately predict whole body energy density, we used a 5-mm diameter dermal punch to remove two small tissue samples (mean = 0.8 g), one from each lateral side below the dorsal fin, from each smallmouth bass. The remaining carcass was cut into pieces smaller than 100 cm³. Each tissue type (testes, viscera including emptied digestive tract, tissue plugs, body) were weighed, then dried at 60ºC to constant weight (± 1%, usually 24-96 h). Next, testes, viscera, and tissue plugs were ground with a mortar and pestle, whereas the body was ground in a Retsch grinder. Ground samples then were dried an additional 24 h. We measured caloric density of the body tissue with a Parr Bomb Calorimeter (Model 1672) and of the testes, viscera, and tissue plugs with a Parr Semi-micro Calorimeter (Model 1425). We calculated caloric density (KJ/g WW) for each tissue and total energetic content (KJ) for each tissue by multiplying by the weight of each tissue type by its caloric density. Whole-body energy content was calculated by summing the energy content of all tissue types, and whole-body energy density as the weighted average (by WW) of energy density for each tissue.

Because energy density can be influenced by fish size (Mackereth et al. 1999), we used the residuals of WW and energetic content (KJ in viscera, testes, or whole body) from regressions on total length (TL) in all analyses (Steinhart and Wurtsbaugh 2003;

Sutton et al. 2000). We used general linear models to explore how residuals of parent WW and energetic content (KJ) varied by TL, lake (Erie and Opeongo), offspring stage (embryo and juvenile), and the lake-by-offspring stage interaction. We used individual contrasts to compare male whole-body energetic content between lakes for males guarding embryos and males guarding juveniles. We used linear regression to test if whole-body energy density was related to tissue plug energy density.

Diet of guarding males

After removing the contents of the digestive tract, all prey larger than 5 mm were identified under a dissecting scope and placed into one of three categories: fish, macro-invertebrates, or crayfish. Fish were identified to species using vertebral counts when necessary (Becker 1983; Trautman 1981). Each prey was dried at 60ºC to constant weight (± 1%, typically 24 h). From these data, we estimated daily ration by using the Eggers model to correct for gut evacuation rate over 24 h (Eggers 1977):

$$\text{Daily ration} = \text{weight of prey in stomach} \times \text{evacuation rate} \times \text{hours} \qquad (1)$$

where the evacuation rate was estimated as 0.1 (Rogers and Burley 1991) and hours = 24 h because samples were collected daily. The Eggers model is a reasonable estimate of daily ration (Boisclair and Leggett 1988). Daily ration was converted to mass-specific ration by dividing it by male smallmouth bass weight. The relationship between daily ration (g/d) at the start of parental care (i.e., males guarding embryos) and at the end of

care (i.e., males guarding juveniles) in each lake was explored with a general linear model: daily ration as the dependent variable and lake (Erie and Opeongo) and offspring developmental stage (embryo and juvenile), and the lake-by-offspring stage interaction as independent variables. We used individual contrasts to ask when daily consumption differed with offspring stage within each lake.

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Bioenergetic simulations

We used a bioenergetic model (Hanson et al. 1997) to estimate the metabolic rate, or activity level, of nest-guarding smallmouth bass in lakes Erie and Opeongo. The model predicted end weight based on wet weight at the start of parental care, energy density at the start and end of the nesting season, total consumption (g), and diet composition of nest-guarding smallmouth bass, in addition to prey energy density and water temperature (Table 1). For each lake, we used regressions to estimate the WW and energy density of an average length smallmouth bass at the start and end of parental care from the observed mean TL.

After running simulations with the base metabolic parameters established for adult smallmouth bass (Whitledge et al. 2003), we adjusted the activity level (ACT) in the model until the model results produced the final WW matching the mean male WW at the end of parental care (± 1 g). The ACT parameter is a constant that is multiplied by standard metabolism (i.e., for the metabolism of an average adult smallmouth bass, ACT = 1; Whitledge et al. 2003). Increasing ACT simulates changes in respiration due to the increased activity associated with swimming and chasing predators. We used lake-

specific estimates of ACT in calculations of net energy expended on parental care. We
first estimated the net amount of energy expended on care by calculating the total change
in energy content of males from start to finish of parental care plus the total consumption
during that time. From this, we subtracted the net change in energy under the assumption
that ACT=1 (i.e., the energetic cost of standard metabolic activities for the simulation
period).

Differences in net energy costs of parental care between Lake Erie and Lake Opeongo
could potentially be the result of differences between the lakes in temperature,
consumption, or ACT. To test how activity level alone influenced final total energetic
cost of guarding nests, we used the Lake Erie ACT (associated with the presence of round
gobies) in a simulation of nest-guarding males in Lake Opeongo, with all other Lake
Opeongo parameters held constant. In this way, we could isolate the influence of round
goby-induced high activity levels on differences in costs of parental care in the two
systems.

RESULTS

Nest-guarding behavior

Nest-guarding smallmouth bass in Lake Erie more aggressively defended their nests
than males in Lake Opeongo. While we placed the camera, smallmouth bass in Lake Erie
remained above or within 1-2 m of their nest and displayed aggression (e.g., "jawing"),
even bumping or biting divers. In contrast, in Lake Opeongo many males disappeared

from view when snorkelers were within 2-3 m of the nest, and did not reappear until snorkelers had left the water. Male TL did not affect chase frequency ($F_{1,46} = 1.15$, $p = 0.29$). Because TL was not a significant factor and we had length measurements for only 51 males, we removed TL from the model to allow us to use our full sample size for these behaviors (67 males). Lake was the only variable that influenced chase frequency ($F_{1,63} = 45.99$, $p < 0.0001$). Nest-guarding smallmouth bass in Lake Erie, regardless of offspring stage ($F_{1,63} = 0.04$, $p = 0.83$) or the lake-by-offspring stage interaction ($F_{1,63} = 0.25$, $p = 0.62$), chased predators 9 times more frequently than smallmouth bass in Lake Opeongo (Figure 6).

Nest-guarding males in Lake Erie chased benthic predators more often than males in Lake Opeongo. Chase orientation by nest-guarding smallmouth bass differed between these two lakes ($\chi^2 = 60.7$, df = 2, $p < 0.0001$). In Lake Erie, 61% of chases were benthic oriented, whereas in Lake Opeongo, horizontal chases were most common (68%; Figure 7). Most predators chased in Lake Erie were benthic species, round goby and log perch (*Percina caprodes*), with occasional chases toward species in the water column, smallmouth bass and rock bass (*Ambloplites rupestris*). In Lake Opeongo, observed predators were in the water column: smallmouth bass, yellow perch (*Perca flavescens*), and pumpkinseed (*Lepomis gibbosus*); we observed only one benthic darter (*Ethostoma* or *Percina* spp.) in a smallmouth bass nest. Because most chases were benthic oriented, and over 99% of predators confirmed in videotapes were round gobies (Steinhart et al. 2004), we believe that nearly all chases in Lake Erie were directed toward this introduced predator.

Although nest-guarding smallmouth bass were more aggressive in Lake Erie than in Lake Opeongo, they left their brood more frequently after their embryos hatched (Figure 6). Leave frequency was not influenced by male TL ($F_{1,46} = 2.95$, $p = 0.09$), nor was percent time away from the nest ($F_{1,46} = 0.37$, $p = 0.54$), so we removed TL from these models. Lake ($F_{1,63} = 7.76$, $p = 0.01$), offspring stage ($F_{1,63} = 7.88$, $p = 0.01$), and their interaction ($F_{1,63} = 28.78$, $p < 0.0001$), all affected leave frequency, driven mostly by the high leave frequency of males guarding hatched embryos in Lake Erie. In both lakes, males spent more time away from the nest once their offspring hatched (Figure 6; lake: $F_{1,63} = 1.89$, $p = 0.19$; offspring stage: $F_{1,63} = 29.13$, $p < 0.001$; lake-by-stage: $F_{1,63} = 0.01$, $p = 0.92$).

Parent condition

In general, male condition and energy content, measured as residuals from population-specific regressions with total length, declined from the start (i.e., guarding unhatched embryos) to finish (i.e., guarding free-swimming juveniles) of parental care (Figure 8). Large males lost more WW and energetic content than small males in Lake Erie, but male size (TL) had no effect in Lake Opeongo (Figure 8; Table 2). Energy density of tissue plugs was correlated with whole-body energetic density ($F_{1,61} = 7.52$, $p = 0.008$). Tissue plug energy density, however, explained only 11% of the variance in whole-body energetic density. Tissue plugs understandably underestimated whole-body energy density (slope $b_1 = 0.42$) as fat reserves are often stored in tissues (e.g., liver) not sampled by tissue plugs.

Residuals of WW and energy content of body and testes were all influenced by offspring stage and the lake-by-offspring stage interaction (Table 3). Males in Lake Erie started with higher residual WW than males in Lake Opeongo ($F_{1,59} = 4.49$, $p = 0.038$), suggesting that males were heavier for a given length at the start of care than at the end of care in Lake Erie. Indeed, males in Lake Erie lost residual WW while providing care ($F_{1,59} = 28.95$, $p < 0.0001$), while males in Lake Opeongo did not lose residual WW during care ($F_{1,59} = 1.12$, $p = 0.29$). When energetic content of all tissues were combined, nest-guarding males in Lake Erie began with higher body energy content than males in Lake Opeongo ($F_{1,59} = 9.41$, $p = 0.003$), and declined 11% in energetic content while providing care ($F_{1,59} = 45.36$, $p < 0.0001$). Nest-guarding males in Lake Opeongo did not decline in energetic content ($F_{1,59} = 0.45$, $p = 0.51$). Energy content of the viscera did not explain the change in whole body energetic content. Viscera content did not change during parental care, although a decline was nearly significant in Lake Erie ($F_{1,59} = 3.63$, $p = 0.062$; Lake Opeongo: $F_{1,59} = 0.01$, $p = 0.91$). Energy content of testes declined during care in both Lake Erie ($F_{1,59} = 51.12$, $p < 0.0001$) and Lake Opeongo ($F_{1,59} = 10.16$, $p = 0.002$), but the contribution of testes to the total energetic content was small ($< 1\%$).

Diet of guarding males

More smallmouth bass ate in Lake Opeongo (64% of males) than in Lake Erie (21%). Smallmouth bass in Lake Erie ate predominantly crayfish (60% by weight) and fish (40%) but, surprisingly, only 3 of 39 guarding males ate round gobies. In Lake Opeongo,

nest-guarding males consumed fish (55% by weight), crayfish (38%), and

macroinvertebrates (7%). Although the trend was for higher consumption by males in

Lake Opeongo than in Lake Erie, lake did not significantly affect mean daily

consumption in our overall model ($F_{1,60} = 3.42$, $p = 0.069$). Offspring stage affected

daily consumption ($F_{1,60} = 9.16$, $p = 0.036$) because males guarding juveniles consumed

more than males guarding embryos in both Lake Erie ($F_{1,60} = 2.29$, $p = 0.026$) and Lake

Opeongo ($F_{1,60} = 2.05$, $p = 0.045$). In addition, percent of males consuming prey

increased from males guarding embryos (Lake Erie: 5%; Lake Opeongo: 50%) to males

guarding juveniles (Lake Erie: 30%; Lake Opeongo: 77%). Daily consumption increased

from start to finish of parental care and was negatively related to male energetic content

(Figure 9).

Bioenergetic simulations

Activity level of nest-guarding smallmouth bass increased above standard metabolism

(ACT = 1) to match field changes in weight and energy density. In Lake Erie,

bioenergetic simulations revealed that guarding males had an ACT of 3.1; in Lake

Opeongo, males had an ACT of 1.2. Increased activity levels substantially influenced

cost of parental care (Figure 10). Although larger (in length) males experienced higher

parental care costs than small males, the differences were small compared to the effects

of changing ACT. A 350 mm smallmouth bass in Lake Erie would spend 381 KJ over

the average of 19 d of care provided. Lower activity levels in Lake Opeongo required

that similar-sized males spent only 53 KJ providing 17 d of care. After correcting for

average number of days of care, male smallmouth bass in Lake Erie invested more than 6 times the energy per day than did males in Lake Opeongo. When male activity level in Lake Opeongo was raised to 3.1, cost of parental care was nearly identical to Lake Erie, with the difference the result of slightly higher metabolic costs associated with 1-2ºC higher temperatures during parental care in Lake Opeongo than in Lake Erie. Consumption differences between the lakes played little role in the field patterns we observed. Indeed, with an activity of 3.1, smallmouth bass expended 7 times more energy on care than energy consumed.

DISCUSSION

The recent round goby invasion into Lake Erie has altered smallmouth bass parental behavior and parental care costs. Nest-guarding smallmouth bass chased predators more than nine times as frequently in Lake Erie (with round gobies) than in Lake Opeongo (without round gobies). Different suites and densities of potential predators in each lake make direct comparison of these lakes as round goby and non-round goby lakes imperfect, but several observations reveal that high predation risk from round gobies caused smallmouth bass to be more aggressive defending their nests. First, limited historical data from Lake Erie (Goff 1984) suggest that chase rates have increased about 3-fold since round goby invaded. Second, predation risk is higher in Lake Erie (post-round goby invasion) than in other smallmouth bass lakes. Predation risk, measured as cumulative number of seconds spent by all predators in a nest left unguarded for 2.5 min, was higher in Lake Erie (750 predator-s; Steinhart et al. 2004) than Lake Opeongo (0

predator-s; G. B. Steinhart, unpublished data), or Lake Opinicon, Ontario, Canada (100 predator-s; Kieffer et al. 1995). Third, benthic-oriented chases were most common in Lake Erie, whereas upward-oriented chases were most common in Lake Opeongo, suggesting that smallmouth bass in these two lakes were indeed chasing different predators. Finally, because round goby are benthic fish lacking a swim bladder and over 99% of nest predators in Lake Erie were round gobies (Steinhart et al. 2004), we believe round gobies are the dominant factor leading to differences in parental behavior between lakes Erie and Opeongo.

Increased chase frequency raised nest-guarding smallmouth bass activity rates by over 300% in Lake Erie, causing male smallmouth bass to lose energy while caring for their broods. Although energetic content did not decline in Lake Opeongo, activity rates for nest-guarding males were higher than standard metabolism. In another study of nest-guarding smallmouth bass in Lake Opeongo, significant energetic declines were observed from start to finish of parental care (Mackereth et al. 1999). We may have failed to find a decline in our study because males may have augmented their energetic content by increasing their consumption, or due to different methodologies. Mackereth et al. (1999) extracted only lipids, ignoring the possibility that lipids may have allocated to growth during parental care, which would reduce lipid content, but result in little change in whole-body energetic content.

Indeed, consumption and foraging behavior were related to energetic content. In both lakes, as the number of days spent guarding the brood increased, male energetic content declined and male daily consumption increased. Mackereth et al. (1999) also reported that nest-guarding males complemented their endogenous energy by feeding during

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parental care. Other organisms that provide parental care increase consumption as their energy reserves decline (Dearborn 2001; Townshend and Wootton 1985) and during stressful conditions (Metcalfe and Thorpe 1992; Pravosudov and Grubb 1998; Steinhart and Wurtsbaugh 2003). When daily consumption increased, males increased leave frequency, spending more time away from their nests than when males were in better condition. Parental investment theory predicts that as the brood ages, it becomes more valuable, so parents should invest more heavily into caring for old broods than young broods (Östlund-Nilsson 2002; Ridgway 1988). But, we observed that males spent less time caring for broods as offspring aged from unhatched and hatched embryos (both non-mobile stages), possibly because guarding males increased their foraging frequency to augment energy reserves. Although males were not observed during leaves, they may have been foraging, as suggested by their increased consumption. Time away from the nest also may have increased if chases and leaves were of longer duration due to capture and handling time of prey. We observed these behavioral changes while offspring developed from unhatched to hatched-embryos. All smallmouth bass embryos are relatively non-mobile, so the decline in parental care occurred while the offspring still required the male to protect them from predators.

Round goby, as an exotic predator, clearly has changed the behavior and cost of parental care for nest-guarding smallmouth bass in Lake Erie. But, the significance of this finding stretches beyond smallmouth bass behavior, as many species alter their parental behavior when faced with different predation risks (Ghalambor and Martin 2000; Ghalambor and Martin 2002; Willson et al. 2001). Changes in parental behavior affect the amount of energy spent on parental care (Coleman and Fischer 1991; Horak et al.

1999; Sabat 1994). In turn, cost of care should affect parental decisions in the context of

lifetime reproductive success (Ghalambor and Martin 2000; Östlund-Nilsson 2002;

Popiel et al. 1996). Exotic species invasions are now common; therefore, we must

consider how invaders may alter reproductive behavior and success of native species.

Because round gobies occur in high densities in Lake Erie (at times more than 100

round gobies per m^2; Charlebois et al. 1997) and enter unguarded nests quickly when

males are removed from nests (Steinhart et al. 2004), the risk to smallmouth bass

offspring is compounded by changes in parental-care behavior. If males should follow

predictions of parental investment theory, smaller broods after round goby predation

should receive less care than large broods (Sargent 1988; Townshend and Wootton

1985). As parental condition declined, and defending nests from round gobies

accelerated this decline, males spent more time away from the nest augmenting their

energy reserves by foraging. By reducing the time males defended their nest, round

gobies may be able to seize these opportunities to consume offspring from unguarded

nests, reducing the reproductive value of the brood. Therefore, small brood size and

declining parental condition both increase the probability that a brood will be abandoned

so that the parent may prepare for future reproductive opportunities.

Many organisms make reproductive decisions based on reproductive value and

perceived risk (Östlund-Nilsson 2002; Rytkönen 2002). But these decisions are complex

and include other factors, such as reproductive lifespan and the probability of future

reproductive success (Ghalambor and Martin 2000; Mauck et al. 1999). Male

smallmouth bass in Lake Erie first reproduce when 3-4 years old and typically have only

4-5 reproductive attempts before death (based on estimated mortality rates). In addition,

frequent storms in Lake Erie destroy many nests and lead to a low probability that a male

will successfully reproduce in any given year (Goff 1986). Therefore, smallmouth bass

in Lake Erie have relatively few reproductive opportunities relative to other, longer-lived

species. In fact, smallmouth bass have a lower probability of reproductive success in

Lake Erie than in Lake Opeongo because smallmouth bass in Lake Opeongo generally

have higher annual survival (due to lower fishing pressure) and higher probability of

success (fewer storms). Thus, smallmouth bass in Lake Erie may be less likely to

abandon their nests, even with round gobies present, because they have a low probability

of successful future reproduction compared to smallmouth bass in Lake Opeongo.

Exotic species, whether nest predators or nest parasites, directly reduce the

reproductive success of native species (Clotfelter and Yasukawa 1999; Popiel et al.

1996). In addition, by increasing the parents' predation risk or care costs, exotic species

can change parental behavior and indirectly affect offspring survival and the future

fitness of the parent (Ghalambor and Martin 2000; Ghalambor and Martin 2002; Ridgway

and Shuter 1994). The cumulative effect of these changes, and how they affect

reproductive decision-making (e.g., abandoning the current brood) has received little

attention, but is no doubt important when considering the manifold effects of exotic

species invasions. We have shown how exotic round gobies affect behavior and

energetics of native smallmouth bass during parental care, thereby potentially altering

smallmouth bass reproductive success.

Model Parameter	Lake Erie	Lake Opeongo
Simulation length (d)	17	19
Consumption (g/g)	34	55
Percent fish in diet	60	55
Percent invertebrates in diet	40	45
Male starting wet weight (g)	852	585
Male ending wet weight (g)	754	571
Male starting energy density (KJ/g)	6004	4949
Male ending energy density (KJ/g)	5355	4831

Table 1. Parameters used in the bioenergetic model (Hanson et al. 1997) to determine activity levels which produced observed changes in weight and energy density of nest-guarding smallmouth bass in Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada. Weight, energy density (KJ/g wet weight), days on nest, and diet data are mean values (Lake Erie, $N = 39$ fish; Lake Opeongo, $N = 25$ fish). Temperatures for the simulations derived from three temperature loggers placed near nests in each lake during nesting. Prey energy densities (6,000 KJ/g WW for fish and 4,000 KJ/g WW for macroinvertebrates) were estimated for a composite of species (Hanson et al. 1997). We used the same consumption, respiration, and egestion/excretion parameters for adult smallmouth bass (Whitledge et al. 2003), regardless of lake.

	Variable	Lake Erie			Lake Opeongo		
		Slope	t	p	Slope	t	p
Early in care	Wet weight	-0.22	-0.41	0.69	0.21	0.86	0.41
(guarding	Body energy	1.77	0.45	0.66	0.79	0.47	0.65
embryos)	Viscera energy	0.27	0.44	0.67	0.27	1.30	0.22
	Testes energy	0.08	1.32	0.21	0.03	0.75	0.47
Late in care	Wet weight	**-0.96**	**-4.38**	**0.001**	-0.02	-0.07	0.99
(guarding	Body energy	**-11.85**	**-4.41**	**0.001**	2.13	0.84	0.42
juveniles)	Viscera energy	-0.86	-2.13	0.01	0.12	0.43	0.67
	Testes energy	**-0.12**	**-6.81**	**<0.001**	0.01	0.12	0.91

Table 2. Individual regressions of residuals of wet weight and body, organ, and testes energy density versus total length for male smallmouth bass early in parental care (i.e., guarding embryos) or late in parental care (i.e., guarding free-swimming juveniles) in Lake Erie, Ohio, USA (2000), and Lake Opeongo, Ontario, Canada (2001; Figure 8). Slopes different from zero (bold results) reveal a significant effect of male length for that variable. Regression results were corrected for number of analyses ($\alpha = 0.003$).

Variable	Source	*F*	df	*p*
Wet weight (g)	Lake	0.01	1	0.99
	Offspring stage	**20.18**	**1**	**<0.0001**
	TL	3.07	1	0.09
	Lake × stage	**6.95**	**1**	**0.01**
Body (KJ)	Lake	0.42	1	0.52
	Offspring stage	**21.42**	**1**	**<0.0001**
	TL	**4.14**	**1**	**0.05**
	Lake × stage	**13.44**	**1**	**0.001**
Viscera (KJ)	Lake	0.01	1	0.94
	Offspring stage	1.25	1	0.27
	TL	1.50	1	0.23
	Lake × stage	1.72	1	0.19
Testes (KJ)	Lake	1.47	1	0.23
	Offspring stage	**48.19**	**1**	**<0.0001**
	TL	0.84	1	0.36
	Lake × stage	**4.47**	**1**	**0.04**

Table 3. General linear models of the factors affecting condition measures of nest-guarding smallmouth bass in Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada. Condition measures were the residuals of wet weight and energetic content of tissues (body, viscera, and testes) derived from population-specific regressions versus smallmouth bass TL. Offspring stage is a surrogate for time in parental care (i.e., males guarded embryos early in care and juveniles late in care). Significant factors are indicated in bold.

Figure 6.   Nest-guarding behaviors for smallmouth bass guarding unhatched and

hatched embryos in Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada. Chases

(**A**) were rapid swimming motions to chase potential predators from a nest and were more

frequent in Lake Erie than in Lake Opeongo (lake effect: $F_{1,63}=45.99$, $p<0.0001$). Both

leave frequency (**B**; stage effect: $F_{1,63}=28.78$, $p<0.0001$) and percent time away from the

nest (**C**; stage effect: $F_{1,63}=29.13$, $p<0.0001$) increased after offspring hatched.
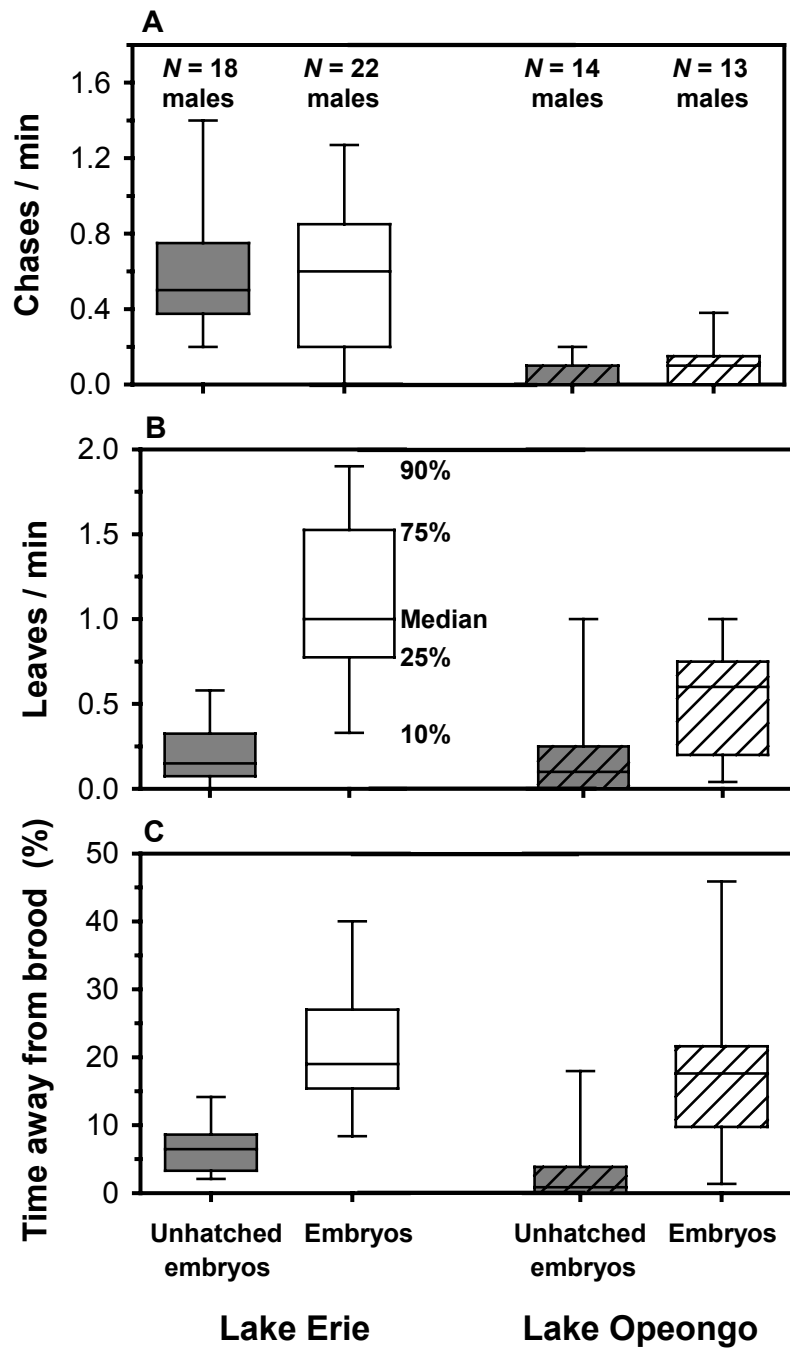
Figure 6.

Figure 7.   Orientation of chases made by nest-guarding smallmouth bass in Lake

Erie, Ohio, USA (1999 and 2000) and Lake Opeongo, Ontario, Canada (2001). We

assumed down-oriented (>10º below horizontal) chases were for pursuing benthic

predators (e.g., round gobies in Lake Erie), while horizontal and up-oriented (>10º above

horizontal) chases were pursuing predators in the water column. Downward chases were

more common in Lake Erie than in Lake Opeongo ($\chi^2 = 60.7$, df $= 2$, $p < 0.0001$).
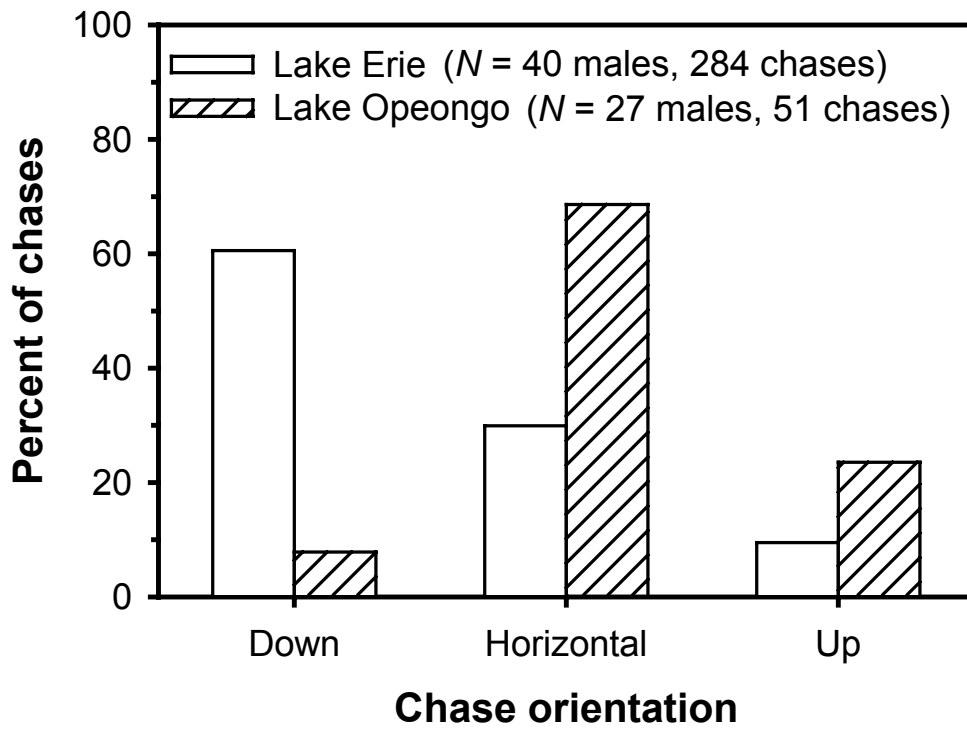
Figure 7.

Figure 8.   Residuals from regressions between smallmouth bass total length and wet

weight and between total length and body, viscera, and testes energy density (KJ/g) in

Lake Erie, Ohio, USA (2000), and Lake Opeongo, Ontario, Canada (2001) plotted

against total length. Data from early and late in parental care were pooled within each

lake to calculate residuals, but regressions versus total length were performed separately

for each period. Positive residuals indicate fish in better than average condition with

significant regressions marked with an asterisk (see Table 2 for regression results).

Figure 8.

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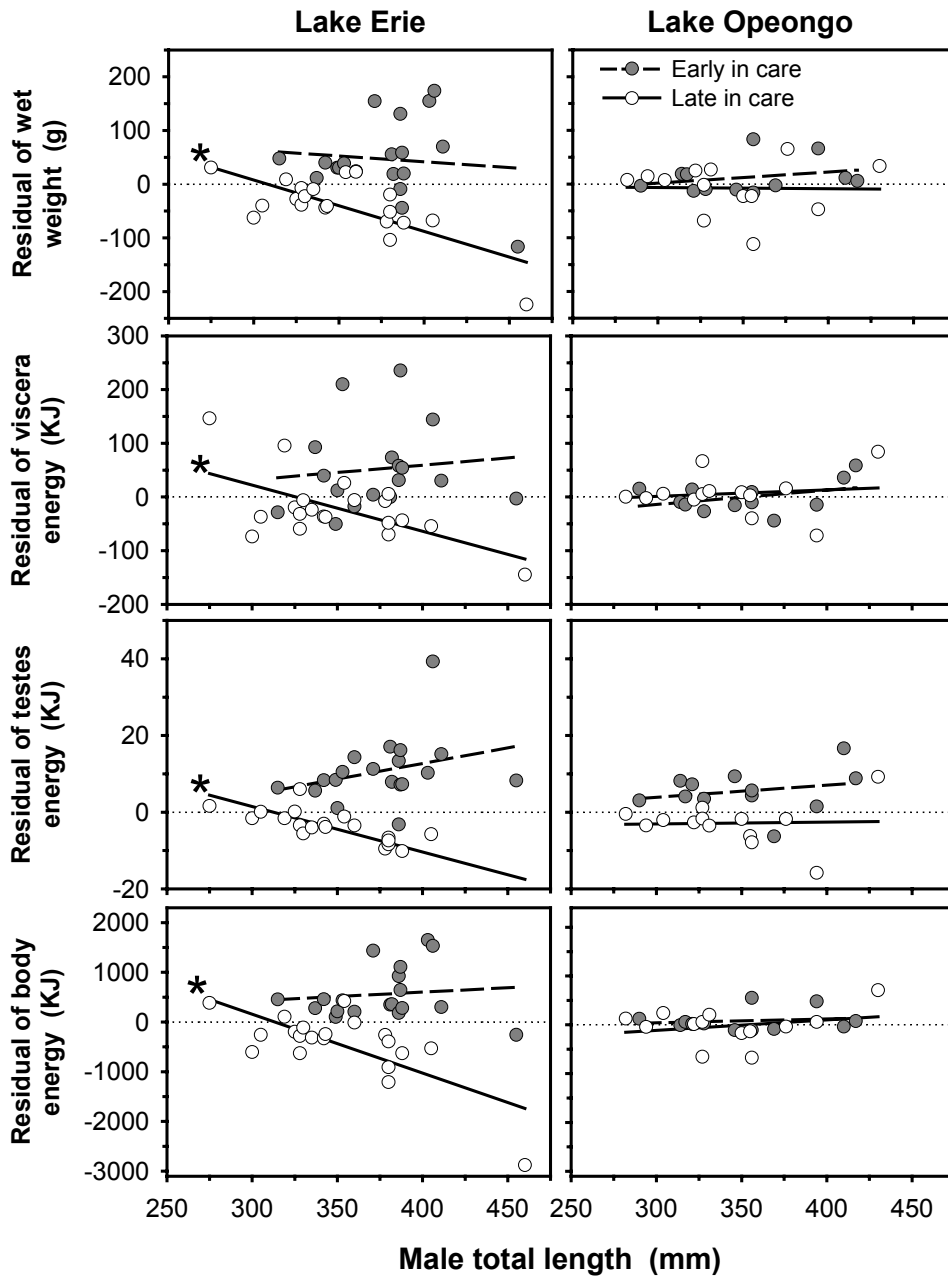
Figure 9.   Estimated daily consumption (g/d) versus whole-body energy density of nest-guarding smallmouth bass, early and late in parental care, in Lake Erie, Ohio, USA (2000), and Lake Opeongo, Ontario, Canada (2001).   Both lake ($F_{1,60}$=4.08, p=0.05) and time (early or late in parental care; $F_{1,60}$=9.77, p=0.003) affected mean consumption.
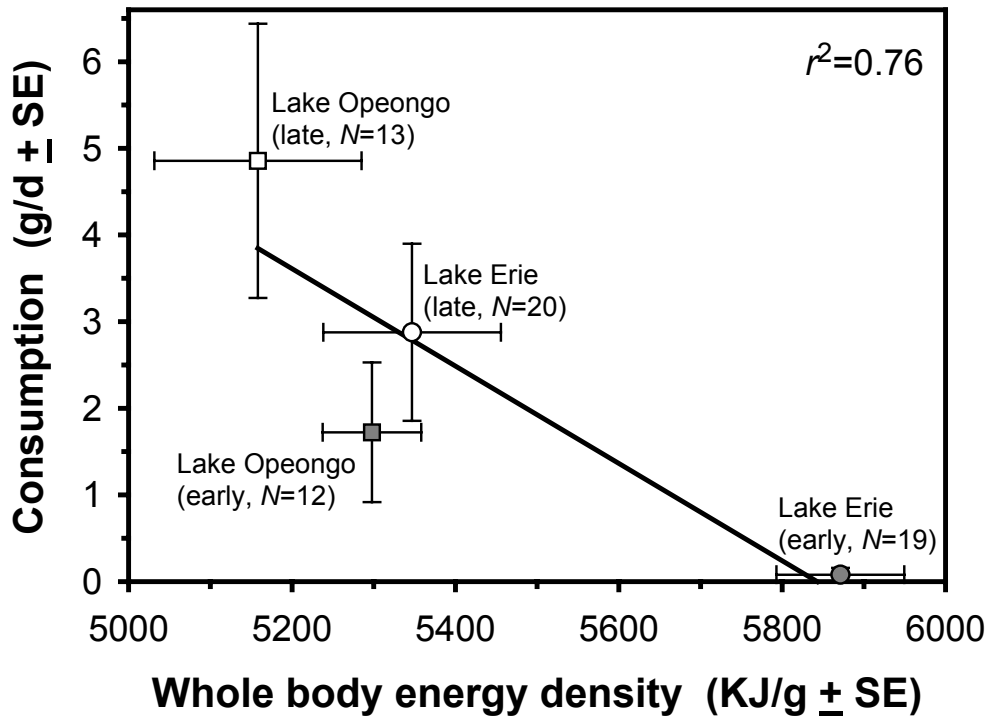
Figure 9.

Figure 10.   Estimated direct costs of parental care from bioenergetic simulations of nest-guarding males in Lake Erie, Ohio, USA (1999-2000, round gobies present), and Lake Opeongo, Ontario, Canada (2001, no round gobies), with expected costs if round gobies occurred in Lake Opeongo. To simulate the effects of round gobies in Lake Opeongo, activity level (ACT) was raised to the level of smallmouth bass in Lake Erie. The cost of care plotted here resulted only from changes in activity level because we assumed constant consumption.
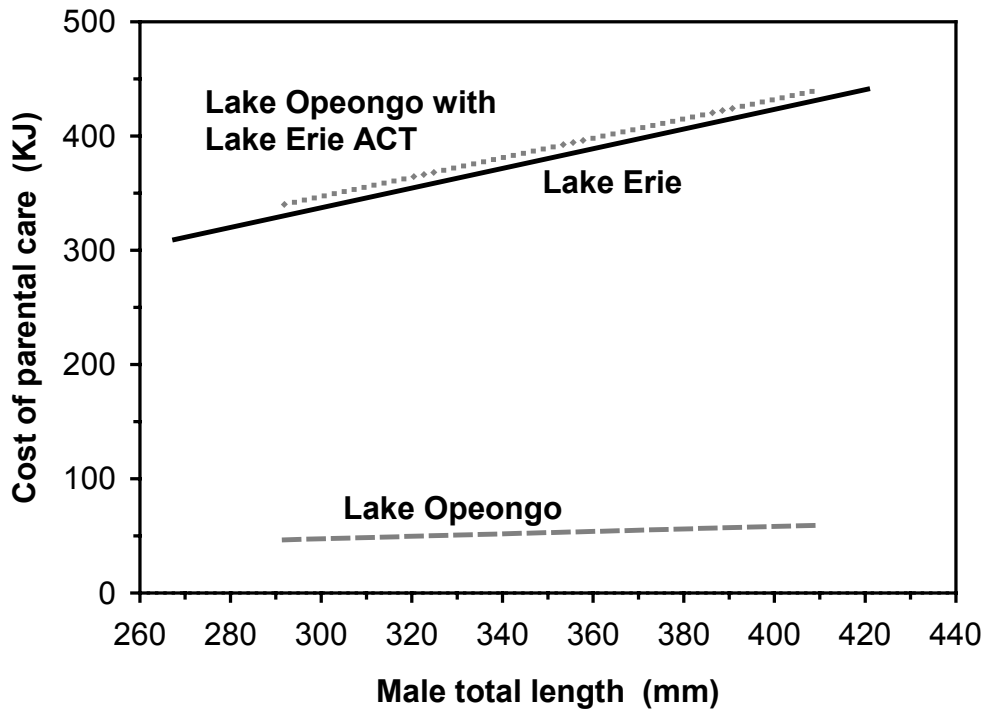
Figure 10.

CHAPTER 4

EFFECTS OF STORMS, ANGLERS, AND NEST PREDATORS ON

SMALLMOUTH BASS NEST SUCCESS

ABSTRACT

We studied how storms, angling, and nest predation affected smallmouth bass
(*Micropterus dolomieu*) nest survival in the Bass Islands, Lake Erie, Ohio. Increasing
angler effort and introduction of an exotic nest predator, round goby (*Neogobious
melanostomus*), have raised concerns about smallmouth bass recruitment in Lake Erie.
We surveyed smallmouth bass nests and calculated daily survival rates for nests assigned
to different angling treatments: control (no angling), angling without predation (guarding
male temporarily removed and nest guarded until his return), or angling with predation
treatments (guarding male temporarily removed and nest left unguarded). Only 30% of
control nests were successful during 1999-2001 spawning seasons, compared with 11%
of angling without predation and 14% of angling with predation treatments. Using
maximum likelihood models in the program MARK, we explored how storms, anglers,

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and treatment affected daily nest survival. Although nest predators consumed about 35% of broods during angling, daily nest survival rates of angling without predation (0.87) and angling with predation treatments (0.88) were similar, but angling reduced nest survival compared to controls (0.91). Although angling reduced nest survival, mean number of anglers counted at sites during our surveys did not contribute to nest survival. Storms, defined as any day with at least 2 h of wind speeds at least 7 m/s, were related to both nest success and daily survival. The best model predicting daily nest survival included the added effects of treatment and number of storms. Thus, whereas storms and angling affected smallmouth bass nest survival, number of anglers and nest predation did not.

INTRODUCTION

Nest success is a critical component in the reproductive biology of species providing parental care for offspring that remain in a confined nest (e.g., many fish, birds, reptiles, and amphibians). Environmental conditions (Goff 1986; Townshend and Wootton 1985), parents' ability to care for their young (Ridgway and Shuter 1994), and parental behavior (Ghalambor and Martin 2000; Sargent 1988) all influence nesting success. In turn, reproductive success can influence population dynamics and affect the evolution of parental behavior (Gross and MacMillan 1981; Popiel et al. 1996). As anthropogenic impacts on climate and species invasions become more widespread, understanding their impacts on nest success is of growing importance. For example, climate warming (Shuter and Post 1990), exotic nest predators (Janssen and Jude 2001), and brood parasites (Pease 1995) affect reproductive success. Therefore, understanding the

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mechanisms controlling nest success will allow better predictions of how environmental changes may affect future reproductive success (Ricciardi and Rasmussen 1998; Shuter and Post 1990).

We chose to examine nest success of smallmouth bass, *Micropterus dolomieu*, where males alone care for their offspring for up to 6 weeks (Friesen 1998; Knotek and Orth 1998). Care involves nearly constant fanning of eggs and protection of offspring from nest predators (Hinch and Collins 1991). During this time, smallmouth bass do not actively forage for prey, although they may consume a limited number of prey available near the nest (Mackereth et al. 1999). Thus, parental care is energetically costly for smallmouth bass (Gillooly and Baylis 1999; Mackereth et al. 1999). Smallmouth bass nest success is influenced by storms (Goff 1986), temperature fluctuations (Friesen 1998; Knotek and Orth 1998), angling (Philipp et al. 1997; Suski et al. 2003), and nest predation (Hinch and Collins 1991; Knotek and Orth 1998).

We examined smallmouth bass nest success in Lake Erie, Ohio, USA, where storms, angling, and nest predators may well determine smallmouth bass nest survival. Lake Erie is a large lake with a long fetch; thus, storms can produce large waves capable of destroying smallmouth bass nests (Goff 1986). Nest predators, which can destroy unguarded smallmouth bass nests within 24 h (Hinch and Collins 1991; Kieffer et al. 1995), are extremely abundant in Lake Erie since the introduction and spread of the round goby, *Neogobious melanostomus* (Charlebois et al. 1997). In addition, angling is allowed during the nesting season in Ohio waters of Lake Erie, so anglers can remove guarding males from their nests. When the guarding male smallmouth bass is removed, the nest becomes susceptible to predators (Kieffer et al. 1995; Philipp et al. 1997). Even

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if anglers practice catch-and-release techniques, nest predators consume offspring while the guarding male is absent (Steinhart et al. 2004). In addition, the stress of angling may result in nest abandonment (Philipp et al. 1997).

Herein, we describe how storms, angling, and nest predation, both singly and in combination, affected smallmouth bass nest success in Lake Erie. Specifically, we sought to determine which factors were more important in determining smallmouth bass nest success and if factors interacted to affect nest success. To do this, we first had to define wind speeds that caused smallmouth bass nest failures. Next, we designed an experiment to separate the effects of storms, angling, and nest predation on smallmouth bass nest success. Assessing nest survival has traditionally relied on reporting only percent nest success or by using techniques that involve assumptions about nest failure date or causes of nest failures (Mayfield 1961). However, recent techniques and software have been developed that allow for more comprehensive analyses (e.g., including individual and time-dependent covariates) of nesting data (Burnham and Anderson 1998; Dinsmore et al. 2002; White and Burnham 1999). For our analyses, we used the recently developed nest success model in the program MARK (White and Burnham 1999).

METHODS

Nest success surveys

We conducted nest surveys at three locations in the Bass Islands, Lake Erie, to monitor smallmouth bass nest survival during 1999-2001 spawning seasons (Figure 11).

We surveyed smallmouth bass nests for a maximum of 64 d, depending on year: 24 May - 3 July 1999, 9 May - 11 July 2000, and 9 May - 9 July 2001. Sites were revisited as frequently as possible (mean every 3 d; range 1-10 d). Sites were known spawning areas with similar substrate (predominantly cobble over a cohesive-clay base) and depth (2.5-3 m deep), but were exposed to different ranges of winds (i.e., different exposure to storms; Figure 11). Within each site, we repeatedly sampled one or two linear transects (6 m by 100 m; 1999) or one 50-m diameter circle (2000-2001). Latitude and longitude of each site were recorded in 1999 and were used to position sites in subsequent years. Nests were individually marked with numbered tiles. In both 2000 and 2001, we found tiles from nests marked in 1999; thus, our sites were located within 100 m of each other across years.

For each survey, a pair of SCUBA divers swam along a metered line marking the transect (1999) or swam in concentric circles by holding a metered line attached to a buoy at the site's center (2000 and 2001) until they had surveyed the entire site. When a new nest was discovered, we marked it with a numbered tile and recorded its location on a site map to aid in relocating nests on subsequent visits. For all nests, we recorded offspring developmental stage as unhatched embryos (i.e., fertilized eggs), hatched embryos, larvae, or juveniles. We defined a successful nest as any nest producing free-swimming larvae because free-swimming offspring, either larvae or juveniles, can leave the nest at any time. Defining successful nests as nests producing larvae may overestimate true nest success because offspring survival increases if offspring remain until metamorphosing into juveniles.

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Angling experiment

We assigned each nest, consecutively, to one of three treatments: 1) control
(unmanipulated); 2) angling without predation (the nest was guarded by a diver during
the male's absence); or 3) angling with predation (predators were allowed to enter the
unguarded nest). The two angling treatments were designed to test direct effects of
angling on nest survival (angling without predation) and effects of nest predation
occurring while guarding males were temporarily removed (angling with predation).
During experimental angling, unguarded nests lost 400 to 1,000 offspring (approximately
25% of the brood; Steinhart et al. 2004). If a nest was destroyed or abandoned before we
assigned it to a treatment or before the treatment was applied, the nest was moved to a
no-treatment category.

To simulate catch-and-release angling, SCUBA divers caught nest-guarding males
using a rod and reel, with a soft-plastic artificial bait on a weighted, single hook as a lure.
We angled nest-guarding males an average of 2 d after their nest was discovered (range
1-16 d). Divers remained suspended above and to the side of the nest, careful not to
disturb the substrate, and extended the rod to place the jig on the substrate within the nest.
Once the smallmouth bass was hooked, the diver swam to the support boat and passed the
rod to a person in the boat, who quickly reeled in the guarding male. Angled fish were
weighed, measured, and jaw-tagged (Monel metal jaw tag, size 10) before release (mean
angling plus processing time 125 s, range 37-238 s). For the angling without predation
treatment, a diver remained by the nest to and chased potential predators with hand
motions to prevent predators from entering while the guarding smallmouth bass was
absent. Nests were guarded until males returned (average 208 s, range 12-885 s). All

males were observed returning to their nests, except one male who did not return until divers left the nest 15 min after the male had been released, but this male was seen guarding his nest the next day. We compared nest success among treatments using a χ^2 test ($\alpha = 0.05$ for all tests).

Defining a storm

To determine the strength and duration of winds required to destroy smallmouth bass nests, we monitored egg losses from artificial nests placed in each survey site during 24 May - 11 July 2000. Artificial nests (21.6-cm diameter and 3-cm tall) were constructed by embedding limestone rocks of two different size classes (small = 3.8 cm ± 0.7; large = 6.2 cm ± 1.2) in concrete (Kwikcrete™). After determining the mean size (2.6-mm diameter) and specific gravity (0.033) of unfertilized smallmouth bass eggs (Crisp 1989; Dudley and Platania 1999), we found a polystyrene bead that mimicked the size and specific gravity of real eggs. Because smallmouth bass eggs adhere to the substrate after fertilization, we experimented with various adhesives to find one that mimicked the adhesive strength of real eggs. Adhesiveness of artificial eggs held to rocks by compounds was compared to egg-covered rocks collected from smallmouth bass nests in Lake Erie. Adhesive strength was tested in a large aquarium, with adjustable flow, by incrementally moving egg-covered rocks closer and closer to the flow source. We recorded distance from the nozzle where 50% of eggs had been washed from the rock. This process was repeated for multiple flows, adhesives, and for rocks covered with real

smallmouth bass eggs. Ultimately, a petroleum-based cream (Vaseline™) most closely mimicked the adhesiveness of real smallmouth bass eggs.

Artificial nests, each with 50 artificial eggs, were placed *in situ* at the three sites to estimate egg loss to waves and currents. At each site, four nests, two each of the different substrates, were deployed at the center of the study sites at 3-m depth, on 35 different site-days (total 140 artificial nests). All nests were left *in situ* overnight (mean 26 h, range 17-48 h). After retrieving nests, we counted the remaining eggs and averaged number of eggs for nests of similar substrate and compared mean egg number across substrate size with a paired *t*-test to determine if substrate size affected egg loss.

To determine storm exposure for each artificial nest deployment, we used continuous wind data (1-h mean speed and direction) from a National Oceanic and Atmospheric Administration (NOAA) weather station located on South Bass Island (Station SBIO1; Figure 11). We included only winds directed into each of our study sites (Figure 11). Using egg loss and wind data from only one of the sites, a two-dimensional Kolmogorov-Smirnov test (2DKS test; Garvey et al. 1998) was used to test for a significant threshold between wind speed (m/s) and number of eggs lost from the artificial nests. The best fit was found using a threshold wind speed of 7 m/s. Next, we used a 2DKS to test for a threshold number of hours of continuous wind with speeds $\geq$ 7 m/s that resulted in significant egg losses from artificial nests at all sites. We used this threshold (hours of continuous wind speeds $\geq$ 7 m/s) as our definition of a storm that was capable of destroying real smallmouth bass nests in our sites.

Modeling nest survival

To quantify the effects of anglers, predators, and storms on daily nest survival, we used the nest survival model in the program MARK (White and Burnham 1999). MARK uses maximum likelihood models and is preferable to other techniques (e.g., Mayfield estimation) because it allows the user to include individual, group, and time-specific covariates when estimating nest survival (Dinsmore et al. 2002). We limited our analyses to a set of pre-determined models that explored the effects of nest treatment (control, angling without predation, and angling with predation), sample site, and storms on smallmouth bass daily nest survival. For angled nests, nest histories included only days post-angling. In addition, we included no-treatment nests as control nests in our models, but not when calculating mean nest success for control nests.

Our candidate models did not include the direct effects of day or year to estimate nest survival. Because storms occurred frequently, our surveys were sometimes separated by several storms, and not all nests were seen on every day; estimating daily survival for 63 intervals, 3 sites, 3 treatments, and 3 years would result in estimation of more parameters than we deemed possible for our sample size. We ignored the effect of year, independent of site, in our model because year effects would be confounded as we had only control treatments during 1999, but applied control, angling with nest predation, and angling without nest predation treatments during 2000-2001. Including storms as a covariate indirectly accounted for annual effects, as models including storms were nested within models containing both site and year. The storm covariate was the number of storms, as defined by our artificial nest experiment, occurring during survey periods for each combination of site and year (i.e., 9 unique storm values). Because we empirically

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defined a storm from artificial-nest experiments at each site, and because our sample sites were all of similar depths, we felt that storms would have similar effects regardless of site or year. The angler covariate was the mean number of anglers observed during each visit to survey smallmouth bass nests in a particular site. An observer in the support boat counted all boats and anglers within the bay where the site was located while SCUBA divers surveyed smallmouth bass nests. Models that incorporated one or more covariates used the *logit* link function and all other models used the *sine* link function (Burnham and Anderson 1998; Dinsmore et al. 2002).

We began with the null model, estimating a single mean daily nest survival without inclusion of any factors (Model 1; see below). We then looked at each of four factors individually: spawning site (Perry's Monument, Gray's Bay, Sonny's Marina, Model 2), nest treatment (control, angling without predation, angling with predation, Model 3), storms (number of storms in a given year at each site, Model 4), and anglers (mean number of anglers seen per day in a given year at each site, Model 5). After determining the effect of storms alone, we explored whether nest treatment affected nest survival when survival estimates were constrained by the effect of storms: an additive effect (both storms and nest treatment affected daily nest survival; Model 6) and the interaction of the two (storms affected daily survival of nest treatments differently; Model 7). In case our definition of a storm was not an accurate description of an event that could destroy smallmouth bass nests, we also tested a model that constrained daily nest survival by the total hours of wind speeds ≥ 7 m/s at each site-by-year combination (Model 8). The models and their simplified notation were as follows:

Model	Notation
1) Single estimate of daily survival	$S_{(.)}$

$$Y_i = \beta_0 + \varepsilon_i$$

2) Effect of site only	$S_{(site)}$

$$Y_i = \beta_0 + \beta_1 site_1 + \beta_2 site_2 + \varepsilon_i$$

3) Effect of nest treatment only	$S_{(trt)}$

$$Y_i = \beta_0 + \beta_1 trt_1 + \beta_2 trt_2 + \varepsilon_i$$

4) Effect of storms only	$S_{(storms)}$

$$Y_i = \beta_0 + \beta_1 storms + \varepsilon_i$$

5) Effect of anglers only	$S_{(anglers)}$

$$Y_i = \beta_0 + \beta_1 anglers + \varepsilon_i$$

6) Effect of treatment plus effect of storms	$S_{(trt + storms)}$

$$Y_i = \beta_0 + \beta_1 trt_1 + \beta_2 trt_2 + \beta_3 storms + \varepsilon_i$$

7) Effect of treatment and storms	$S_{(trt \times storms)}$

$$Y_i = \beta_0 + \beta_1 trt_1 + \beta_2 trt_2 + \beta_3 storms +$$
$$\beta_4 storms{\cdot}trt_1 + \beta_5 storms{\cdot}trt_2 + \varepsilon_i$$

8) Effect of treatment plus effect of storm hours	$S_{(trt + storm\ hours)}$

$$Y_i = \beta_0 + \beta_1 trt_1 + \beta_2 trt_2 + \beta_3 storm\ hours + \varepsilon_i$$

We compared the fit of models using Akaike's Information Criterion (AIC; Akaike 1985). Models were ranked according to AIC_c (Burnham and Anderson 1998; Dinsmore et al. 2002). Differences in AIC_c (ΔAIC_c) were used to determine which model(s)

provided the best fit for nest survival (Burnham and Anderson 1998; Dinsmore et al. 2002). As a rule of thumb, a ΔAIC_c value less than 2 indicates equal support for the candidate models, and ΔAIC_c values greater than 7 indicate considerable support for a difference between models (Burnham and Anderson 1998). In addition, normalized Akaike weights (w_i) were used to evaluate the degree of uncertainty for model selection (Burnham and Anderson 1998). Akaike weights were used to measure the model likelihood of the better fitting model in relation to a poorer fitting model: the ratio of two w_i values, the relative plausibility, is interpreted as the likelihood of the better model (Burnham and Anderson 1998).

RESULTS

Nest success

We monitored nest success of 326 smallmouth bass nests during the 3 study years: 131 controls, 70 angling without predation, 65 angling with predation, and 60 no-treatment nests. Nest success varied by site and treatment (Figure 12), with treatment having a significant effect on nest success ($\chi^2 = 11.18$, df = 2, $p = 0.004$). Nest success did not differ between angling without predation and angling with predation treatments ($\chi^2 = 0.18$, df = 1, $p = 0.68$) despite significant losses of offspring from angling with predation nests (Steinhart et al. 2004). Inspection of data, including χ^2 residuals, found control nests had higher nest success (29.8%) than nests exposed to either angling without predation (11.4%) or angling with predation (14.0%) treatments. Smallmouth bass nest success in Lake Erie was lower than reported for many other systems (Table 4).

Storms and nest success

From artificial nest experiments, we defined a storm capable of destroying smallmouth bass nests as at least 2 h of consecutive wind speeds of at least 7 m/s directed toward the sample site: wind speeds of this strength and duration resulted in significant egg losses from artificial nests (Figure 13; 2DKS test, $N = 33$, $D = 0.12$, $p = 0.03$). Egg losses from nests with small or large substrates did not differ ($t = 1.98$, df $= 138$, $p = 0.51$). Using this definition of a storm, smallmouth bass nest success (controls only) was negatively correlated with number of storms across sites and years (Figure 14). No successful nests were observed at Gray's Bay in 2000 or Perry's Monument in 2001. Total number of days with storms (from all directions) was higher during the 2000 and 2001 spawning seasons (24 storms each season) than during the 1999 spawning season (20 storms; 20-y average = 20.3 storms; Figure 15).

Modeling nest survival

Daily survival of smallmouth bass nests was a function of number of storms and treatment, but not mean number of anglers per survey visit (Table 5). The best model, $S_{(trt + storms)}$ was more than 5 times more likely to describe nest survival than the next best model, $S_{(storms)}$. From the best model, storms negatively affected nest success ($\beta_{storms} = -0.074$), as did angling ($\beta_{angling\ without\ predation} = -0.45$, $\beta_{angling\ with\ predation} = -0.41$). When we considered each of these factors alone, storms and nest treatment had equal weight in determining nest success ($S_{(trt)}$ AIC$_c$ - $S_{(storms)}$ AIC$_c$ = 0.23; Table 5). Using total number of storm hours did not explain nest success as well as using total number of storms ($S_{(trt +}$

$_{\text{storms}}$ AIC$_c$ - $S_{\text{(trt + storm hours)}}$ AIC$_c$ = 5.10; Table 5). In other words, storm duration was not as important as absolute number of storms in determining daily nest survival. In addition, the model including only additive effects of storm number and nest treatment was 7 times more likely than the model with an interaction between the effects of storm number and nest treatment, suggesting these covariates only had additive effects on daily nest survival.

Mean daily nest survival ranged from a low of 0.83 (angling without predation treatment at Perry's Monument 2000, 10 storms) to a high of 0.93 (control treatment at Perry's Monument 1999, 2 storms). Overall, mean daily survival for control nests (0.91; includes no-treatment nests) was higher than for angling without predation (0.87) and angling with predation (0.88) treatments. Including no-treatment nests as controls may have underestimated daily nest survival because no-treatment nests were, by definition, nests that failed soon after discovery (i.e., before we could assign them to a treatment). Implications of differences in daily survival are magnified when considering that smallmouth bass offspring typically require at least 2 weeks to develop into free-swimming larvae (for successful nests, mean = 13 d in Lake Erie), and parental care can last up to 43 d (Friesen 1998; Knotek and Orth 1998). When expanding daily survival rates to 20-d survival rates, nest survival rates were 0.09 to 0.25 for control nests and 0.02 to 0.1 for nests of either angling treatment (Figure 16).

DISCUSSION

Smallmouth bass nest success in the Bass Islands, Lake Erie, was lower than reported in many other systems, except for studies in the Great Lakes, because of frequent, powerful storms. Storms may destroy smallmouth bass nests by causing upwelling of cold water that kills developing offspring, but how temperature influences smallmouth bass nest success is not consistent. In the laboratory, transferring smallmouth bass embryos from 18ºC to 10ºC had no adverse affect (Webster 1948). But in field observations, fungus infected and killed smallmouth bass offspring when temperatures dropped below 18ºC (Knotek and Orth 1998). In addition, evidence from Lake Opeongo suggests that temperature declines greater than 2ºC may cause nest failures (G. B. Steinhart, unpublished data; Friesen 1998) and that smallmouth bass spawn in areas that experience higher temperatures than non-spawning sites (Rejwan et al. 1999). In contrast, many studies have concluded that storms and high flows flush offspring from nests (Goff 1986; Lukas and Orth 1995). In particular, a study in Long Point Bay, Lake Erie, documented that storms destroyed smallmouth bass nests when wind speeds were greater than 4.6 m/s (Goff 1986). We found that higher wind speeds were required to destroy smallmouth bass nests, but our smallmouth bass nests were in deeper water (average nest was in 3 m of water) than in Long Point Bay (average nest was in 1.6 m of water). Future work should focus on estimating water velocities that wash smallmouth bass embryos (both hatched and unhatched embryos) from nests on different substrates. Then, by using hydrodynamic equations, researchers can define wind speeds capable of destroying smallmouth bass nests in a variety of systems and water depths.

In Lake Erie, nest success was negatively related to angling, but not to nest predation. Catch-and-release of nest-guarding males also has been shown to reduce the probability of nest success (Philipp et al. 1997), but the mechanism has not been clearly defined. Some researchers have suggested that angling may cause males to abandon when the male returns and finds a smaller brood following nest predation (Kieffer et al. 1995; Suski et al. 2003). In Lake Erie, nest predators consumed more than 800 offspring every time a male smallmouth bass was caught-and-released (Steinhart et al. 2004). Despite these offspring losses, we found that nest predation during angling did not cause a reduction in smallmouth bass nest success in Lake Erie. Additional offspring losses may occur during recovery from angling-related physiological stress if nest-guarding fish are not able to adequately defend their nest (Kieffer et al. 1995; Schreer et al. 2001); thus, post-angling nest-predation also has been suggested. We have no evidence that brood predation occurred after the male returned to its nest in Lake Erie (Steinhart et al. 2004). Furthermore, in experimental brood reductions (25-75% of offspring removed) in Lake Erie, 10 of 11 males continued to guard their broods for at least 2 d (mean = 6 d, range 0 - 19 d) after brood reduction and, except for one nest that was abandoned within 1 d, all other nests were guarded until a storm occurred (G. B. Steinhart, unpublished data). However, experimental brood reductions in other lakes reduced male brood defense (Ridgway 1989; Suski et al. 2003) and nest success (Suski et al. 2003). For other fish species, brood reduction causes either no difference (Jennions and Polakow 2001) or an increase (Coleman et al. 1985) in brood abandonment. Different behavioral responses to brood size might be explained by probability of successful future reproduction and expected future fitness. In Lake Erie, owing to low adult survival, males behaving so as

to optimize their expected lifetime fitness almost always guarded their nests, regardless of brood size (Chapter 5). In other systems (e.g., those with high adult survival) optimal males abandon when their brood becomes too small (Chapter 5; Coleman et al. 1985; Suski et al. 2003).

Angling had a direct negative effect on smallmouth bass nest success. For both angling treatments, nest success and daily survival rate were reduced compared to control nests. Although we found no effect of the mean number of anglers present during our surveys on smallmouth bass nest success, anglers can reduce nest success (Philipp et al. 1997; Suski et al. 2002). Our estimate of angling pressure was from limited dates and assumed those anglers were targeting smallmouth bass. Our experimental angling may have overestimated nest abandonment due to angling because jaw-tagged males may have been more likely to abandon. In one study, however, mortality of jaw-tagged male smallmouth bass was the same as non-jaw tagged males (~10%) during nesting (MacCrimmon and Robbins 1979). Jaw tags also can reduce adult growth rates (Shetter 1967), but this should have had little effect during the short time nests were present after the angling treatment (maximum of 16 d).

Several explanations exist as to why angling may have reduced smallmouth bass nest success. First, angling can cause smallmouth bass mortality, but immediate (less than 1 h) and short-term (less than 72 h) mortalities are low (Dunmall et al. 2001), even when fish were subjected to repeated handling and extensive confinement in tournaments (0-11% mortality; Hartley and Moring 1995). Others have hypothesized that angling-related physiological stress causes angled parents to abandon. Indeed, as the number of times a male is caught increases, nest success decreases (Philipp et al. 1997). Because males

expend large amounts of energy on nest defense (Gillooly and Baylis 1999; Mackereth et al. 1999), physiological stress and energetic expenditures during catch-and-release angling may push smallmouth bass over a threshold where nest abandonment becomes the favorable choice to insure survival until the following spawning season. It is unlikely that males are assessing angling risk, abandoning, and then moving to a different area to spawn because smallmouth bass typically return to the same area to spawn year after year (Rejwan et al. 1997).

What remains to be determined is whether patterns in smallmouth bass nest success drives patterns in adult abundance. Many studies have failed to find a relationship between nest success or young-of-the-year abundance and ultimate adult abundance (Gillooly et al. 2000; Post et al. 1998; Serns 1984); however, many studies have suggested that warm temperatures promote high growth and survival of juvenile smallmouth bass and lead to increased recruitment to adulthood (Casselman et al. 2002; Post et al. 1998; Serns 1984; Shuter et al. 1980). But temperature also reduces offspring development time and, therefore, increases the probability that a nest is successful, so there are multiple explanations why warm temperatures increase smallmouth bass recruitment.

We conclude that storms had the greatest impact on smallmouth bass nest success in Lake Erie, but that angling also caused some males to abandon their nests. The effects of storms and angling were independent; that is, angled and control nests were affected by storms equally. While storms destroyed many smallmouth bass nests in the Bass Islands, storms might have little effect on smallmouth bass nest success in small lakes where storms are not as intense than large lakes. Although nest predators are extremely

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abundant in Lake Erie, nest predation had no effect on nest survival, possibly because

nest-guarding males in Lake Erie will continue to guard even very small broods. In lakes

where males are more prone to nest abandonment than in Lake Erie, nest predation may

influence nest survival if males chose to abandon nests after predators consume a portion

of the brood. While the effects of storms and nest predation on nest survival may depend

on the lake or population of interest, this study corroborates other research that

demonstrates that angling for nest-guarding bass reduces nest success.

Study site	Year(s)	N	% Success	Study
Nebish Lake, Wisconsin	1985	49	96%	(Raffetto et al. 1990)
Nebish Lake, Wisconsin	1983	45	93%	(Raffetto et al. 1990)
South Branch Lake, Maine	1972	26	88%	(Neves 1975)
Lake Erie, Ontario	1983	87	87%	(Goff 1986)
Nebish Lake, Wisconsin	1984	47	87%	(Raffetto et al. 1990)
Lake Huron, Ontario	1973	13	85%	(Hurley 1975)
Mississippi River, Ontario	1990-1995	452	84%	(Philipp et al. 1997)
Lake Opeongo, Ontario	1993	76	82%	(Friesen 1998)
Lake Opeongo, Ontario	1989	123	79%	(Friesen 1998)
Lake Opeongo, Ontario	1992	92	77%	(Friesen 1998)
Lake Opeongo, Ontario	1988	63	75%	(Friesen 1998)
South Branch Lake, Maine	1971	15	67%	(Neves 1975)
North Anna River, Virginia	1994	56	64%	(Knotek and Orth 1998)
St. Lawrence River, Ontario	1990-1995	1,864	58%	(Philipp et al. 1997)
Lake Michigan, Michigan	1954	20	55%	(Latta 1956)
Lake Michigan, Michigan	1955	28	54%	(Latta 1956)
Charleston Lake, Ontario	1990-1995	1,536	54%	(Philipp et al. 1997)
Lake Opeongo, Ontario	2001	36	50%	G. B. Steinhart, unpublished data
Lake Opeongo, Ontario	1991	72	47%	(Friesen 1998)
Tadenac Lake, Ontario	1966	20	45%	(Turner and MacCrimmon 1970)
Lake Opinicon, Ontario	1990-1995	1,376	44-63%	(Philipp et al. 1997)
North Anna River, Virginia	1992	105	43%	(Lukas and Orth 1995)
Lake Erie, Ohio	1999	54	41%	This study
Lake Erie, Ontario	1982	33	33%	(Goff 1986)
Lake Huron, Ontario	1974	40	33%	(Hurley 1975)
Lake Erie, Ohio	2001	30	23%	This study
Lake Erie, Ohio	2000	47	21%	This study

Table 4. Smallmouth bass nest success (shown in descending order of % of nests reaching the free-swimming, larval stage) for various lakes and rivers, including sample year(s), number of nests observed (N), percent nest success, and data source.

Model	Deviance	Number of parameters	AIC_c	$\Delta\,AIC_c$	Model weight (w_i)	Model likelihood
$S_{(trt\,+\,storms)}$	589.58	4	597.60	0.00	0.62	1.00
$S_{(storms)}$	596.82	2	600.83	3.22	0.12	0.20
$S_{(trt)}$	595.03	3	601.05	3.45	0.11	0.18
$S_{(trt\,\times\,storms)}$	589.36	6	601.42	3.81	0.09	0.15
$S_{(trt\,+\,storm\,hours)}$	594.67	4	602.70	5.10	0.05	0.08
$S_{(anglers)}$	603.42	2	607.42	9.82	0.00	0.01
$S_{(.)}$	606.94	1	608.94	11.34	0.00	0.00
$S_{(site)}$	606.84	3	612.86	15.26	0.00	0.00

Table 5. Summary of model results for smallmouth bass nest survival in Lake Erie, Ohio, USA, 1999-2001. Models are ranked by ascending $\Delta\,AIC_c$. Factors in the models include storms, nest treatment (trt; control, angling, angling plus nest predation), average number of anglers seen, and site.

Figure 11. Map of locations for studying smallmouth bass nest survival in the Bass Islands, Lake Erie, Ohio, USA. Arcs indicate the approximate wind ranges included when calculating number of storms at each site: Perry's Monument (PM, 60-180˚); Sonny's Marina (SO, 210-280˚); Gray's Bay (GB, 290-315˚ and 10-60˚). Continuous wind data were from NOAA weather station SBIO1, located on South Bass Island.
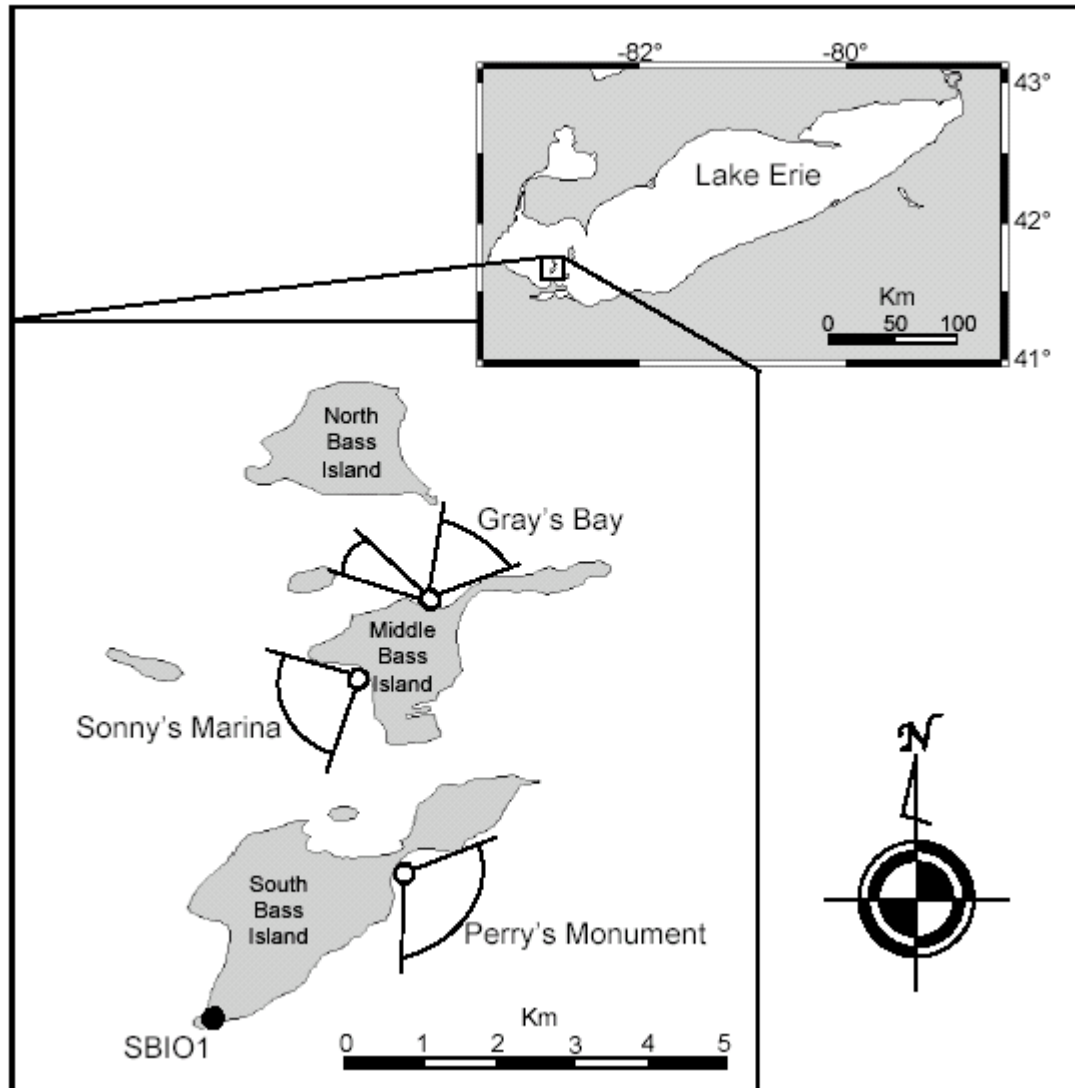
Figure 11.

Figure 12. Smallmouth bass percent nest success in the Bass Islands, Lake Erie, Ohio,

USA, during 1999-2001 for A) Perry's Monument, B) Sonny's Marina, C) Gray's Bay,

and D) all sites combined. Successful nests were those nests producing free-swimming

larvae. Nests were assigned to either a control treatment (only observation), angling

without predation (guarding male smallmouth bass temporarily removed by angling and

nest guarded during his absence), or angling with predation (guarding male smallmouth

bass temporarily removed by angling and predators allowed to enter unguarded nest).

For angling with predation treatments, nests lost more than 800 offspring to nest

predators (Steinhart et al. 2004).
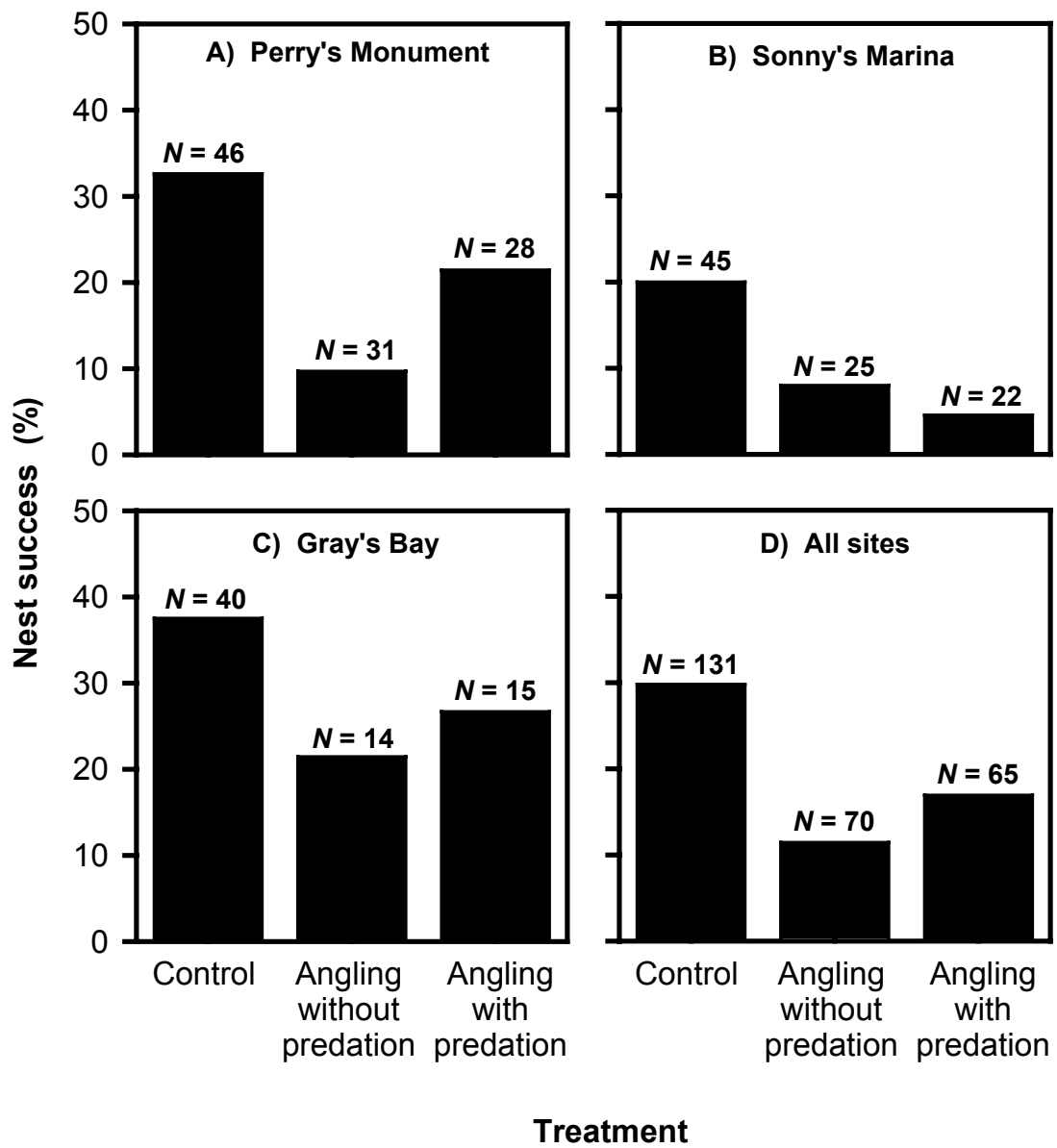
Figure 12.

Figure 13. Number of artificial eggs remaining in simulated smallmouth bass nests after exposure to different numbers of consecutive hours with wind speeds $\geq$ 7 m/s. Nests were seeded with 50 eggs, then placed at 3-m depth and retrieved after 24 h. A two-dimensional Kolomogorov-Smirnov (2KDS) test found a significant threshold at 1.8 h. Therefore, we defined a storm capable of destroying smallmouth bass nests as any 2 consecutive hours with wind speeds $\geq$ 7 m/s.
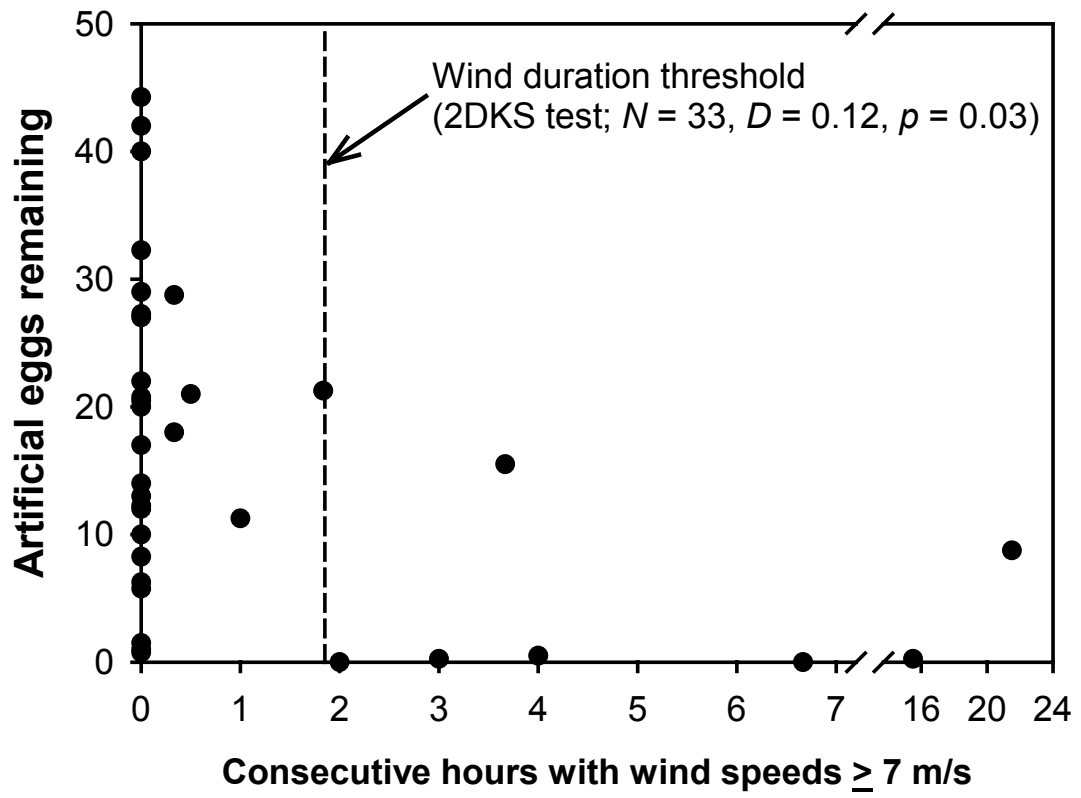
Figure 13.

Figure 14. Smallmouth bass nest success as a function of number of storms occurring at

different sampling sites during 1999-2001 spawning seasons in the Bass Islands, Lake

Erie, USA. Successful nests were defined as any nest producing free-swimming larvae.

Nest success data were arcsine-square root transformed to calculate the regression

equation.
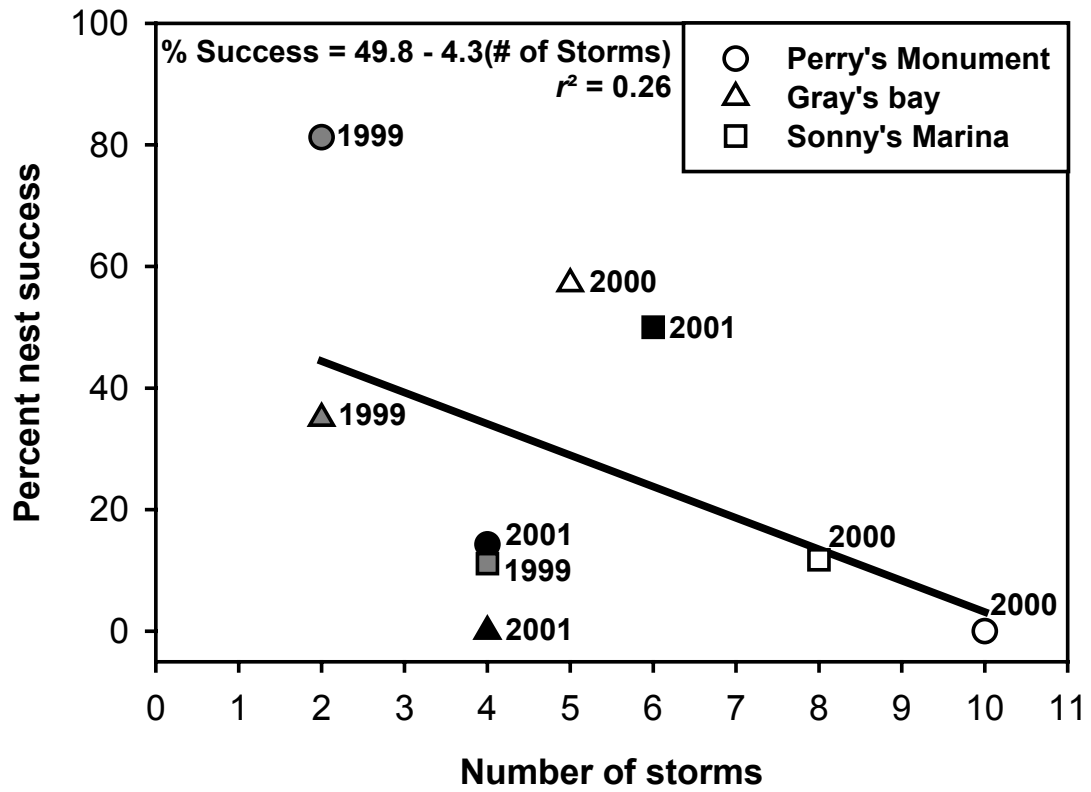
Figure 14.

Figure 15. Number of days with storms in the Bass Islands, Lake Erie, Ohio, USA,

during 1982-2001 smallmouth bass spawning seasons (1 May to 30 June). All days with

at least 2 h of consecutive wind speeds $\geq$ 7 m/s (from any direction) were counted as

storm days. The line indicates the 20-y average and numbers indicate the total number of

storms during the 1999-2001 spawning seasons.
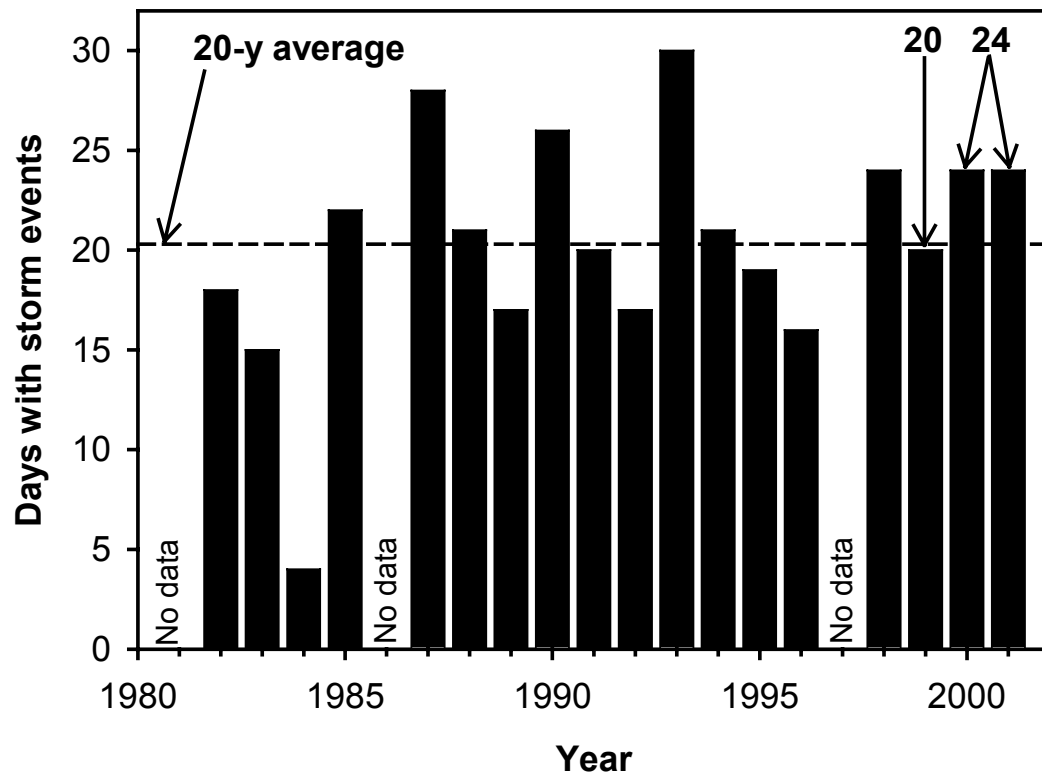
Figure 15.

Figure 16. Probability a smallmouth bass nest survives 20 d in the Bass Islands, Lake

Erie, Ohio, USA. Survival probabilities for each site and nest treatment are from the

best-fit model calculated in the program MARK ($S_{(trt + storms + anglers)}$), raised to the power of

20 to adjust daily survival to typical duration of parental care.
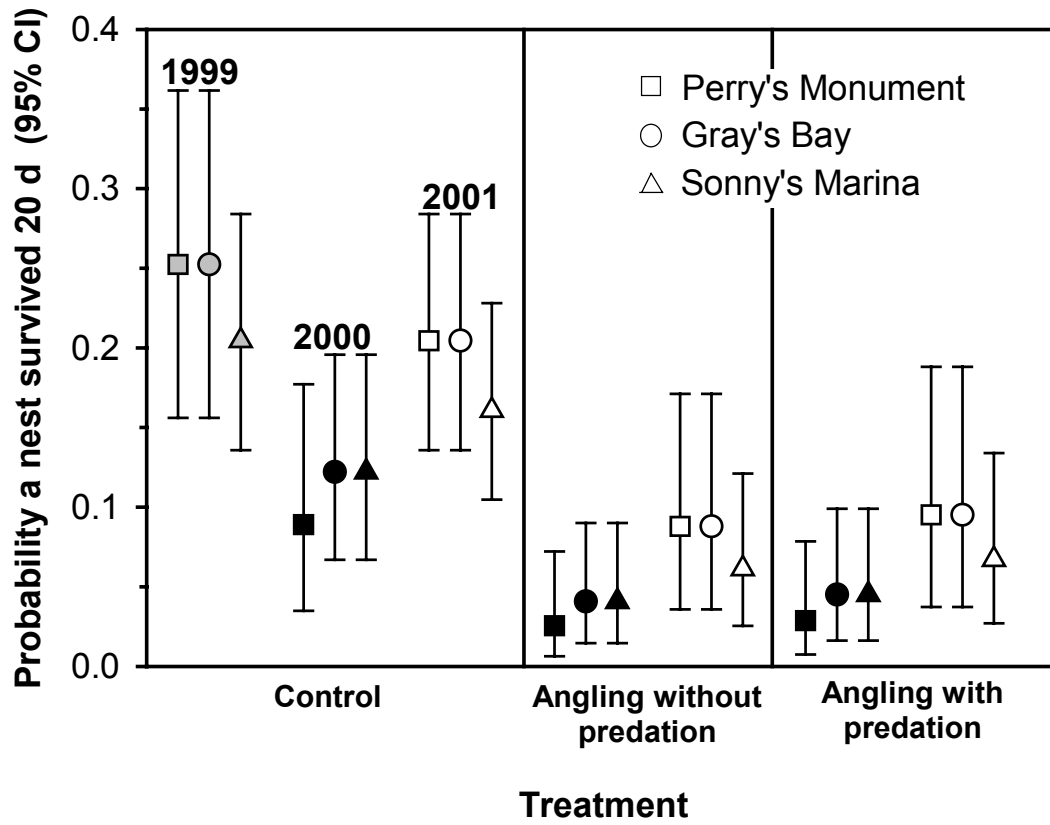
Figure 16.

CHAPTER 5

SHOULD I STAY OR SHOULD I GO: FACTORS DETERMINING VARIATION

IN OPTIMAL PARENTAL CARE DECISIONS OF A NEST-GUARDING FISH

ABSTRACT

Parental care reduces future reproductive success; thus, parents must balance the

value of guarding offspring versus their future fitness if they abandon their offspring. We

explored how environmental conditions affected optimal reproductive behavior for a fish

in which males provide parental care (smallmouth bass, *Micropterus dolomieu*). Using a

stochastic dynamic programming model, we determined how parent age, days of care

already provided, and brood size affected optimal brood abandonment decisions. We

compared optimal decisions for males from two lakes with different demographics and

environmental conditions. Next, we explored how adult and offspring survival,

probability of nest success, angling pressure, and parental care costs affected optimal

decisions. In general, when variables were examined independently, optimal decisions

followed parental investment theory: nests nearing independence were less likely to be

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abandoned than young nests and as adult annual survival and offspring daily survival decreased, males were less likely to abandon than when survival was high. Increased parental care costs led males to abandon larger broods than when costs were low. The addition of an exotic nest predator, which both decreased offspring survival and increased parental care costs, caused males to abandon more frequently than when the nest predator was absent. Given the suite of conditions in each lake, however, Lake Opeongo males displayed a larger behavioral response to changes in model parameters than males in Lake Erie, due to differences in adult survival and male fecundity between the lakes. Adult annual survival, including reduced annual survival from providing care, was the most significant factor in determining optimal parental care decisions for smallmouth bass. We concluded that age-dependent parameters (e.g., adult survival or cost of providing care) that affected current and future fitness differently, were more important in determining parental behavior than variables that were age independent (e.g., offspring survival or probability of nest success). Variations in optimal decisions, and subsequent affects on reproductive success, may have important consequences for understanding population dynamics.

INTRODUCTION

Providing parental care is costly and, therefore, invokes tradeoffs among components of fitness (Sargent 1997; Stearns 1992). Trade-offs in parental care for birds have been considered as a balance between offspring number with offspring survival, resulting in an optimal clutch size (Lack 1947). Lack's (1947) ideas, however, only dealt with trade-offs

within a breeding season. Williams (1966) elaborated on Lack's idea, but proposed that the more important tradeoff is between current and future fitness. That is, organisms must balance the value of their current brood against the fitness gained from their future reproductive efforts in order to maximize their lifetime reproductive fitness. Thus, an individual investing too heavily in its current brood may sacrifice future reproductive gains (Williams 1966).

The risks and costs of parental care affect the balance between current and future fitness, and vary depending on reproductive behavior and by environment. When faced with increased risk of detection and death by visiting their brood, parents in high predation-risk environments provide less care than parents in low predation-risk environments, especially in populations where adult survival is already low (Ghalambor and Martin 2000; Ghalambor and Martin 2002; Mallory et al. 1998). In species where extrapair fertilizations occur, low or uncertain relatedness also may cause parents to provide less care than when relatedness and, thus, fitness are high (Mauck et al. 1999; Östlund-Nilsson 2002). Energetic expenditures on parental care can reduce adult survival, growth, and future fitness (Balshine-Earn 1995; Sabat 1994; Smith and Wootton 1994; Townshend and Wootton 1985). Consequently, when the energetic cost of parental care increases or food availability decreases, parents are more likely to abandon their current reproductive effort (Townshend and Wootton 1985). However, when parents are caring for a brood that is either large or near independence, they are more likely to accept the cost of providing care, and even provide more intense care, than when their brood is small or young (Coleman and Fischer 1991; Coleman et al. 1985; Skolbekken and Utne-Palm 2001).

We chose to explore reproductive decisions using smallmouth bass, *Micropterus dolomieu*, as a model organism. Male smallmouth bass provide parental care for their offspring by fanning the nest to provide oxygen and defending the nest from potential predators. Providing care is energetically costly for smallmouth bass due to direct energetic expenditures on nest defense (Gillooly and Baylis 1999; Mackereth et al. 1999), and indirectly because providing care may limit foraging opportunities (Hinch and Collins 1991). Although prematurely abandoning a nest will result in total brood failure, it does allow smallmouth bass to spend more time growing during spring and summer. Indeed, spawning smallmouth bass experience lower annual survival than non-spawning individuals (Ridgway 1986; Wiegmann et al. 1997). In addition, forgoing reproduction for increased growth should result in larger size at next reproduction, which is important because large male smallmouth bass tend to receive more eggs than small males (Mackereth et al. 1999; Wiegmann et al. 1992). Other factors that might influence smallmouth bass nest abandonment decisions include reproductive lifespan, probability that a nest will be destroyed by stochastic events, and offspring daily survival.

To understand how this complex suite of interactions affects reproductive decisions, we used dynamic programming to simulate optimal parental decisions for individual smallmouth bass in two lakes that differed in smallmouth bass growth, survival, cost of care, and probability of nest success. We explored how parental behavior (i.e., optimal decisions) and sensitivity of behavior to different environmental conditions (e.g., adult or offspring survival, probability of nest success, cost of parental care) varied between lakes. In one of these lakes, the round goby (*Neogobious melanostomus*), a recently arrived exotic nest-predator (Jude et al. 1992), poses a new selective pressure on

smallmouth bass reproductive behavior; hence, we examined how this novel nest predator might change smallmouth bass reproductive behavior in both lakes. Dynamic programming is ideally suited for addressing these types of questions because it finds the behaviors, based on an individual's current state, that optimize lifetime reproductive fitness (Mangel and Clark 1988). We hypothesized that when factors that increased the probability of future reproductive success (i.e., adult survival rate, probability of nest success, and offspring survival) were high, parents would be more likely abandon their current brood than when those factors were low. In addition, when costs or risks of providing care decreased future reproductive success (i.e., high energetic cost of care and high probability of death while providing care), we predicted that parents would abandon large broods that they would normally guard if the costs and risks of care were low. Therefore, owing to lake-specific cost of care (Chapter 3) and adult growth and survival, we expected that the sensitivity of behavioral responses to different factors would vary between lakes.

METHODS

Smallmouth Bass Reproductive Ecology

Male smallmouth bass are the sole providers of parental care for their developing offspring. In spring, as water temperatures approach 15ºC, male smallmouth bass clear an area for a nest, usually over cobble. After the female deposits her eggs, the male remains to guard developing offspring as the young pass through several developmental

stages. As embryos, smallmouth bass are non-mobile and, therefore, extremely vulnerable to nest predators. During this stage, the male chases potential predators and fans the nest to provide oxygen and clear the nest of debris (Hinch and Collins 1991; Ridgway 1986). Even after the offspring develop into free-swimming larvae, males provide constant care until larvae metamorphose into juveniles. Total duration of care ranges from 17 to 43 d (Friesen 1998; Knotek and Orth 1998). Providing care causes nesting males to lose energy and weight (Gillooly and Baylis 1999; Mackereth et al. 1999). As with many fishes, providing care can reduce future fecundity (Sabat 1994) and decrease parental survival (Ridgway 1986).

Study Sites

We studied nesting smallmouth bass in Lake Erie, Ohio, USA, and in Lake Opeongo, Ontario, Canada, to estimate parameters necessary for our model. In mesotrophic Lake Erie, we surveyed nesting smallmouth bass in the Bass Islands, located in the western basin of Lake Erie (41° 40' N, 82° 50' W), during May and June 1999-2001. In oligotrophic Lake Opeongo (45° 42' N, 78° 22' W, Algonquin Park, Ontario), we observed nesting smallmouth bass during June 2001, and used published data and communication with researchers familiar with Lake Opeongo smallmouth bass to obtain appropriate parameter values.

Lake Erie and Lake Opeongo were chosen as contrasting systems because they differ in ways that affect smallmouth bass life history and reproductive behavior. Smallmouth bass are native to Lake Erie, but were introduced into Lake Opeongo in the early 1920's,

rapidly establishing a self-sustaining population (Ridgway 1986; Shuter et al. 1987).

Angling and harvesting of spawning smallmouth bass has been allowed in Lake Erie

prior to 2004, but fishing during spawning is prohibited in Lake Opeongo. In Lake Erie,

which has a more productive and longer growing season than Lake Opeongo, smallmouth

bass grow faster than individuals from other lakes (Doan 1940), including Lake Opeongo.

As a result of differences in fishing pressure and life-history characteristics (e.g., growth

rate), adult survival is generally lower in Lake Erie than in Lake Opeongo (R. Knight,

Ohio Division of Wildlife, Columbus, Ohio, personal communication; Ridgway 1986;

Shuter et al. 1987). Lakes Erie and Opeongo differ in nest-predator densities, with

smallmouth bass progeny experiencing a higher risk of nest predation in Lake Erie than

in Lake Opeongo (Steinhart et al. 2004). Nest predators are extremely abundant in Lake

Erie since the invasion of the round goby, which was first seen in Lake Erie in 1993 and

reached high densities (sometimes exceeding 100 individuals/m^2) in the Bass Islands in

1998 (M. Thomas, Ohio State University Stone Laboratory, Put-In-Bay, Ohio, personal

communication; Jude et al. 1992). Storms, by creating waves, depositing sediment, and

causing temperature fluctuations, are significant sources of nest failures in both lakes

(Friesen 1998; Goff 1986), but Lake Erie, owing to its large fetch, is exposed to more

violent storms than Lake Opeongo (G. B. Steinhart, unpublished data). Thus, overall nest

success is lower in Lake Erie than in Lake Opeongo (G. B. Steinhart, unpublished data).

Model summary

We built and explored a stochastic dynamic programming (SDP) model that predicted optimal behavior of nest-guarding smallmouth bass. The model is based on the assumption that guarding males will behave such that they maximize their lifetime fitness, herein defined as the number of offspring surviving until metamorphosis. Using backward iteration (Mangel and Clark 1988), the SDP model predicted whether males should abandon or guard broods based on a male's state: his age, days of care already provided, and current brood size. In daily time steps, the model calculated expected offspring production for the remainder of a male's lifetime (i.e., expected future fitness) when he guarded or abandoned his current brood and, then, males selected the behavior that maximized their lifetime fitness. Abandonment caused males to gain no fitness for that year. Thus, for abandonment to be an advantageous behavior, there must be some cost of providing care. In our model, the direct costs of care for guarding males were reductions in survival and growth (resulting in lower future fecundity). The indirect cost of care was an increased probability of being captured and killed by an angler; non-nesting males were not vulnerable to angling during the spawning season. During each day, nest-guarding males lost a fixed proportion of offspring to natural mortality, had some probability of being caught and, if caught, kept (resulting in death of the brood and the male) or released (resulting in brood reduction by nest predators). On each day, nests had a probability of being destroyed by a storm. If parental care was successfully completed, males added their current brood to their lifetime fitness and then had to survive until the next year before spawning again.

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Our base models simulated behavior of male smallmouth bass from Lake Erie (before the invasion of round gobies) and Lake Opeongo. We used these models to explore how male state (age, days of care already provided, and brood size) affected optimal decisions and expected lifetime fitness. Next, we tested model sensitivity to several different parameters to determine which factors had the most influence on optimal behavior and to understand how differences in the suite of conditions that characterize Lakes Erie and Opeongo (angling, system productivity, probability of nest success, etc.) interacted to affect optimal behavior. Because we suspected that the most influential difference between the lakes was the presence of round gobies and its interactions with angling effects, we compared optimal decisions in both lakes in simulations with and without round gobies. As a final test of which parameters were most important in determining optimal nest abandonment behavior, we changed parameters in Lake Erie simulations in a step-wise fashion in an attempt to make Lake Erie smallmouth bass behave similarly to smallmouth bass in Lake Opeongo.

Model derivation

On each simulation day d ($d = 1, 2,…D$-1) of every spawning season y ($y = 1, 2,…Y$), a male smallmouth bass first made the decision to guard or abandon his brood, based on expected probabilities of future events influencing current and future fitness. Next, males lost offspring to natural mortality and, then, had some probability of being caught by an angler, and, finally, had some probability of losing all of its offspring to a storm. At the start of the last day D of any season, offspring left the nest and males received fitness

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equal to their brood size (B) on that day; males did not make a decision or experience

reductions in offspring on day D. A male's behavioral decision was made based on his

state: his current brood size (B), days of care provided (d), and his age (y). We used male

age (in years) as a state variable, but age was really a surrogate for male size (total length

in mm, TL). Male TL was estimated from length-at-age relationships specific to either

Lake Erie or Lake Opeongo (Table 6). In turn, male size is positively related to the

number of eggs it receives (Mackereth et al. 1999; Wiegmann et al. 1992). We calculated

starting brood size on day $d = 1$ (B_0) for males of different ages from a TL-brood size

relationship:

$$B_0 = a \cdot TL + b \tag{1}$$

where the coefficients a and b varied by lake (Table 7). We considered brood size in 100

offspring increments when calculating brood size at the start of the day (i.e., brood size

rounded to nearest 100), and used linear interpolation for values between these

increments when calculating expected future fitness.

A modeled male began day d with brood size B, and made its decision to guard or

abandon based on its expected future fitness, which was a combination of several

probabilistic events. Many smallmouth bass offspring die from disease, predation, and

anoxia (Friesen 1998; Knotek and Orth 1998), but daily survival varies with offspring

age, so we included separate embryonic ($d = 1$-13) and larval ($d = 14$-20) daily survival

rates (DSR; Table 7). Next, guarding males had a fixed, daily probability of capture by

an angler (p_A; Table 7). In simulations in which smallmouth bass harvest was allowed,

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males were released with a size-dependent probability (p_R), because anglers often are more likely to release small fish than large fish:

$$p_R = 1 - i \cdot e^{j \cdot TL} \qquad (2)$$

where coefficients i and j varied by lake (Table 7). Where harvest was prohibited (i.e., the base simulation in Lake Opeongo), $p_R = 0.99$. When a male was caught and kept, the entire brood failed. If caught and released when round gobies were present, males lost 500 offspring to nest predators in addition to offspring daily mortality. Thus, a male that guarded his brood and was not caught on day d began with brood size B' on day $d+1$:

$$B' = B \cdot DSR \qquad (3)$$

But a male that guarded his brood and was caught and released on day d began with brood size B'' on day $d+1$

$$B'' = \begin{cases} B'-500, \text{ with round gobies} \\ B', \text{ without round gobies} \end{cases} \qquad (4)$$

In addition, because storms can destroy many smallmouth bass nests (Friesen 1998; Goff 1986), we included the daily probability a nest was destroyed by a storm (p_S; Table 7). Destruction of a nest did not affect the male, but did result in total brood failure (B' and $B'' = 0$).

Our model incorporated parental care costs because providing care causes male

smallmouth bass to lose weight and energy (G. B. Steinhart, unpublished data; Mackereth

et al. 1999). Our model used male length instead of weight or energetic content, so we

modeled care costs as a decline in *TL* (Δ *TL*; Table 7) for each day of care, resulting in a

smaller male size at the beginning of the next spawning season. Because starting brood

size B_0 was a function of *TL* (equation 2), a new starting brood size B_0' for year *y*+1was

calculated based on whether a male guarded or abandoned on day *d* in year *y*:

$$B_0' = \begin{cases} a \cdot TL - \Delta TL \cdot d + b, \text{if male guards} \\ a \cdot TL - \Delta TL \cdot (d-1) + b, \text{if male abandons} \end{cases} \tag{5}$$

with *a* and *b* defined as for equation 1. In addition, providing care reduces annual

survival rate; nesting males experience lower annual survival (*ASR*) than non-nesting

males (E. S. Dunlop, unpublished data; Ridgway 1986). In our model, adult *ASR* was

age-dependent, decreasing with male age, and we included a daily reduction of annual

survival rate (Δ *ASR*; Table 6) for males providing care.

So, the expected future fitness for a male of age *y* with brood of size *B* on day *d*,

F(B,d,y), is made up of the probabilities of different events multiplied by the expected

fitness value if each of those events occurred. Therefore, the expected fitness values (*V*)

varied based on male decisions and probabilistic events. For a male making the decision

to guard on day *d* and then not encountering a storm or an angler that day, the expected

fitness value is:

$$V_0 = F(B', d+1, y) \tag{6}$$

While the expected fitness value of deciding to guard on day d and then encountering a storm, assuming the male is not caught and kept by an angler, is its probability of surviving to the next nesting season and its expected fitness from that point on:

$$V_S = (ASR - \Delta ASR \cdot d)F(B_0', 1, y+1) \tag{7}$$

The expected fitness value of deciding to guard the nest when the male is caught and released by an angler, given that the brood is not destroyed by a storm, is:

$$V_{A,R} = F(B'', d+1, y) \tag{8}$$

If a male is caught and kept by an angler, regardless of whether his brood is destroyed by a storm, its expected fitness value is 0.

If a male chose to abandon its nest, the expected fitness value is determined by its probability of surviving to the next nesting season and its expected fitness from that point on:

$$V_{ab} = (ASR - \Delta ASR(d-1))F(B_0', 1, y+1) \tag{9}$$

These expected fitness values (equations 7-10) result in the expected future fitness on day d to be:

$$F(B,d,y) = \max \begin{cases} \text{Guard} : (1-p_S)\left[(1-p_A)V_0 + p_A p_R V_{A,R}\right] + p_S V_S \\ \text{Abandon} : V_{ab} \end{cases} \qquad (10)$$

On the last day D of each nesting season $y < Y$, offspring left the nest, males received fitness equal to their brood size, and expected future fitness is:

$$F(B,D,y) = B + (ASR - \Delta ASR \cdot D)F(B_0',1,y+1) \qquad (11)$$

On the last day D of the last spawning season Y, expected future fitness is:

$$F(B,D,Y) = B \qquad (12)$$

Parameterization of simulations

Our simulation assumed a minimum of 20 days of care was required to raise offspring to independence and that males could spawn once each year. Duration of parental care within a season is variable and temperature dependent (Friesen 1998). It is generally assumed that parental care may end, and the offspring survive, once offspring metamorphose into juveniles (Ridgway 1986), requiring anywhere from 14 to 43 days (Friesen 1998; Knotek and Orth 1998). Our simulations assumed that developing

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offspring would metamorphose (i.e., reach the minimum age at which they could survive without care) at the start of day 21. Male smallmouth bass begin spawning at age 3 in Lake Erie and age 4 in Lake Opeongo (G. B. Steinhart and E. S. Dunlop, unpublished data; Ridgway 1986); however, because only a few males reproduce at these ages, most comparisons were made with males spawning at age 4 (Lake Erie) and age 5 (Lake Opeongo). Males over age 13 are rarely seen in either lake, but to avoid behavioral effects of an artificially constrained lifespan, the model allowed fish to spawn for 20 years ($Y = 20$), reaching age 23 in Lake Erie and age 24 in Lake Opeongo, in the very unlikely event that they survived that long.

For males of a given age, length (TL) was estimated from catch-at-age data. Males in Lake Erie were larger at any given age than males in Lake Opeongo (Table 6). We assumed males reached their maximum TL at age 15 y in both lakes, thereafter maintaining a constant length at older ages. For the base simulations, brood size on day 1 (B_0), probability of release if caught (p_R), adult annual survival rate (ASR), and change in annual survival by providing care (ΔASR) were related to age-specific TL (Tables 6 and 7). Daily probability that an angler caught a guarding male, p_A, for base simulations was 0.05 in Lake Erie and 0.01 in Lake Opeongo. We calculated age-specific p_R (equation 2) that, when weighted by abundance of smallmouth bass of all ages in Lake Erie, yielded a mean release probability of 0.2, approximating mean release rate from Lake Erie creel surveys (R. Knight, Ohio Division of Wildlife, unpublished data). When simulating no-fishing conditions (the base condition in Lake Opeongo), p_R was 0.99. Base offspring daily survival rate (DSR) was 0.9 for embryos ($d = 1\text{-}13$) and 0.92 for larvae ($d = 14\text{-}20$),

based on values from Lake Opeongo and other systems (Friesen 1998; Knotek and Orth 1998).

To calculate the daily probability that a nest was destroyed by a storm, p_S, we used Mayfield estimation (Mayfield 1961) on data from smallmouth bass nests monitored *in situ* in Lakes Erie and Opeongo (G. B. Steinhart, unpublished data). Base p_S values were 0.065 in Lake Erie and 0.015 in Lake Opeongo (Table 7).

We estimated parental care costs (Δ *TL* and Δ *ASR*) from empirically measured changes in wet weight (converted to change in *TL*) in Lake Erie, with round gobies present, and from changes in wet weight and annual survival in Lake Opeongo (G. B. Steinhart and E. S. Dunlop unpublished data; Ridgway 1986). Activity level of nest-guarding males in Lake Erie, with round gobies present, was about 2.5 times higher than activity levels in Lake Opeongo where round gobies were not present (Chapter 3). Therefore, we assumed that when round gobies were absent the cost of care would be only 40% (i.e., 1/2.5) the cost when round gobies were present. In Lake Erie, we measured Δ *TL* as 2 mm/day of care when round gobies were present and adjusted Δ *TL* to 0.8 mm/day of care without round gobies. In Lake Opeongo, we measured Δ *TL* as 0.5 mm/day of care when round gobies were absent. Change in annual survival, Δ *ASR*, varied by male age and was based on annual survival differences between nesting and non-nesting males in Lake Opeongo (Table 6; Ridgway 1986; E. S. Dunlop, unpublished data). We arrived at Lake Erie Δ *ASR* by first using the Δ *ASR* from a similar length smallmouth bass in Lake Opeongo then, because high growth rates in Lake Erie likely reduce the effect of care on annual survival compared to Lake Opeongo, we reduced Δ

ASR values by half. For all simulations, *ASR* could not drop below 0.01 after adjustments

for parental care.

Model Simulations

   After running base simulations for Lakes Erie and Opeongo with parameters as

defined above, we ran a series of simulations to understand how various model

parameters affected smallmouth bass reproductive decisions. For these simulations, we

changed only one parameter at a time, keeping other conditions as described for the base

simulations. First, we looked at parameters that affected the fitness value of broods

within a spawning season. In each lake, we varied: 1) daily probability that a nest was

destroyed by a storm (p_S) by multiplying the base values by 0.5 and 2, and 2) offspring

daily survival rate (*DSR*) by $\pm$ 0.05 in each lake. We then tested the effects of changing

adult survival within the spawning season by varying the probability that a male was

caught from its nest while guarding (p_A = 0.01, 0.05, 0.1). Because the base model in

Lake Opeongo assumed that 99% of males caught by anglers were released (p_R=0.99),

when we tested the effect of angling-related adult survival during the spawning season in

Lake Opeongo, we simulated that anglers would keep some smallmouth bass. Therefore,

we assumed that anglers in Lake Opeongo kept smallmouth bass with p_R calculated from

equation 2, with parameters i = 0.01 and j = 0.009. These parameter values resulted in a

mean p_R similar to Lake Erie. Next, we examined the effects of varying adult annual

survival between spawning seasons by varying *ASR* by $\pm$ 0.1. Finally, we examined how

the cost of parental care, which affected both ΔTL and ΔASR, influenced optimal

abandonment decisions by running simulations with no care costs and double care costs in each lake.

Next, we investigated how round gobies might affect smallmouth bass nest guarding behavior in both lakes. Although round gobies are not present in Lake Opeongo, they have invaded Lake Erie and they will likely spread to inland lakes with characteristics more similar to Lake Opeongo than Lake Erie. When including round gobies in our simulations, we assumed round gobies consumed 500 offspring every time a male was caught and released by an angler (Steinhart et al. 2004). In addition, we modified the cost of parental care when round gobies were present, because round gobies increased energetic losses for nest guarding males in Lake Erie (G. B. Steinhart, unpublished data). For Lake Erie, we used the daily change in male wet weight while guarding when round gobies were present and converted it to Δ TL (2 mm/day of care). Again, because activity level of nest guarding males in Lake Erie was about 2.5 times higher than standard metabolism when round gobies were present (G. B. Steinhart, unpublished data), we assumed Δ ASR would be 2.5 times higher than in the base simulation: 0.01 for age 3, 0.019 for age 4, and 0.013 for males age 5 and older. Similarly, to simulate round goby presence in Lake Opeongo, we multiplied Lake Opeongo Δ TL and Δ ASR values by 2.5.

Finally, once we observed the base results from each lake, we changed parameters to try to force male smallmouth bass in Lake Erie to behave as male smallmouth bass in Lake Opeongo. Our objective was to determine which parameters were most important in defining underlying differences in parental decisions in the two lakes. We began with the base simulation in Lake Erie and then changed model parameters and examined their effects on parental behavior. To the base Lake Erie simulation, we individually added

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Lake Opeongo values for 1) angling (both p_A and p_R), 2) *ASR*, 3) p_S, 4) Δ *TL* and 5) Δ

ASR. Then, in a step-wise fashion, we ran simulations in Lake Erie with combinations of

these parameter values from Lake Opeongo until we determined the minimum set of

parameters that produced optimal behaviors in Lake Erie that were most similar to

optimal behaviors in Lake Opeongo.

RESULTS

Male Age

Older males were less likely to abandon their brood than young males in both lakes

(Figure 17).   In Lake Erie, males age 3-5 abandoned their nests only when their broods

became extremely small, but in Lake Opeongo, males abandoned their broods after only

slight reductions in brood size. In fact, our model predicted that an age 4 male in Lake

Opeongo would always choose abandonment on day 1, but males age 5 and 6, behaving

optimally, would not abandon on day 1 unless their broods reached 65% and 30% of

starting brood size. In addition, as days of care provided increased, optimal male

smallmouth bass were less likely to abandon their broods, even when broods were very

small, than early in parental care (Figure 17).

Optimal behavior when varying in-season parameters p_S and *DSR*

Reduction in daily probability of nest destruction by storms caused little difference in

optimal male behavior (Figure 18). It is important to consider that with a minimum

brood size increment of 100 offspring in our model, the lowest positive percent of offspring remaining in our models were 3% for an age 4 male in Lake Erie and 9% for an age 5 male in Lake Opeongo. With these levels of remaining brood size, abandonment might actually occur anywhere from 1 offspring to 3% of offspring remaining in Lake Erie and 9% of offspring remaining in Lake Opeongo. Daily probability of nest destruction by storms did have a large effect on expected lifetime fitness in Lake Erie. Under base probability of nest destruction, optimally behaving males had an expected future lifetime fitness of 205 offspring in Lake Erie and 148 offspring in Lake Opeongo but, when p_S was halved, expected future lifetime fitness dropped to 51 offspring in Lake Erie and 120 offspring in Lake Opeongo.

Changing offspring daily survival rate caused small changes in optimal behaviors for males in Lake Opeongo but not consistent changes in Lake Erie (Figure 18). With increased offspring daily survival rate in Lake Opeongo, optimal males abandoned broods that were normally guarded under base offspring daily survival. Increased offspring daily survival rate increased expected future lifetime fitness in both Lake Erie (from 205 to 600 offspring) and Lake Opeongo (from 148 to 426 offspring).

Optimal behavior when varying adult survival via p_A and *ASR*

In Lake Erie, decreased probability that a male was angled from its nest caused optimal males to guard nests they normally would have abandoned (Figure 19). Although the difference appeared small, this may have been because males in Lake Erie were already predisposed to guarding small broods. In Lake Opeongo, however,

probability of being angled had no effect on behavior. In both lakes, there was relatively little change in expected future lifetime fitness when p_A was increased: 167, 205, and 245 offspring in Lake Erie and 115, 130, and145 offspring in Lake Opeongo for p_A = 0.01, 0.05, and 0.1, respectively.

Changing adult annual survival rate by ± 0.1 led to changes in optimal male behavior (Figure 19). Optimal males in Lake Opeongo abandoned larger broods when adult annual survival was increased than when adult annual survival was reduced. The same pattern was true for Lake Erie, but the change in brood size when males would abandon was small. It was somewhat surprising that increased adult annual survival increased the abandonment threshold in both Lake Opeongo and Lake Erie, but indirectly increasing adult survival by decreasing the probability of being angled led to the opposite effect in Lake Erie and no change in Lake Opeongo (Figure 19). Increasing adult annual survival increased expected future lifetime fitness from 205 to 245 offspring in Lake Erie and 148 to 204 offspring in Lake Opeongo.

Optimal behavior and cost of parental care

Removing all costs of parental care caused optimal male smallmouth bass to always guard their broods in Lake Opeongo (Figure 20). In Lake Erie, where parental care costs were lower than in Lake Opeongo, removing the energetic costs of parental care (Δ *TL* and Δ *ASR*) caused optimal males to guard some smaller broods that they normally would have abandoned. But, because the indirect cost of care (i.e., the risk of being caught and kept while defending the nest) was greater in Lake Erie than in Lake Opeongo, optimal

males would still abandon very small broods in Lake Erie. Because of different risks of being caught and kept and different base cost of care, changing the cost of care had a larger effect on expected lifetime fitness of optimal males in Lake Opeongo (309 expected future offspring with no cost, 148 expected future offspring with base cost, and 104 expected future offspring with double cost) than in Lake Erie (219 expected future offspring with no cost, 205 expected future offspring with base cost, and 192 expected future offspring with double cost).

Optimal behavior with nest predators

Including nest depredating round gobies in our simulations caused optimal males to abandon their nests with more offspring remaining than if round gobies were absent (Figure 21). Although round gobies indirectly decreased offspring survival by consuming offspring when males were angled from their nests, this result was opposite to the effect of decreasing offspring survival directly. Differences in parental behavior were larger in Lake Opeongo than in Lake Erie, most likely because the cost of parental care was higher in Lake Opeongo than Lake Erie, especially when round gobies were present. In addition to increasing the abandonment threshold, round gobies also reduced expected future lifetime fitness for optimal males by 54 offspring in Lake Erie and 53 offspring in Lake Opeongo.

Forcing optimal males in Lake Erie to behave as optimal males in Lake Opeongo

When we examined how changing single model parameter values affected optimal

male behavior in Lake Erie, we found that including Lake Opeongo p_A and p_R values

caused optimal males in Lake Erie to always guard their broods. In fact, by reducing the

risk of being caught and kept in Lake Erie, optimal males always guarded even when we

added one or more of the following parameter values from Lake Opeongo: adult annual

survival, daily probability of a nest being destroyed by a storm, and effect on male size

for providing care. Adding only adult survival, daily probability of a nest being

destroyed by a storm, or cost to adult survival of providing care all increased the

abandonment threshold (i.e., optimal males abandoned broods they normally would have

guarded). The cost to adult survival for providing care had the largest single effect,

followed by daily probability of a nest being destroyed by a storm, then adult annual

survival rate. Thus, we determined these three parameters were most important in

causing differences in optimal male behavior between the two lakes. When we changed

these three parameters in the Lake Erie simulation to Lake Opeongo values in a step-wise

fashion, the cost of care to adult survival (Δ *ASR*) from Lake Opeongo raised the

abandonment threshold in Lake Erie (Figure 22). Adding Lake Opeongo probability that

a nest was destroyed by a storm (p_S) to the Lake Erie simulation caused another increase

in abandonment threshold, but adding Lake Opeongo adult annual survival rate (*ASR*) to

both of these produced only a small increase in abandonment (Figure 22). Without

changing length-at-age or *TL*-brood size relationships between lakes, this combination of

Lake Opeongo parameter values in Lake Erie resulted in the closest match in optimal

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behavior, even when we added more Lake Opeongo parameter values to the Lake Erie model.

DISCUSSION

Optimal male behavior and its response to parameter values differed between Lake Erie and Lake Opeongo. In general, our model predicted that optimal males in Lake Erie should rarely abandon their broods, even when their broods become very small. In contrast, optimal males in Lake Opeongo should be more prone to abandoning their nests and abandonment thresholds fluctuated when parameter values were changed. This fundamental difference in behavior between the lakes is likely the consequence of underlying differences in the characteristics of each smallmouth bass population. In Lake Opeongo, annual survival rates were higher than in Lake Erie, possibly due to high angling pressure throughout the year in Lake Erie. Because smallmouth bass in Lake Erie had a lower base probability of surviving from spawning season to spawning season than in Lake Opeongo, males in Lake Erie placed more value on their current broods because they were less likely to survive to reproduce again than males in Lake Opeongo. In addition, males in Lake Erie grew faster and received more eggs than similar sized males in Lake Opeongo. Thus, the expected future fitness from broods guarded in the first few spawning attempts was higher in Lake Erie than in Lake Opeongo. Indeed, our model predicted that during its first spawning attempt in Lake Opeongo, at age 4, a male should always abandon its brood on day 1. At first, this suggested a problem with our parameterization of the model, but it demonstrates that an average-length male should not

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reproduce at age 4 in Lake Opeongo. Field surveys of nesting smallmouth bass in Lake Opeongo confirm that many males do not spawn until they reach age 5 or 6.

Model parameters that consistently produced the greatest change in optimal male behaviors were associated with adult annual survival. As mentioned above, reduced adult annual survival rate had an obvious direct negative effect on expected future fitness and it also caused optimal males to guard smaller broods than when survival was high. But, other factors associated with annual survival also played a significant role in determining optimal behaviors. One cost of providing parental care is reduced adult survival (Sabat 1994). In our simulations, increasing the cost of parental care (i.e., reduced annual survival) caused males to abandon larger broods than when care costs were low. Therefore, when annual survival was guaranteed to be low (i.e., *ASR* low), males placed more value on their current brood than future broods. But, when providing care reduced annual survival (i.e., Δ *ASR* high), males placed more value on future broods, which are expected to be larger due to fecundity with increasing with age, than guarding their current brood. Decreasing adult survival directly caused males to abandon less frequently, but when presented with . In addition, in lakes where anglers may keep smallmouth bass during the spawning season (e.g., Lake Erie), risk of death during the spawning season may cause some males to abandon larger broods that they normally would guard. But, when there was very little risk of being angled and kept during the spawning season (i.e., increased probability of surviving to reproduce again even if guarding) in Lake Erie optimal males always guarded even small broods. While we did not observe a similar change in behavior in Lake Opeongo, we believe that the high cost of care on adult survival masked any effects of angling probability. Therefore, in some

systems, increasing parent mortality during reproductive periods (e.g., via angling or hunting) may affect reproductive success in two ways: not only will some broods fail when their parent is killed, but parents also alter their level of investment based on whether adult survival is guaranteed or influenced by amount of care provided.

Offspring mortality resulting from disease, predation, or accidental removal from the brood, can affect optimal parental behavior, but only in certain situations. When the probability of successfully reproducing in the future was relatively high, for example, when adult survival was high and probability of nests being destroyed or depredated was low (e.g., Lake Opeongo), increased offspring survival caused males to abandon larger broods than when offspring survival was low. Because starting brood size was a function of male size, older males received larger broods than young males and the difference between maximum ending brood size for an old male and a young male grows larger as offspring daily survival increases. As the gap in expected fitness from the current brood and expected fitness from future broods grows, young males will devalue their current brood in favor of later broods. But, in systems where expected future fitness is low to begin with (e.g., Lake Erie), offspring daily survival makes little difference.

Changing the probability of nest destruction from storms had the least affect on optimal behaviors in either lake. This result was contrary to our prediction, because when nest success is high, we presumed that males would be more likely to abandon their broods because they had a high probability of succeeding in subsequent attempts. The lack of a behavioral response to fluctuating the probability of nest failure may have resulted from the over-riding importance of adult annual survival to the model, or because probability of nest failure was not an age dependent variable. When parents

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have a similar probability of succeeding in any year, regardless of age, changing the probability that they are successful would not affect the ratio of expected future fitness from their current brood with their future broods. In contrast, all other parameters tested were either directly related to parent age and size (adult annual survival, probability of being kept if caught by an angler, cost of parental care), indirectly related to age (effect of offspring daily survival on the difference between maximum ending future brood size-current brood size), or reduced the probability a parent survived to reproduce again (cost of parental care).

Adding an exotic nest predator, the round goby, to each lake caused optimal males to abandon larger broods than before round gobies invaded. Round gobies have already invaded Lake Erie, and they continue to spread throughout the Great Lakes (Jude et al. 1992). Round gobies increase parental care costs (Chapter 3) and consume offspring when smallmouth bass are temporarily removed from their nests in Lake Erie (Steinhart et al. 2004). In our simulations, we found that the effect of round gobies on parental care (increased care costs led to a higher abandonment threshold) caused more of an effect than their role as nest predators (decreased offspring survival sometimes led to a lower abandonment threshold). Because round gobies are not frequently consumed by nesting smallmouth bass, their effect on cost of parental care will not be compensated for by increased consumption of nest-guarding males. Round gobies, however, are a common in diets of young-of-the-year smallmouth bass, leading to increased young-of-the-year growth rates (G. B. Steinhart, unpublished data). Therefore, by increasing smallmouth bass growth rate, round gobies may have another effect on reproductive decisions that we did not explore. Although round gobies may never arrive in Lake Opeongo, there is little

doubt that they will invade some inland systems, and some of those systems may have characteristics more similar to Lake Opeongo than Lake Erie. But in both lakes, despite differences in base and round-goby-present costs of care, the net effect of adding round gobies was for males to abandon larger broods than before round gobies invaded. So, the presence of a nest predator not only reduces the number of offspring produced through direct consumption of offspring, but also through an increase in brood abandonment.

In conclusion, optimal parental behavior was influenced most by adult annual survival rate. Other parameters that either affected adult annual survival rate or were age-dependent also caused changes in optimal behavior. However, even though parental care theory predicts that individuals with a high probability of successfully reproducing in the future should be more likely to abandon their offspring than individuals with a low probability of successful future reproduction, we found that this was only the case when probability of reproducing was tied to an age dependent variable. Therefore, factors affecting reproductive success that are completely independent from age of the parent (i.e., storm probabilities when storms always destroy the entire brood, or predation risk if predators always depredate the entire brood) have little effect on offspring abandonment.

Lake Erie				Lake Opeongo			
Age	TL	ASR	Δ ASR	Age	TL	ASR	Δ ASR
3	303	0.59	0.004	3	na	Na	na
4	342	0.55	0.008	4	259	0.7	0.025
5	372	0.47	0.0005	5	280	0.6	0.015
6	396	0.39	0.0005	6	300	0.5	0.008
7	417	0.31	0.0005	7	322	0.45	0.0015
8	435	0.21	0.0005	8	350	0.4	0.001
9	450	0.11	0.0005	9	372	0.4	0.001
10	465	0.07	0.0005	10	395	0.4	0.001
11	473	0.04	0.0005	11	411	0.3	0.001
12	485	0.02	0.0005	12	430	0.2	0.001
13	496	0.01	0.0005	13	445	0.1	0.001
14	504	0.01	0.0005	14	458	0.05	0.001
15	510	0.01	0.0005	15	465	0.01	0.001

Table 6. Age-dependent parameter values for male smallmouth bass included in the stochastic dynamic programming model. Smallmouth bass in lakes Erie and Opeongo had a different age range (i.e., no age 3 spawning males in Lake Opeongo), total length at age (*TL,* in mm), adult annual survival rate (*ASR*), and cost of parental care (Δ *ASR*; daily reduction in *ASR* when guarding). For males age 16 and older, we assumed *TL*, *ASR*, and Δ *ASR* were the same as for an age 15 fish.

Parameter	Lake Erie	Lake Opeongo
B	$a = 14, b = -1246$	$a = 13, b = -2500$
DSR (embryos, larvae)	0.90, 0.92	0.90, 0.92
p_S	0.065	0.015
p_A	0.05	0.01
p_R	$i = 0.01, j = 0.007$	0.99
Offspring consumed during angling	0	0
Δ TL	0.67	0.5

Table 7. Lake-specific parameters for a stochastic dynamic programming model of nest-guarding male behavior in Lakes Erie and Opeongo. Values shown are for base simulations in each lake: age specific brood size, daily survival rate (DSR), probability a nest was destroyed by a storm p_S, probability an angler captures a male p_A, probability a male is released if caught p_R, offspring consumed, and daily cost of care in male total length (Δ TL) and annual survival rate (Δ ASR).

Figure 17. Male smallmouth bass reproductive behavior (guard or abandon current brood) as a function of current brood size (B, as percent of starting brood size B_0) and days of care already provided (d) in Lake Erie and Lake Opeongo. Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon. Results are displayed for the first three years in which at least some males are reproductively mature in each lake.
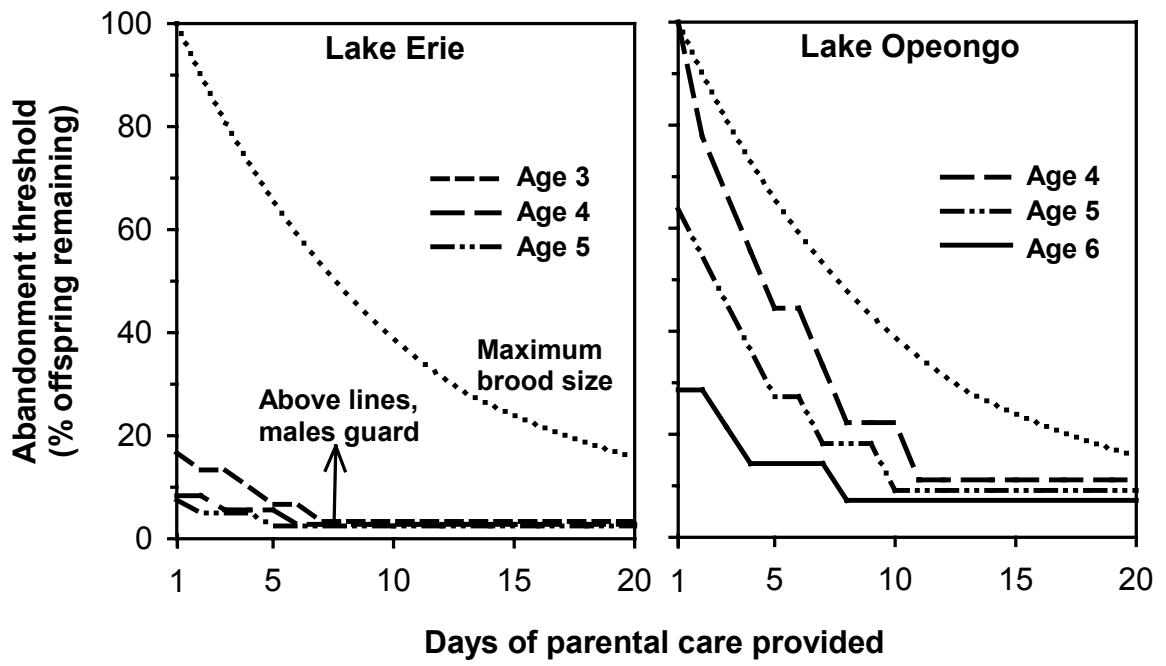
Figure 17.

Figure 18. Optimal smallmouth bass behavior as a function of current brood size (B, as percent of starting brood size B_0) and days of care already provided (d) under different daily probabilities that a nest was destroyed by a storm (p_S) and different offspring daily survival rates (DSR). Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon.
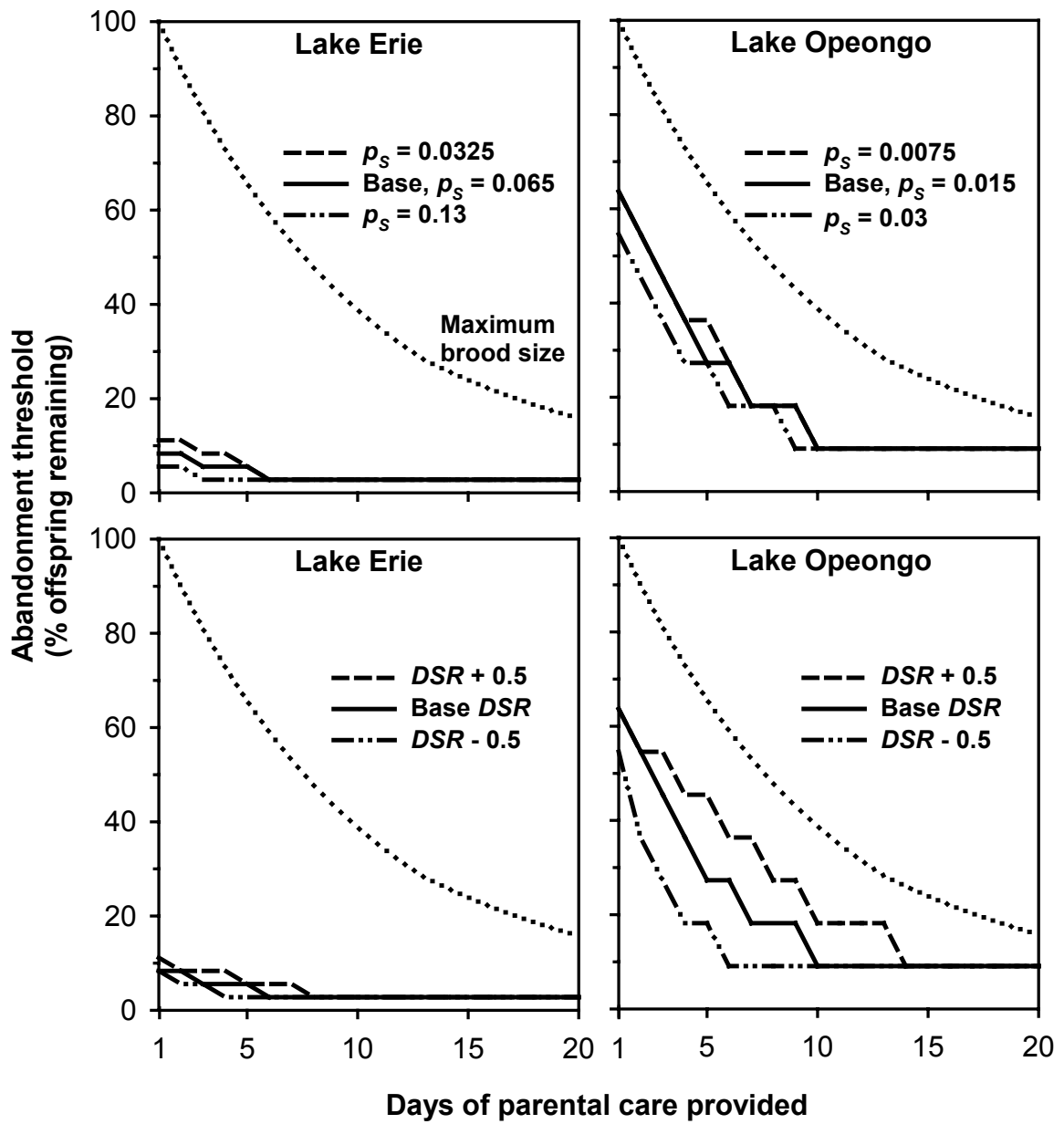
Figure 18.

Figure 19. Optimal smallmouth bass behavior as a function of current brood size (B, as percent of starting brood size B_0) and days of care already provided (d) under different daily probabilities that a male was caught by an angler (p_A) and different adult annual survival rates (ASR). Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon.
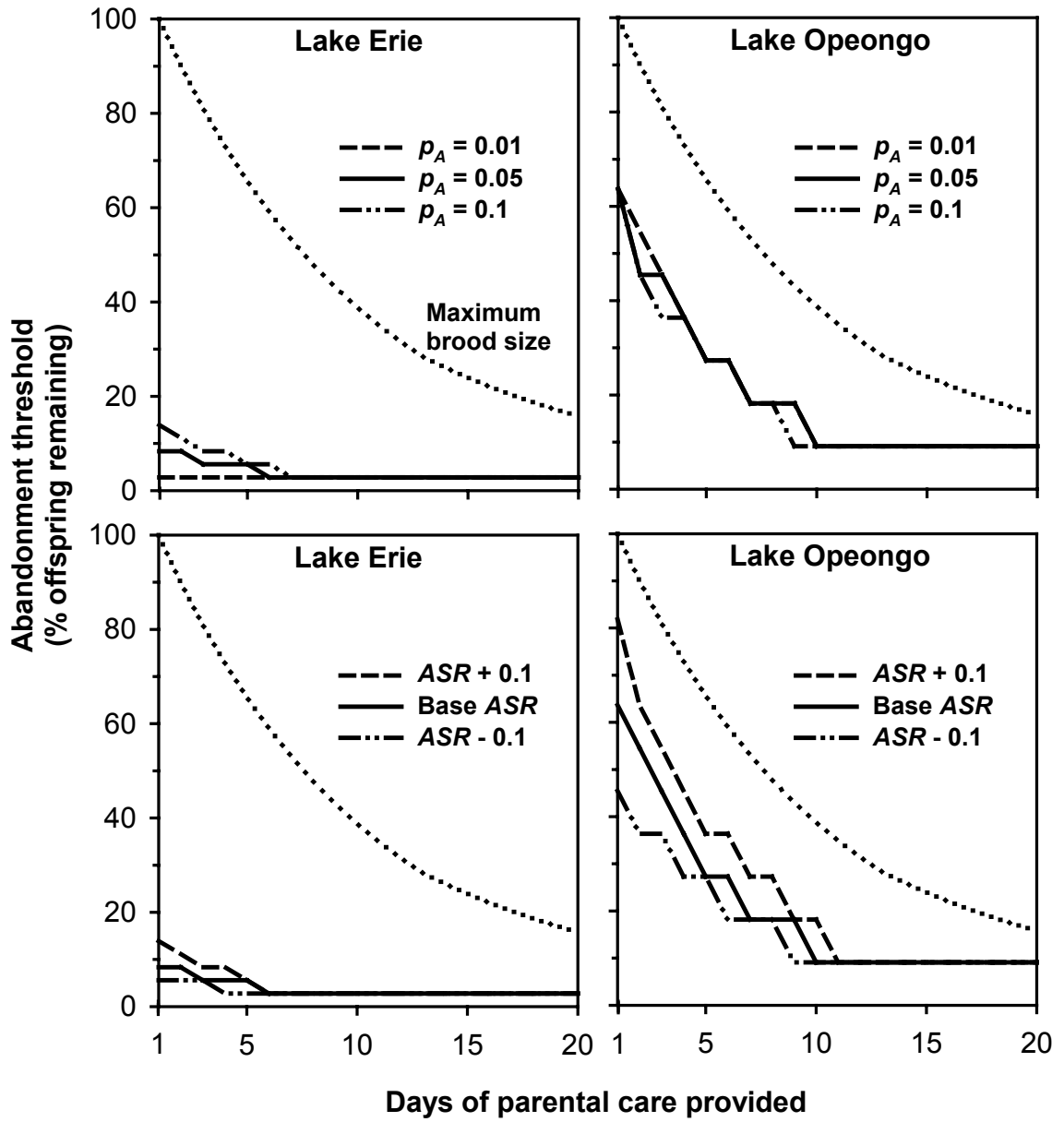
Figure 19.

Figure 20. Optimal smallmouth bass behavior as a function of current brood size (B, as percent of starting brood size B_0) and days of care already provided (d) under different parental care costs. Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon.
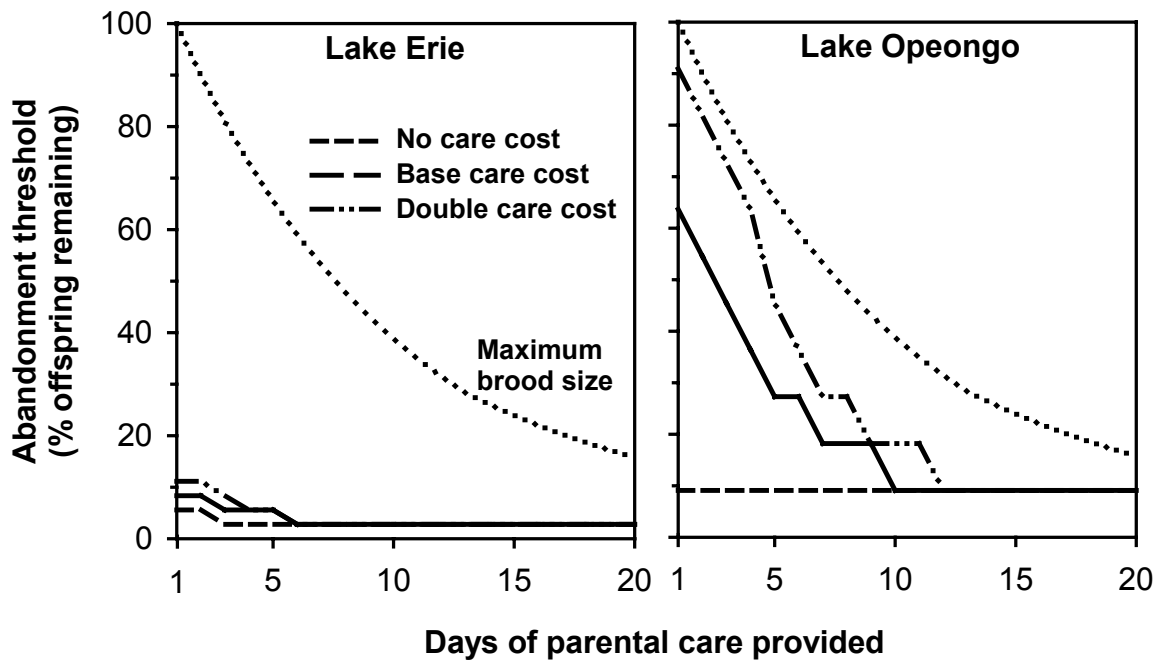
Figure 20.

Figure 21.   Optimal smallmouth bass behavior as a function of current brood size (B, as percent of starting brood size B_0) and days of care already provided (d) when a nest predator, round goby, were present or absent. Results are for an age-4 male in Lake Erie and an age-5 male in Lake Opeongo. Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon.
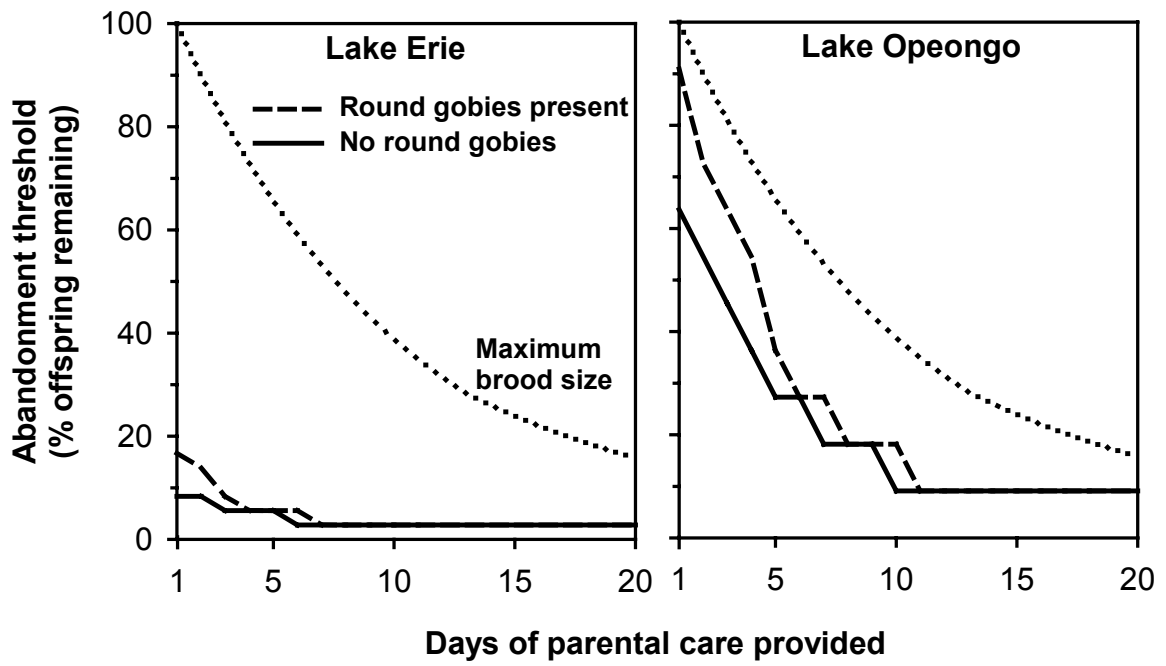
Figure 21.

Figure 22. Optimal smallmouth bass behavior as a function of current brood size (B, as percent of starting brood size B_0) and days of care already provided (d) for an age-4 male in Lake Erie, but with the addition of model parameter values from Lake Opeongo. To the base Lake Erie simulation, we added, step-wise, Lake Opeongo values for cost to annual adult survival of providing care (Δ ASR), probability that a nest was destroyed by a storm (p_S), and adult annual survival rate (ASR) to try to force an optimal age-4 male in Lake Erie to behave as an optimal age-5 males in Lake Opeongo (i.e., males in their second year of spawning in both lakes). Lines indicate thresholds at which males should guard or abandon: above the lines, males should guard; below the lines, they should abandon.
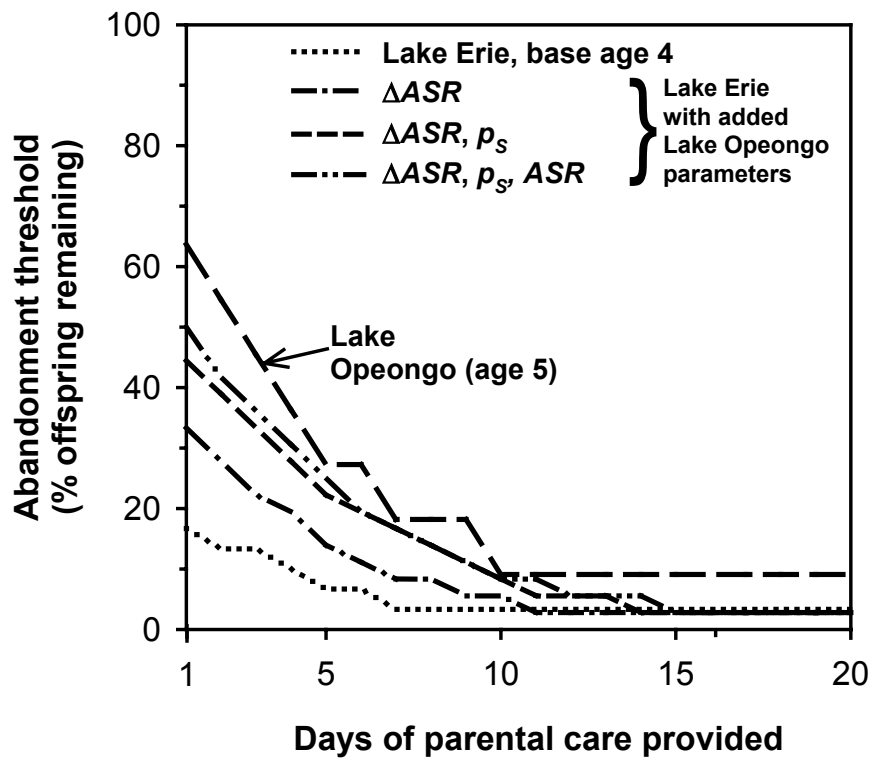
Figure 22.

CHAPTER 6

PARENTAL BEHAVIOR, ANGLING, EXOTIC SPECIES, AND REPRODUCTIVE SUCCESS: MANAGING SMALLMOUTH BASS IN A CHANGING WORLD

ABSTRACT

We used an individual based model to explore how angling pressure, an exotic nest predator (round goby, *Neogobius melanostomus*), and parental behavior affected how different fishing regulations influenced smallmouth bass (*Micropterus dolomieu*) reproductive success in two very different systems: Lake Erie, Ohio, USA, and Lake Opeongo, Ontario, Canada. Our model assumed smallmouth bass made nest-guarding decisions that optimized their lifetime fitness under historical conditions in each lake. As fishing pressure increased, offspring production declined proportionally in both systems; however, when round gobies were included in simulations (currently, round gobies are present only in Lake Erie), offspring production declined more in Lake Opeongo than in Lake Erie. Responses to regulation changes (e.g., season closures, catch-and-release, and

size limit) varied by lake because of lake-specific behaviors and population demographics. For example, high adult survival in Lake Opeongo caused smallmouth bass to devalue current broods and to abandon more offspring than smallmouth bass in Lake Erie. When we allowed males in Lake Opeongo to evolve new optimal behaviors to cope with high fishing pressure and presence of nest predators, males abandoned fewer offspring than when following old, sub-optimal behaviors; however, juvenile production remained constant, possibly because of unavoidable sources of offspring mortality (e.g., storms and daily offspring mortality). Differences in optimal nest-guarding behavior, resulting from population-specific demographics and probability of nest success in lakes Erie and Opeongo, played a role in success of angling regulations, but behavioral changes within lakes had only a small effect on offspring production.

INTRODUCTION

Understanding reproductive success of a species is paramount to appreciating their ecological role and managing their abundance. To understand and predict how fish recruitment may vary, ecologists often turn to simulations that operate on individual or population levels (DeAngelis et al. 1993; Ridgway and Shuter 1997). What has been missing from these models, however, is individual behavior, especially important when examining reproductive success. Population-specific individual behaviors and energy allocation strategies have partially explained individual growth differences (Garvey and Marschall 2003; Munch and Conover 2002) and, presumably, also affect reproductive success. According to the theory of natural selection, individuals should behave in a

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manner that maximizes their lifetime fitness (Williams 1966). These optimal behaviors change as an individual ages and grows, or when an individual's environment changes (Gross 1991). Global change, exotic species introductions, over-harvesting, habitat alteration, and management activities can rapidly change the environment to which optimal reproductive behaviors have evolved (Adams et al. 2001; Clark et al. 2001) and, ultimately, may lead to evolution of new optimal behaviors (Gross 1991). To fully understand how these different environmental conditions affect reproductive success, we can compare how behavior varies across different ecosystems and, in turn, how behavioral differences affect reproductive success.

Reproductive success depends upon parental behavior, which then influences offspring production. For example, male smallmouth bass (*Micropterus dolomieu*) provide sole parental care for their offspring for up to 7 weeks (Ridgway 1988). Care, particularly defending the offspring from predators, is required during embryonic and larval stages or broods will fail (Hinch and Collins 1991; Steinhart et al. 2004). But providing care is energetically costly for smallmouth bass (Gillooly and Baylis 1999; Mackereth et al. 1999) and can reduce future fecundity and survival of the parent (Ridgway 1986; Sabat 1994). Therefore, individuals must balance the fitness tradeoff between guarding their brood and abandoning their brood to prepare for future spawning attempts (Williams 1966). In many species, parents decide to guard or abandon their brood based on the balance between current and future fitness, a combination of their probability of successfully reproducing in the future, current condition, and current brood size (Jennions and Polakow 2001; Östlund-Nilsson 2002; Townshend and Wootton 1985).

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Smallmouth bass, native to eastern North America, are dominant predators often controlling fish communities through top-down impacts (MacCrimmon and Robbins 1975; Vander Zanden et al. 1999). Because they often support popular recreational fisheries, smallmouth bass also are subjected to a wide range of management practices to improve fishing and assure sustainability (Fox 1975; Noble 2002). When anglers catch and keep nesting bass (both smallmouth and largemouth bass, *M. salmoides*), nest predators quickly consume unguarded offspring (Hinch and Collins 1991; Kieffer et al. 1995; Steinhart et al. 2004). Even if nesting bass are released, angling causes physiological stress that can lead to nest abandonment (Cooke et al. 2002; Philipp et al. 1997) and even a short absence can lead to substantial offspring losses due to nest predators (Kieffer et al. 1995; Steinhart et al. 2004). Therefore, angling can both directly reduce reproductive success and indirectly influence reproductive success if males decide to abandon their nests following brood reduction by predators. Thus, managers often implement angling restrictions to protect smallmouth bass during spawning and parental care (Kubacki et al. 2002; Suski et al. 2002). Managing smallmouth bass fisheries traditionally has employed limits on size and number of fish harvested, enforcement of catch-and-release regulations, and seasonal closures (Fox 1975; Noble 2002).

Lakes supporting healthy smallmouth bass populations attract anglers, which may, in turn, increase the probability of environmental change. Changes in angling pressure modify adult survival and, especially when nest predators are abundant, offspring survival (Ridgway and Shuter 1997; Steinhart et al. 2004). Highly mobile anglers may increase the likelihood of introduction of exotic species by intentional introductions of "desirable" species, release of live bait, or accidental transportation of non-indigenous

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species on boats and trailers (Johnson et al. 2001). Because nest-abandonment behavior presumably evolves to local conditions, these angler-induced changes may lead to shifts in which behaviors are optimal. Parents making sub-optimal decisions based on previous conditions may experience dramatically reduced reproductive success. Even though parental decisions (i.e., guard or abandon) can lead to reproductive failure, behavior has rarely been considered when deciding on fishing regulations.

Here, we describe how reproductive success of smallmouth bass is influenced by interactions with their environment. We do this with an individual-based model incorporating optimal and sub-optimal behaviors, weather, nest predators, and angling under different regulations. Within this framework, individual fish make reproductive decisions based either on expectations of historical experience or expectations of conditions in their new environment. We simulated reproductive success of two smallmouth bass populations, each population with very different demographics. In our view, increased angling pressure and nest predation should reduce offspring production when parental behavior had not yet responded to these changes. However, once optimal male behavior has evolved to the new environment, we hypothesized that offspring production would increase relative to males that made sub-optimal decisions.

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METHODS

Study Sites

We studied nesting smallmouth bass in Lake Erie, Ohio, USA, and in Lake Opeongo, Ontario, Canada, to estimate parameters necessary for our model. In mesotrophic Lake Erie, we surveyed nesting smallmouth bass in the Bass Islands, located in the western basin of Lake Erie (41° 40' N, 82° 50' W) during May and June 1999-2001, and in oligotrophic Lake Opeongo (45° 42' N, 78° 22' W, Algonquin Park, Ontario), we surveyed nesting smallmouth bass during June 2001 and combined these data with published and unpublished records to estimate parameter values.

Lakes Erie and Opeongo differ in aspects of smallmouth bass life history and reproductive behavior. Smallmouth bass are native to Lake Erie, but were introduced into Lake Opeongo in the early 1920's, rapidly establishing a self-sustaining population (Ridgway 1986; Shuter et al. 1987). Angling and harvesting of spawning smallmouth bass has been allowed in Lake Erie, but angling during spawning is prohibited in Lake Opeongo. As a result, adult survival is generally lower in Lake Erie than in Lake Opeongo (R. Knight, Ohio Division of Wildlife, Columbus, Ohio, personal communication; Ridgway 1986; Shuter et al. 1987). Smallmouth bass in Lake Erie, which is more productive and has a longer growing season than Lake Opeongo, grow faster than smallmouth bass in most other systems (Doan 1940), including Lake Opeongo. Lake Erie supports higher nest-predator densities than Lake Opeongo (Steinhart et al. 2004). Nest predators have been extremely abundant in Lake Erie since

the invasion of the round goby, first seen in Lake Erie in 1993 and reaching high densities (at times exceeding 100 individuals/m^2) in the Bass Islands in 1998 (Charlebois et al. 1997; Jude et al. 1992). By creating waves, depositing sediment, and causing temperature fluctuations, storms contribute to nest failures in both lakes (Friesen 1998; Goff 1986). Lake Erie, owing to its large fetch, is exposed to more violent storms than Lake Opeongo (G. B. Steinhart, unpublished data).

Modeling overview

We used a dynamic programming (DP) model described in Chapter 5 to generate optimal parental decisions of nest-guarding smallmouth bass in lakes Erie and Opeongo based on the age of the guarding male, number of offspring remaining in the current brood, and days of parental care already provided. For each combination of male age, brood size, and day, the model determined the optimal decision, to guard or to abandon the current brood, so as to maximize a male's expected lifetime reproductive fitness. Optimal decisions then were used in an individual-based model (IBM) in which a population of smallmouth bass was exposed to random storms and angling (with different angling pressures), presence or absence of an exotic nest predator (round goby), and different fishing regulations. Because the fitness value of behavioral responses that have evolved to one environment may be different following a change in the environment (e.g., an invading nest predator), we tested both old (i.e., sub-optimal under the new conditions) and evolved (optimal under the new conditions) decisions, but only in Lake Opeongo where male behavior had more flexibility than in Lake Erie (Chapter 5). The

IBM described the number of offspring reaching an age (20 d) at which they had

metamorphosed and no longer required parental care. Although survival to independence

is not a direct measure of recruitment to the fishery or to the adult population, it serves as

a first step in predicting potential smallmouth bass recruitment.

Dynamic programming model

The DP model used backward iteration (Mangel and Clark 1988) to calculate expected

lifetime fitness (number of offspring reaching independence) when a nest-guarding male

chose to guard or abandon its current brood. The model assumed males sought to

maximize their fitness; thus, males chose the optimal behavior, guard or abandon, that

produced the largest expected lifetime offspring production. Expected future fitness was

calculated based on empirically measured probabilities of nest failure, nest predation,

offspring survival, and adult annual survival, and estimated probabilities of being caught

by an angler and being released when captured. Cost of parental care was expressed as a

reduction in a male's future survival and fecundity for each day of care provided. All

optimality model parameters were derived separately for Lake Erie (see Chapters 2-5)

and Lake Opeongo (E. S. Dunlop, University of Toronto, unpublished data). Full details

on construction and exploration of the DP model are available in Chapter 5.

Individual based model

The IBM simulated offspring production for a population of 1,000 male smallmouth

bass during a single spawning season. Males were placed randomly in one of three

spawning areas in a given lake to allow simulation of localized storms and angling pressure. Each male was randomly assigned an age, based on observed age distributions in each lake (minimum age 3 in Lake Erie and age 4 in Lake Opeongo; maximum age 13 in both lakes). In both the DP model and the IBM, male total length (*TL*) was assigned from length-at-age data for each lake (G. B. Steinhart, unpublished data; E. S. Dunlop, University of Toronto, unpublished data). Because larger males receive more eggs than smaller males (Mackereth et al. 1999; Ridgway 1986; Wiegmann et al. 1992), starting brood size was estimated as a function of *TL*:

$$\text{brood size} = a\ TL - b \tag{1}$$

where $a = 14$ and $b = 1200$ in Lake Erie and $a = 13$ and $b = 2500$ in Lake Opeongo (G. B. Steinhart and E. S. Dunlop, unpublished data).

Based on observed spawning season length in each lake, in the IBM we simulated a 60-d spawning season in Lake Erie and 40-d season in Lake Opeongo. To ensure that spawning was initiated only when a brood had sufficient time to complete 20 d of care before the last day of the spawning season *D*, all males could begin spawning on any day $d=1$ to D-20. On each simulation day *d*, a male initiated its first spawning attempt with a probability of $d/40$ in Lake Erie and $d/20$ in Lake Opeongo. The DP model results assigned behaviors to males only after they began spawning. Nests were considered successful and parental care terminated when offspring reached metamorphosis after 20 d (total duration of parental care ranges from 17 - 43 d and depends on temperature; Friesen 1998). When a male's first spawning attempt failed, he began a second attempt

with a daily probability of 0.15. This value was chosen because it resulted in about 5%

of males re-nesting in our simulation, similar to empirically measured re-nesting rates

observed in Lake Erie during 2 years of study (G. B. Steinhart, 2000 and 2001,

unpublished data; note: multiple spawning was not allowed in the DP model to generate

male decisions). Males that successfully reared a brood through 20 d or failed in two

spawning attempts could not spawn again in this model because males meeting these

criteria were never observed spawning again within a year (G. B. Steinhart, unpublished

data).

   During each simulation day, nesting males were exposed to angling, while non-nesting

males were not. Daily probabilities of capture for simulations of current conditions were

0.05 in Lake Erie (open smallmouth bass season during spawning) and 0.01 in Lake

Opeongo (closed to smallmouth bass fishing during spawning). As in the DP model,

captured males were released with a size-dependent probability because anglers released

more small fish than large fish:

$$p_R = 1-(r \cdot e^{(s \cdot TL)}) \quad\quad\quad (2)$$

where $r = 0.01$ and $s = 0.008$ in Lake Erie, and $r = 0.01$ and $s = 0.009$ in Lake Opeongo

(R. Knight, Ohio Division of Wildlife, Sandusky, Ohio, personal communication). Age-

specific p_R, when weighted by smallmouth bass abundance by age in Lake Erie, yielded a

mean release probability of 0.2, approximating the reported release rates from Lake Erie

creel surveys (R. Knight, Ohio Division of Wildlife, Sandusky, Ohio, personal

communication). We modified the coefficients in the Lake Opeongo release probability

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equation to yield a similar weighted-mean release probability. When simulating no-fishing regulations (e.g., current conditions in Lake Opeongo) or catch-and-release regulations (e.g., current conditions for males smaller than 355-mm TL in Lake Erie), p_R was 0.99.

If a male was captured and kept, nest predators consumed all offspring in his nest. When males were captured and released, either 500 or no offspring were consumed when round gobies were present or absent, respectively (Steinhart et al. 2004). When caught and released, guarding males had a 0.05 probability of abandoning their brood, regardless of brood size (G. B. Steinhart, unpublished data). Because developing smallmouth bass offspring can die from disease, lack of oxygen, and predation while males are guarding (Friesen 1998; Knotek and Orth 1998), number of offspring remaining after angling was reduced by 10% per day for embryos (day 1-13) and 8% per day for larvae (day 14-20; Friesen 1998; Knotek and Orth 1998).

We modeled storms as stochastic events that affected all nests at a spawning site. In Lake Erie, high winds (two or more hours of winds greater than 7 m/s) destroyed many smallmouth bass nests (Chapter 4), but a single storm typically affected only discrete spawning areas. We simulated the effect of localized spawning populations in bays and reaches, each with different exposure to storms, by allowing a storm to affect only one site per day. We calculated a daily storm probability (range: 0.25-0.44) for each weekly simulation interval (only 4 d in last interval) using 18 y of continuous winds data from a NOAA weather station (Station SBI01). In Lake Opeongo, smallmouth bass nest failures were associated both with wind events and rapid drops in temperature (both related to storms; G. B. Steinhart, unpublished data; Friesen 1998). Daily storm probability was

lower in Lake Opeongo, 0.12, based on the frequency of storms during the 2001-spawning season. When a storm occurred, its impact was manifested in one, randomly selected site, and each nest in the exposed site had a fixed probability of surviving. Nest survival probabilities following storms were estimated from field observations of smallmouth bass nest encounter histories (0.44 in Lake Erie, 0.36 in Lake Opeongo; G. B. Steinhart, unpublished data), but survival probabilities (0.4 in Lake Erie and 0.65 in Lake Opeongo) were adjusted in the model to produce a mean nest success rate that matched mean nest success in each lake. The adjusted survival probability for Lake Opeongo was quite different from our estimated survival probability because we had only one year of nesting data from which to estimate nest survival following storms.

At the end of a simulation day, each male made the decision to guard or abandon its brood based on offspring number, male age, and days of parental care already provided. We ran 200 iterations of 1,000 males each for each simulation. Model output included the total number of offspring produced by the population (dividing total offspring production by 1,000 males provides the mean number of offspring produced per male), number of offspring lost to predators as a result of angling, and number of offspring abandoned.

Effects of angling pressure and nest predators

We tested how angling pressure influenced offspring production and offspring abandonment by varying the daily probability of capture (0.01, 0.05, and 0.1), probability of release (p_R as per equation 2 or 0.99), and presence of round gobies (i.e., 500 offspring

consumed during catch-and-release angling only when round gobies were present). For

Lake Erie, simulating current conditions included assumption of a 355-mm (14 in)

minimum size limit (i.e., p_R = 0.99 if male *TL* >355, equation 2 if *TL* ≥ 355). In Lake

Opeongo, the simulation of current conditions used a daily probability of capture of 0.01

and a probability of release of 0.99 because we assumed some smallmouth bass would be

caught and kept by poachers or anglers unaware of the regulations. In all other

simulations in which angling and harvest were allowed, p_R was size-based, as per

equation 2. In all angling simulations, males made nest abandonment decisions under the

expectation of angling pressure from the current conditions and absence of round gobies,

not the adjusted angling parameters, with one exception; in Lake Erie, the 355-mm

minimum size limit was not introduced until 2000, so we assumed males expected the

historical p_R as described in equation 2.

Effects of nest-guarding behavior

To examine how male behavior, based on expectation of probabilities of capture,

release, storms, etc., affected offspring production, we explored how offspring production

and abandonment varied for males making old (i.e., suboptimal under the new angling

regime that included angling and nest predators) and evolved (i.e., optimal under the new

angling regime) decisions. We explored how behavior affected offspring production and

abandonment only for Lake Opeongo males because smallmouth bass in Lake Opeongo

displayed more flexible behavior than smallmouth bass in Lake Erie when simulation

parameters were modified (Chapter 5). Therefore, any effect of behavior should be larger

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in Lake Opeongo than in Lake Erie. For all IBM simulations testing behavior, we assumed the angling regime included increased angling pressure (0.05 daily probability of capture), size-based probability of release, and 500 offspring consumed per catch-and-release of the male (i.e., round gobies present). First, we used decisions generated from the DP model that were based on previous conditions in Lake Opeongo (no angling, no round gobies) to simulate what might happen immediately following an increase in angling combined with a round goby invasion. Next, we tested if evolution of new nest-guarding behaviors affected offspring production and abandonment by generating new optimal decisions with our DP model. Three sets of behavioral decisions were generated corresponding to behavioral evolution to 1) new angling pressure with no round gobies, 2) old angling pressure with round gobies, and 3) new angling pressure with round gobies. In addition, because behavioral responses were quite sensitive to adult survival (Chapter 5) and adult survival would, presumably, decline as fishing pressure increased, we generated decisions for males exposed to new angling pressure, presence of round gobies, and a 0.1 decrease in annual adult survival.

Testing angling regulations

We explored how different angling regulations commonly used by fisheries managers could affect smallmouth bass offspring production. Because the rate at which male behavior may evolve in response to new angling regulations is unknown, we simulated only the immediate affect of angling regulations in IBM simulations using guarding-male behaviors from the DP model that corresponded to current angling conditions in each

lake. In addition to simulating current conditions in the IBM, we simulated 1) no regulations, 2) a 355-mm minimum size limit, 3) a sanctuary, 4) catch-and-release only, and 5) no fishing (Table 8). Establishment of a sanctuary area was simulated by exposing 1/3 of the population (i.e., one site) to no fishing and 2/3 of the population to no regulations. Each of these simulations included only old behaviors evolved under the current-conditions simulations

In Lake Erie, frequent storms early in the spawning season cause most nests initiated in May to fail, resulting in most offspring production from nests guarded during June (Steinhart et al. 2004). In such situations, a closed season may be needed only when nests with a high probability of survival (e.g., late spawned nests) are active. We tested the effect of closing the smallmouth bass fishery during only 1-31 May and only 1-30 June and compared these closures with simulations of no regulations, catch-and-release only, and no-fishing regulations (Table 8). The distribution of successful and failed nests in our IBM model did not match the distribution observed *in situ* during 1999-2001, possibly because the occurrence of storms during 1999-2001 was different from storm probabilities generated from average wind data during 1981-2001 (excluding 2 y with no data). Therefore, we made several modifications to our IBM to simulate the observed distribution of successful and failed nests during 1999-2001 by forcing more nests to fail in May and more nests to succeed during June: 1) increased daily storm probabilities during May (to 0.8 from a range of 0.25-0.43), 2) reduced daily storm probabilities in June (to 0.3 from a range of 0.3-0.43), and 3) forced males to attempt a second spawning only after day 30 and with a daily probability of 0.2. With these changes, total offspring

produced in these simulations were not comparable to previous simulations, but the

differences between closure-date simulations were directly comparable.

RESULTS

Effects of angling pressure and nest predators

An increase in angling pressure reduced total juvenile production (Figure 23).

Increasing the probability of being caught by an angler from 0.01 to 0.05 reduced mean

offspring production by 21% in Lake Erie and 18% in Lake Opeongo when round gobies

were absent. When probability of angling was increased from 0.01 to 0.1, mean offspring

production declined by 38% and 37% in lakes Erie and Opeongo, respectively.

Round gobies also reduced juvenile production in both lakes, but by greater percents

in Lake Opeongo than Lake Erie (Figure 23). In Lake Erie, adding round gobies to 0.01,

0.05, and 0.1 daily angling probability simulations resulted in 5, 11, and 26% reductions

in mean offspring produced compared to the same angling probabilities with round

gobies absent. Round gobies caused larger changes in offspring produced in Lake

Opeongo: 5, 27, and 52% reductions compared to the same angling probabilities without

round gobies.

With round gobies present, offspring abandonment increased as probability of male

capture increased, and offspring abandonment and change in abandonment rates were

higher in Lake Opeongo than in Lake Erie (Figure 24). Males in Lake Erie abandoned

only 0.2% of all offspring when angling probability was low (0.01) and abandoned

approximately 2.1% of all offspring when angling probability was high (0.1). In Lake Opeongo, males abandoned a greater percent of their offspring than in Lake Erie: 2.9% abandoned with low angling pressure and 6.2% when angling pressure was high.

Effects of nest-guarding behavior

New optimal male behaviors (i.e., male adapted to new angling pressure, round goby presence, and new adult survival) affected abandonment of offspring, but not production of juveniles, in Lake Opeongo (Figure 25). Abandonment of offspring declined when male behavior had adapted to new (i.e., increased) angling pressure and adult annual survival, but behavioral responses to round gobies had little impact on offspring abandonment. When males had full knowledge of angling pressure, presence of round gobies, and annual survival, they abandoned 61% fewer offspring than when they had not evolved to these new conditions. Offspring production, however, changed little with male behavior. In fact, for all simulations where male behavior had evolved to at least one of the new conditions, juvenile production was slightly lower than when male behavior had not yet adapted current conditions (Figure 25).

Testing angling regulations

Offspring production generally increased with more restrictive angling regulations, but regulation effectiveness differed between lakes Erie and Opeongo (Figure 26). In general, angling restrictions had a greater effect in Lake Opeongo than in Lake Erie. In Lake Erie, in order from highest to lowest offspring production, were no fishing, catch

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and release only, a sanctuary protecting 1/3 of the spawning population, a 355-mm minimum size limit, and no regulations. In Lake Opeongo, however, a catch and release regulation resulted in fewer offspring produced than a sanctuary. The difference was small, only 4%, but the direction was opposite that observed between catch and release and sanctuary regulations in Lake Erie (Figure 26). In addition, offspring production was similar in Lake Opeongo with either a 355-mm minimum size limit or no angling regulations, as in Lake Erie. In Lake Opeongo, 90% of spawning males were below the 355-mm minimum size limit, so it was surprising that the minimum size-limit did not increase offspring production compared to Lake Erie, where only 40% of spawning males were below the 355-mm minimum size limit (Figure 27).

Our modified model testing season closures caused 70% of successful nests in Lake Erie to start after 1 June (Figure 28), successfully mimicking the observed distribution of successful nests during 2000-2001 (Steinhart et al. 2004). With this distribution of successful nests, timing of angling closure was an important component in driving juvenile production by smallmouth bass (Figure 29). When fishing was prohibited only during 1-31 May, offspring production increased by 10% compared to an open season during the entire spawning season. Closing the fishery during 1-30 June, however, resulted in 25% more offspring compared to an open season, 13% more offspring than a closed season in May only, and 6% more offspring than a catch-and-release regulation.

DISCUSSION

Fishing pressure and, therefore, angling regulations affected smallmouth bass offspring production but the effectiveness of regulations depended on unique characteristics of each lake in our simulations. Unfortunately, managers sometimes assign lake-specific regulations, and often regulations in specific lakes are only used only when large differences exist among water bodies (e.g., Great Lakes states often have separate regulations for inland waters and Great Lakes waters for the same species). Managers may have difficulty enforcing a wide range of regulations and anglers may find it confusing to sort through dozens of unique regulations but, at a minimum, managers must consider how regulations affect the range of waters to which they are applied. Our results demonstrated how angling regulations and nest predators affected offspring production. In addition, we report how differences in smallmouth bass demographics across different systems affected guarding-male abandonment behavior and the consequences for the success of different angling regulations.

Effects of angling pressure and nest predators

Obviously, increasing angling pressure and nest predators should be accompanied by a decline in offspring production. However, response in a lake depends on several facets of smallmouth bass life history in individual lakes. In Lake Erie, smallmouth bass rarely abandon their nests because adults experience relatively high annual mortality compared to Lake Opeongo. Because of high mortality, smallmouth bass have evolved to expect

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few reproductive opportunities; thus, they guard smaller broods than males in Lake Opeongo. Similarly, in bird populations characterized by high adult mortality (similar to Lake Erie), parents are more vigilant in caring for their young, even if it compromises parental survival (Mauck et al. 1999; Ghalambor and Martin 2000). When we simulated the presence of an exotic nest predator (round goby), differences in offspring production between the lakes grew larger as angling pressure increased. Nest predators, combined with angling, reduced brood sizes of captured nest-guarding males and, because males in Lake Erie were more willing to guard smaller broods than males in Lake Opeongo, resulted in lower offspring abandonment in Lake Erie than in Lake Opeongo.

Starting brood size also may play a role in determining how angling regulations and nest predators influence offspring production. Not only are smallmouth bass in Lake Erie larger at a given age than males in Lake Opeongo, but they also receive more eggs than similar-sized individuals in Lake Opeongo. Because round gobies consume about 500 offspring every time a nest-guarding male is caught-and-released, regardless of current brood size (Steinhart et al. 2004), nest predation during catch-and-release angling reduced brood size by a larger proportion in Lake Opeongo than in Lake Erie. The direct (brood predation) and indirect (abandonment following brood predation) effects of nest predators are likely to be more important in systems where males have relatively small broods and males are less tenacious in their nest defense (e.g., Lake Opeongo).

Effects of nest-guarding behavior

Nest-guarding smallmouth bass behavior results from a complex interaction of a male's expectations of future fecundity and mortality, probability of successful reproduction, and offspring mortality (Chapter 5). Because parents evolve behaviors that maximize their lifetime fitness, distinct differences in parental behavior occur across environments differing in adult survival and fecundity, food availability, and predation risk (Badyaev and Ghalambor 2001; Ghalambor and Martin 2000; Townshend and Wootton 1985). Faced with a changing environment, new optimal behaviors may evolve that improve reproductive success given new selective pressures (Gross 1991; Skulason 1995). In simulations in which smallmouth bass were exposed to new environmental conditions and behaved differently based on their underlying expectations of these new conditions, smallmouth bass did abandon fewer offspring than when smallmouth bass behavior was based on expectations of their old environment. But, offspring production did not increase, even though abandonment of offspring decreased, possibly because smallmouth bass offspring experience high mortality that swamped the effect of brood abandonment. In our simulations, 85% of offspring died due to unavoidable daily mortality and nest success was only about 35% in Lake Erie. So, even when males behaved with full knowledge of their new environment, offspring production was likely limited more by offspring mortality and nest success rates than male abandonment of broods. In some systems, however, where offspring mortality and nest success are high, parental behavior may be more important in determining offspring production than the lakes used in our simulations.

Testing angling regulations

Restricting angler catch and harvest of smallmouth bass can be an effective tool to increase smallmouth bass abundance, but the effectiveness of regulations has been mixed: similar regulations established in different systems do not always produce the same results (Fox 1975; Noble 2002). Our results revealed some potential causes for the success or failure of regulations. Proceeding from least restrictive to most restrictive regulations, consider the effects of establishing a minimum-size limit for smallmouth bass. Because more spawning smallmouth bass were protected by a 355-mm *TL* limit in Lake Opeongo than in Lake Erie, we would have predicted that offspring production should increase more in Lake Opeongo than in Lake Erie when a minimum-size limit was simulated. However, offspring production did not differ between the no regulation and size-limit regulation in either lake.

We included nest depredating round gobies in these simulations, thus affording round gobies opportunities to consume offspring while nests were left unguarded. All males could still be caught, but anglers had to release fish less than 355 mm. Because a larger proportion of spawning males exceeded the minimum size in Lake Erie than in Lake Opeongo, more broods failed due to anglers keeping males in Lake Erie. Even though anglers kept fewer males in Lake Opeongo than in Lake Erie, round goby consumption of offspring from unattended nests in Lake Opeongo, and subsequent nest abandonment by the male, apparently made up for differences in adults kept by anglers. Male behavior also may have contributed to the similarity in offspring production under a minimum-size

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limit. Because of their smaller starting brood size and their propensity to abandon depredated broods, male smallmouth bass in Lake Opeongo were more likely to abandon broods after angling than males in Lake Erie, thus reducing the effectiveness of a minimum size-limit in Lake Opeongo.

Although we maintain that offspring production in these systems may be governed more by other sources of offspring mortality and nest failure, there is further evidence that male behavior can play a role when we examine the simulations of a catch-and-release regulation. Offspring production under a catch-and-release regulation and minimum-size limit regulations were similar in Lake Opeongo (only 3% higher for catch-and-release). But in Lake Erie, catch-and-release fishing resulted in a 13% more offspring produced than a 355-mm size limit. We believe these differences demonstrate that offspring losses from nest predation and subsequent male abandonment were more important in Lake Opeongo (little difference between catch-and-release and minimum size) than in Lake Erie, because males in Lake Erie continued to guard their broods even after nest predation during catch-and-release angling.

Establishing sanctuaries, where fish are protected from fishing, has been gaining in popularity as a technique for protecting fishery resources (Roberts et al. 2001; Suski et al. 2002). In Lake Opeongo, a sanctuary protecting 1/3 of the spawning males resulted in the second highest offspring production. But in Lake Erie, establishing a sanctuary was only the third best option, behind no angling and catch-and-release angling. Again, this demonstrates that protecting male smallmouth bass from anglers during spawning has a larger effect on offspring production in lakes where brood predation during angling causes males to lose a significant portion of their offspring (i.e., lakes with many

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predators or small brood sizes), or where brood reduction or angling ultimately lead to nest abandonment (i.e., lakes with long-lived males that are more prone to abandonment).

Our results demonstrate how offspring production varies as a function of angling pressure, nest predation, and parental behavior. While offspring production may not translate directly to recruitment to adulthood or the fishery, we demonstrated that offspring production could vary widely not only with angling pressure and regulations, but that changes in offspring production varied by system due parents' willingness to guard small brood sizes. Managers should consider variation in environmental conditions (e.g., storm frequency, nest predators) and population characteristics (e.g., survival and fecundity) when deciding how to regulate fish populations. However, we recognize that management decisions involve much more than maximizing offspring production; angler opportunity, regulation enforcement, desired fish size-structure, among others, also influence management decisions. However, in addition to traditional factors involved assessing the value of different regulations, we assert that consideration must be given to the specific life-history characteristics that ultimately regulate the behavior of individuals from different populations.

Simulation	Probability of capture	Probability of release
No regulations	0.05	Equation 2
355-mm size limit	0.05	0.99 when $TL \leq 355$ mm;
		Equation 2 when $TL > 355$ mm
Sanctuary	0.01 at sanctuary site;	0.99 at sanctuary site;
	0.05 at two sites	Equation 2 at two sites
Catch-and-release	0.05	0.99
No fishing	0.01	0.99
Limited angling season	0.01 during closed season;	0.99 during closed season;
	0.05 during open season	Equation 2 during open season

Table 8. Probability of capture and release of nest-guarding smallmouth bass used when simulating the effect of different angling regulations on offspring production in Lakes Erie and Opeongo. A sanctuary was simulated by exposing 1/3 of the population (i.e., one site) to no fishing and 2/3 of the population (i.e., remaining two sites) to no angling regulations.

Figure 23. Smallmouth bass offspring production as a function of angling pressure and round gobies for simulated smallmouth bass populations (200 iterations of 1,000 spawning-age males) in Lake Erie, USA, and Lake Opeongo, Canada. Arrows mark the current conditions in each lake and percentages indicate change in mean offspring production from current conditions. Current conditions in Lake Erie included a 355-mm minimum length limit, while in Lake Opeongo, current conditions included $p_R = 0.99$ (see text for full details). Horizontal lines indicate the median juvenile production, box ends represent the 25th and 75th percentiles, error bars represent the 10th and 90th percentiles. Note that y-axis scales differ for the two lakes.
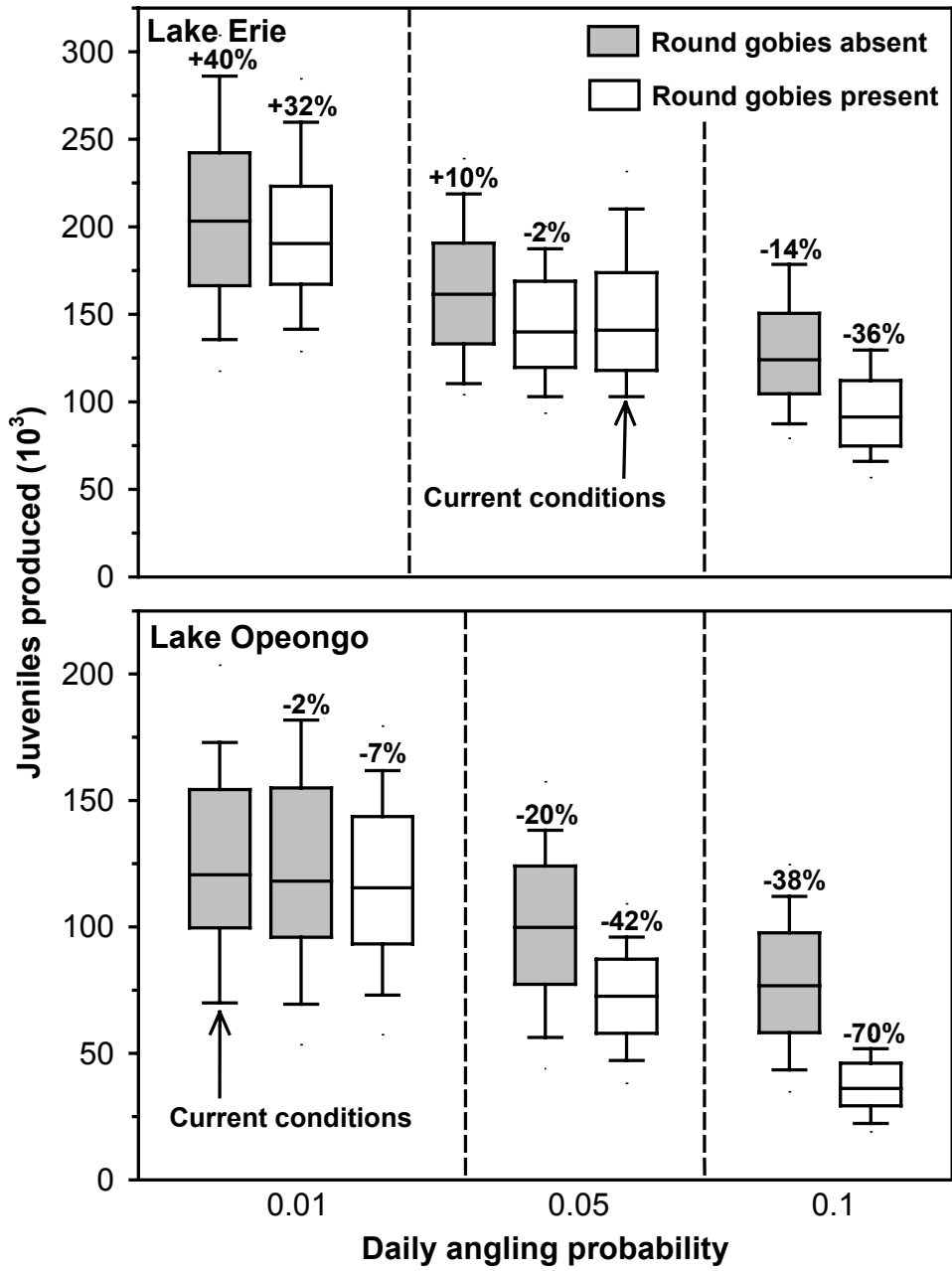
Figure 23.

Figure 24. Offspring abandoned (percent of all offspring) by male smallmouth bass as a function of angling pressure for simulated smallmouth bass populations (200 iterations of 1,000 spawning-age males) in Lake Erie, USA, and Lake Opeongo, Canada. All models assumed a size-dependent release probability and presence of round gobies. Predators quickly consume all abandoned offspring (Hinch and Collins 1991; Steinhart et al. 2004).
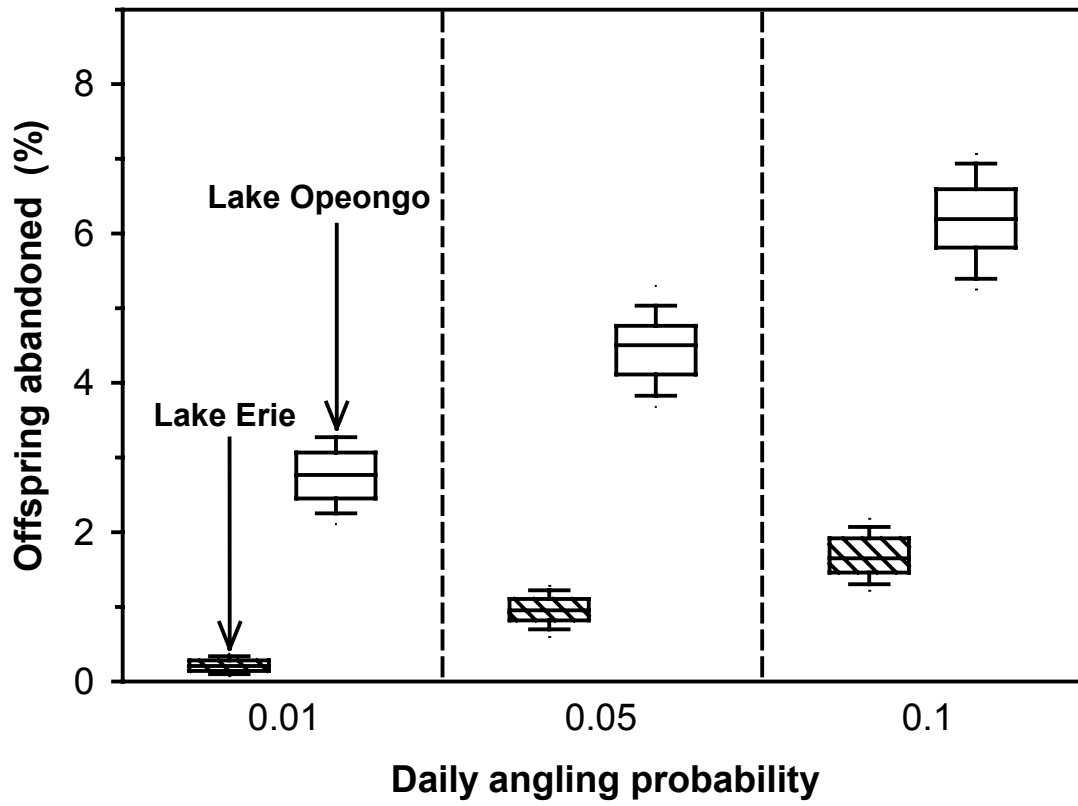
Figure 24.

Figure 25. Offspring abandoned and produced as a function of parental behavior for a simulated smallmouth bass population (200 iterations of 1,000 spawning-age males) in Lake Opeongo, Canada. In all simulations, round gobies were present and consumed 500 offspring during catch-and-release angling of guarding males (0.05 daily probability of capture and size-dependent probability of release). In simulations, individual males made decisions based on their "evolutionary knowledge" of angling pressure, round gobies, and adult annual survival.   Males began with no knowledge of these conditions (i.e., their behavior under current conditions in Lake Opeongo, see text), but subsequently evolved new optimal behaviors to one or more factors. Percentages indicate change in mean offspring production or abandonment from the no knowledge condition ("None").
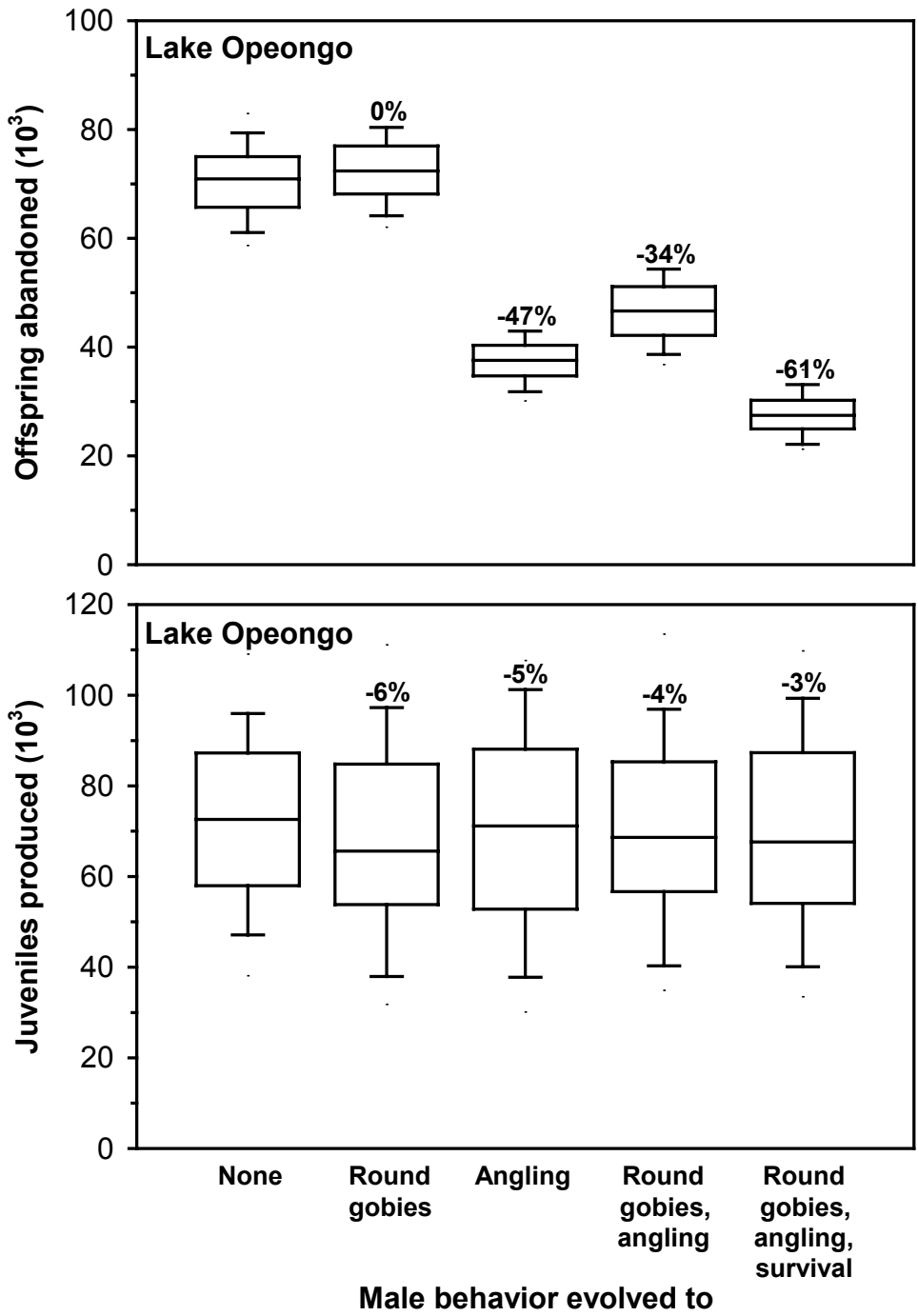
Figure 25.

Figure 26. Change in offspring production under different fishing regulations for simulated smallmouth bass populations (200 iterations of 1,000 spawning-age males) in Lake Erie, USA, and Lake Opeongo, Ontario, Canada. Arrows mark the current conditions in each lake and percentages indicate change in mean offspring production from current conditions. See text for a description of the simulations and Table 8 for simulation parameters. Note different y-axis scales.
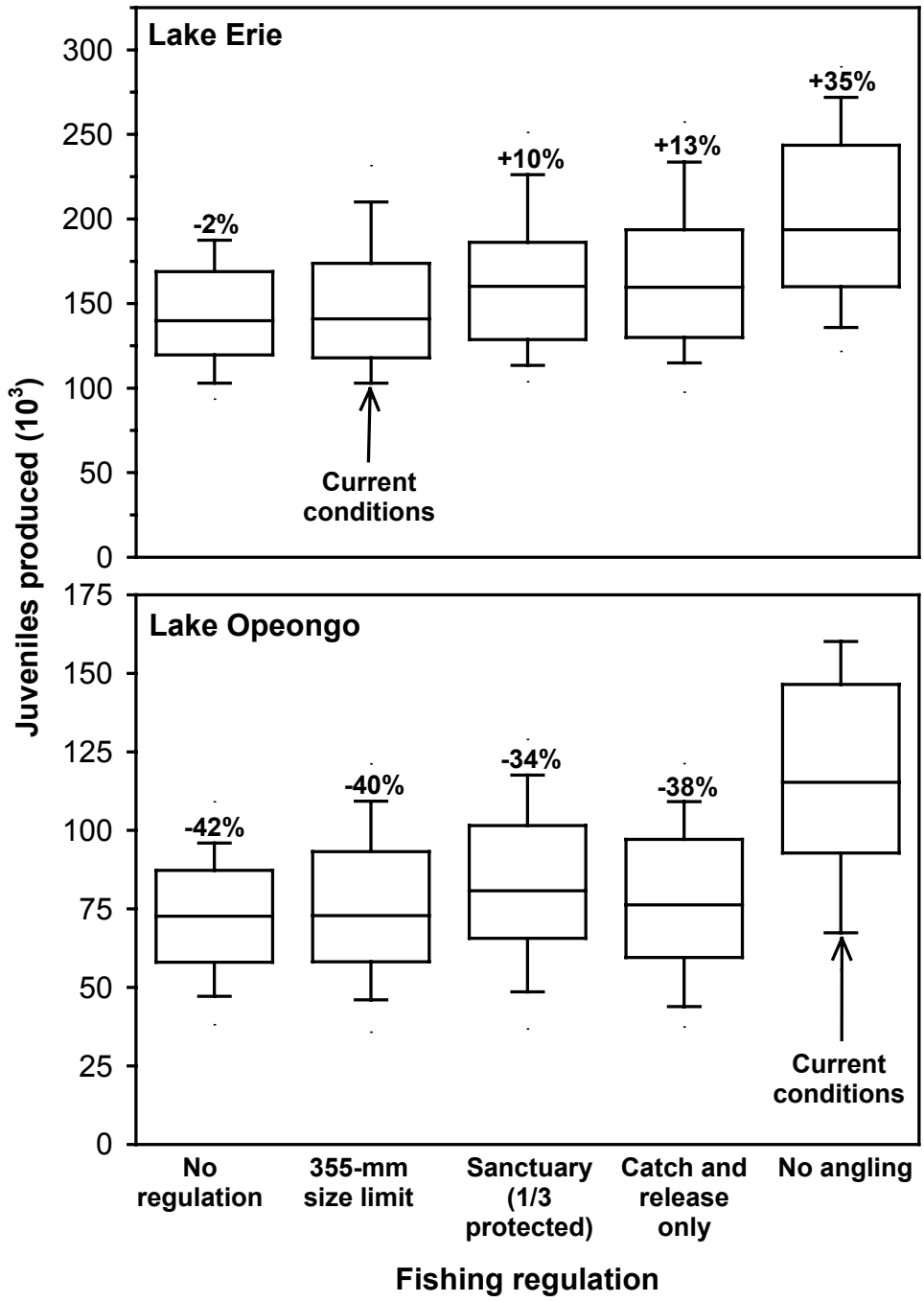
Figure 26.

Figure 27. Length-frequency distribution of spawning male smallmouth bass from

simulated populations in Lake Erie, USA, and Lake Opeongo, Ontario, Canada. Data are

from simulated populations, but were generated from length-at-age and age-frequency

distributions observed in Lake Erie during 1999-2001 and Lake Opeongo during 2001.

Males to the left of the vertical line were protected by a 355-mm minimum length limit,

currently in effect in Lake Erie.
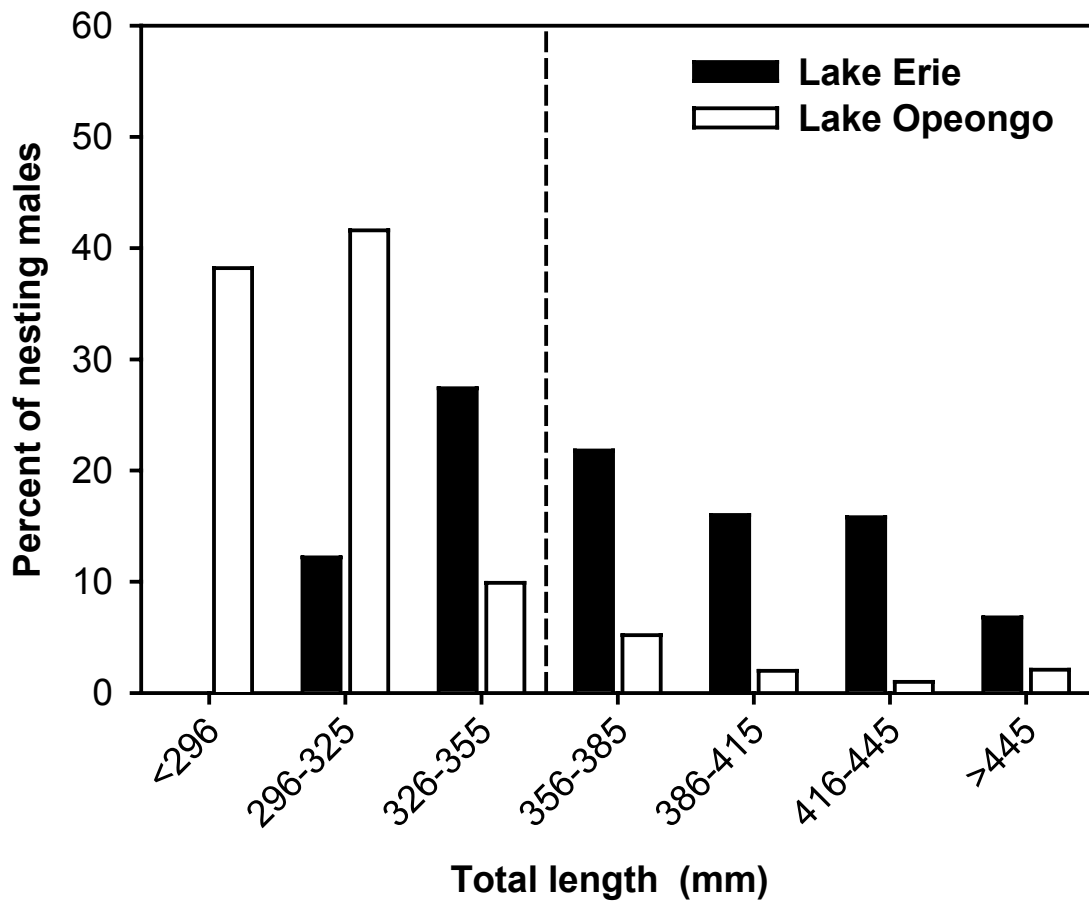
Figure 27.

Figure 28. Cumulative percent of successful and failed nests by their initiation date for a simulated smallmouth bass population (200 iterations of 1,000 spawning-age males) in Lake Erie, USA. Model parameters were adjusted to force 70% of successful nests to begin after 1 June to test the effectiveness of fishing closures during only 1-31 May or 1-30 June (see text for details).

Figure 28.

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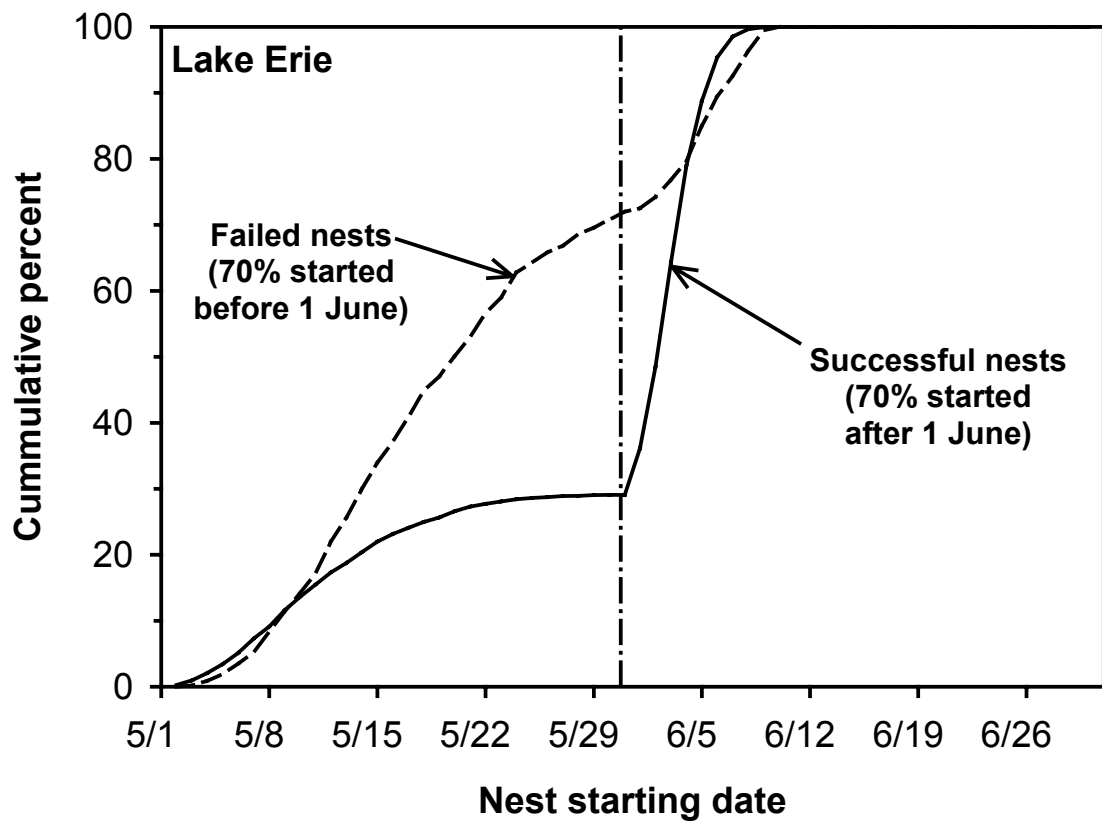
Figure 29. Offspring production under different angling regulations for a simulated smallmouth bass population (200 iterations of 1,000 spawning-age males) in Lake Erie, USA. The arrow marks the current conditions in Lake Erie and percentages indicate change in mean offspring production from current conditions. These simulations used adjusted model parameters to force 70% of successful nest to begin after 1 June (Figure 28); therefore, offspring produced are not directly comparable to data in other figures. See text and table for a description of parameter modifications.
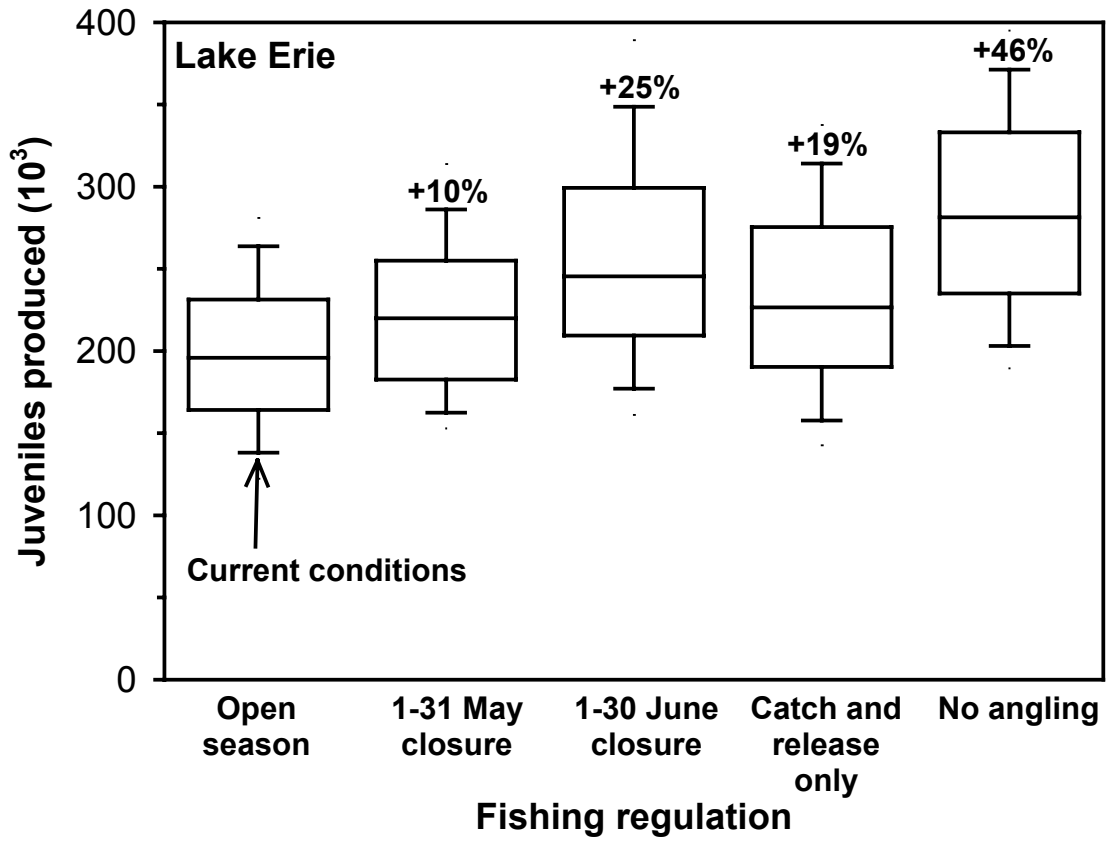
Figure 29.

CHAPTER 7

HIGH GROWTH RATE OF YOUNG-OF-THE-YEAR SMALLMOUTH BASS IN

LAKE ERIE: A BENEFIT OF THE ROUND GOBY INVASION?

ABSTRACT

The round goby (*Neogobius melanostomus*) first appeared in Lake Erie in 1995, quickly reaching extremely high densities (>100/m^2) in nearshore habitats frequented by juvenile smallmouth bass (*Micropterus dolomieu*). As round gobies are both potential competitors and prey for smallmouth bass, we investigated changes in young-of-the-year (YOY) smallmouth bass diet and growth between pre- and post-round goby invasion in the Bass Islands, Lake Erie. During 1999-2001, YOY smallmouth bass fed more frequently on fish than in either 1919 or 1975. Fish comprised 21% of YOY smallmouth bass (21-100 mm total length) diets by weight in 1975 and 51% of the diet during 1999-2001, but increased to 90% for YOY >100 mm during 1999-2001. Of fish consumed by first-year smallmouth bass during 1999-2001, 75% were round gobies. YOY smallmouth bass in 1999-2001 grew faster (1.2 mm/d) than those in the 1940's, 1950's, or 1970's

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(0.58-0.85 mm/d). Bioenergetic analyses revealed that a diet shift to include more fish, including round goby, generated a more energy-rich diet than before round goby invaded Lake Erie. In addition, predicted consumption by YOY smallmouth bass increased after the round goby invasion, possibly facilitated by current, high round goby densities. By consuming round gobies, juvenile smallmouth bass growth rate has increased, which has possible consequences for survival, reproduction, and age at maturity. Although the round goby invasion may have increased smallmouth bass growth rate, there are negative effects: round gobies are also predators, changing energy and contaminant transfer through the Lake Erie food web.

INTRODUCTION

Introduced species, especially those considered invasive, compete with native fauna for space, nutrients, and food (Janssen and Jude 2001; Vander Zanden et al. 1999), or reduce survival of native species through predation (Krueger et al. 2001; Mason and Brandt 1996). Invasive or nuisance species often have reproductive traits or defense mechanisms permitting them to out-compete or avoid predation by indigenous species, thus magnifying their damaging impact (Kolar and Wahl 1998; Mather and Stein 1993; Rejmánek and Richardson 1996). With increased mobility of humans has come a rise in the spread of non-indigenous species through accidental releases via global shipping and travel as well as intentional introductions into existing ecosystems (Dukes and Mooney 1999; Ricciardi and MacIsaac 2000). The alarming rate of species introductions and

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global homogenization of fauna has become a primary concern of conservationists and ecosystem ecologists (Rahel 2000; Ricciardi and Rasmussen 1998).

Exotic species also may benefit native or desirable species (Slobodkin 2001) and are often purposefully introduced by fisheries managers to provide forage or for biocontrol (Lafferty and Kuris 1996). For example, gizzard shad (*Dorosoma cepedium*) and threadfin shad (*D. petenense*) have been stocked into impoundments across the United States to provide food for popular sportfish (DeVries and Stein 1990). In the Great Lakes, exotic Pacific salmonids have been stocked both to control alewife (*Alsoa psedoharengus*) populations and to provide new angling opportunities (Kitchell and Crowder 1986; Magnuson et al. 1980). Even with planned introductions, however, introduced species often have undesirable consequences, as demonstrated in the dramatic decline of cichlids in Lake Victoria following the unauthorized introduction of Nile perch (Kaufman 1992) or the cascade of negative effects after *Mysis* were intentionally introduced into Flathead Lake, Montana (Spencer et al. 1991). Once a new species becomes established, it is essential to completely understand its complex role in the ecosystem because reducing its abundance can have a variety of effects upon the ecosystem (Zavaleta et al. 2001). As it is often difficult and expensive to extirpate a non-native species, or even to ameliorate its effects, the preferred management option often is to limit the introduction and spread of exotics into new systems (Kolar and Lodge 2002).

The Great Lakes have been colonized by an incredible number of exotic species in the last 50 years, and many have established large, self-sustaining populations with far-reaching effects on native fauna (Mills et al. 1993; Ricciardi and MacIsaac 2000). A recent invader of the Great Lakes, the round goby (*Neogobius melanostomus*) first

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appeared in the St. Claire River in 1990 (Jude et al. 1992) and were soon found in Lake Michigan (1993), Lake Huron (1994), Lake Superior and the eastern basin of Lake Erie (1995), and Lake Ontario (1997; Charlebois et al. 1997). As a benthic fish that reaches 15 cm and is quite prolific, with multiple spawnings per year, round gobies can now reach extremely high densities ($> 100/m^2$) in Lake Erie (Charlebois et al. 1997; Corkum et al. 1998). Although not ecologically dissimilar from native benthic fishes, [e.g., sculpin (*Cottus* spp.) and darters (*Ethastoma* spp.)], round gobies are found in higher densities than native predators and could drive substantial changes in the ecosystem as competitor, predator, and food source for native species (Charlebois et al. 1997; Chotkowski and Marsden 1999; Janssen and Jude 2001). Understanding how round gobies interact with the current species assemblage in the Great Lakes is of primary concern when considering if and how to control round goby numbers, their spread to new ecosystems, and possible ways to ameliorate the consequences of their invasion.

We assessed the effects of round goby on native smallmouth bass (*Micropterus dolomieu*) in Lake Erie by sampling young-of-the-year (YOY) smallmouth bass to determine if their growth rates or diet have changed since the introduction of round goby. As benthic foragers, round gobies may compete with smallmouth bass for macro-invertebrate prey, which are common to both species (Charlebois et al. 1997; Hair 1979; Wickliff 1920). Round goby may, however, provide a new food source for smallmouth bass. Therefore, while competition with round gobies could reduce YOY smallmouth bass growth, the addition of a new, calorie-rich prey source (i.e., round goby) could increase growth if incorporated into smallmouth bass diets. Because first-year growth can be important to survival, fecundity, and age of maturation, understanding the role of

round goby in the Lake Erie ecosystem will determine their potential to harm to native fish populations.

METHODS

Smallmouth bass growth

We collected young-of-the-year smallmouth bass in the Bass Islands, a belt of islands and reefs located in the western Basin of Lake Erie (41°40' N, 82°50' W) during June through September 1999-2001. Fish were collected with a variety of equipment and in a range of habitats (weeds, rocks, and human-made structures). During 8 June through 7 July 1999, we used dip nets to sample YOY smallmouth bass from nests (446 fish from 50 nests). After they had left their nests, we captured YOY smallmouth bass (414 fish) with a 23-m by 1.8-m bag seine (7-mm mesh), deployed either from a boat or as a beach seine, during late June through early September 1999-2001. We collected 60 additional fish with sinking multi-panel gillnets (13, 19, 25, and 38-mm stretch mesh) during late July through early September 1999-2000, and 212 juveniles via electrofishing in early September 1999-2001. Combined, we collected 1132 YOY smallmouth bass on 42 different days.

After capture, smallmouth bass were preserved either in 95% ethanol (EtOH; dip-netted fish) or frozen (all other fish). Total length (TL, $\pm$ 1 mm) and wet weight (WW, $\pm$ 0.001 g) were measured within 3 mos of collection. For samples preserved in EtOH, we

corrected for preservation effects by assuming a 1.35% TL loss and a 5.35% WW gain (DiStefano et al. 1994; Engel 1974; Johnson and Swanson 1974; Stobo 1972).

Historical growth data

Historical YOY smallmouth bass growth rates were determined from length and weight of fish specimens stored at the Ohio State University's Museum of Biological Diversity and F.T. Stone Laboratory. Samples were grouped by decade, including only those decades when sample dates ranged from at least early July through early September: 1940's (5 dates, 53 fish), 1950's (7 dates, 48 fish), and 1970's (5 dates, 113 fish). When collected, these samples were fixed overnight in 10% formalin, rinsed, soaked in a jar of tap water for > 3 d, and placed in successively higher concentrations of EtOH until reaching a final concentration of 70% EtOH. Total length ($\pm$ 1 mm) and wet weight ($\pm$ 0.001 g) were adjusted for typical changes in length (1.35% loss) and weight (5.35% gain) during preservation of similar-sized, spiny-rayed fishes (DiStefano et al. 1994; Engel 1974; Johnson and Swanson 1974; Stobo 1972). In addition, we used YOY smallmouth bass TL data (340 fish total), measured during June through September 1975-1977 (means for 15 dates; Hair 1979). Wet weights for these fish were estimated from a length-weight regression created from museum samples collected during the same years:

$$\text{Wet Weight} = 0.000023 \cdot (\text{Total Length})^{2.86} \quad (R^2 = 0.99, N = 177) \tag{1}$$

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We compared growth rates (mm/d) between the 1940's, 1950's, 1970's, and 1999-2001 using analysis of covariance (ANCOVA; SAS PROCGLM; $\alpha=0.05$) with decade as the class variable and day-of-year the covariate used to predict total length. The model included the decade by day-of-year interaction to test whether sample year had a significant affect on growth rate. Finally, we tested if growth rates (mm/d) from earlier decades were different from the current growth rate using t-tests to compare slopes.

Diet analyses

We quantified diet composition of 34 YOY smallmouth bass (21-47 mm TL) captured from nests during 23 June through 6 July 1999. All prey items were removed from excised stomachs, identified, counted, and measured under a compound microscope using a digitizing tablet and SigmaScan software. Prey weight was calculated from length-weight regressions (Culver et al. 1985).

Prey from YOY smallmouth bass ($N = 269$, 37-156 mm TL) captured during July-September 1999-2001, after they left their nests, were identified, counted, and weighed. Though used in growth rate estimates, gillnet-caught smallmouth bass were not used for diet analyses. Prey items were separated into categories (round goby, other fish, crayfish, Diptera, amphipods, mayflies, and other insects). Fish were further identified to species, when possible, by counting vertebrae (Becker 1983; Trautman 1981). Once classified, we dried prey at 60˚C until dry weights were stable ($\pm$ 1%), usually <48 h. Fish without complete vertebral columns were first designated as unidentified, weighed, then

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partitioned into either round goby or other fish categories based on their occurrence in identified stomach contents (75% round goby and 25% other fish, by weight).

Diet data were available for YOY smallmouth bass captured in 1919 and in the 1970's (Hair 1979; Wickliff 1920).   For both data sets (1919 and 1975), frequency of fish in diet of smallmouth bass of different sizes (9-100 mm TL in 15-mm groups) was compared with data from 1999-2001 using Mann-Whitney U-Tests. In addition, Hair (1979) quantified diets of 177 YOY using the "points method" to estimate the percent composition for different prey types. We used a G-Test to compare 1975-1976 and 1999-2001 YOY smallmouth bass diet composition by prey type.

Bioenergetic simulations

To test the assumption that differences in growth may be explained by a combination of prey caloric density and total consumption, we used a bioenergetic model to estimate consumption by YOY smallmouth bass (Hanson et al. 1997).   Two simulations, one using 1975-1977 data and one using 1999-2001 data, were run from 9 June through 10 September (93 d). Default model parameters for YOY smallmouth bass were used for respiration, egestion, and excretion equations (Shuter and Post 1990). Additional model inputs included temperature (mean daily temperature from 1980-2001; NOAA buoy data), growth and diet composition (our observations and historical data; Hair 1979). We used estimates for prey caloric density (J/g wet weight): copepods (2,800 J/g), cladocerans (2,300 J/g), diptera larvae (2,600 J/g), mayflies (5,400 J/g), amphipods (4,800 J/g), crayfish (3,000 J/g), and fish (4,500 J/g; (Cummins and Wuycheck 1971;

Hanson et al. 1997; Kershner 1998). Round goby caloric density was estimated as 3,766 J/g (personal communication, G. Kim, Ohio State University, June 2003; D. Bunnell, Ohio State University, June 2003).

Three possible explanations for differences in observed growth were tested with the bioenergetics model. First, we compared the total amount of prey (g/d) consumed in both simulations to test the hypothesis that consumption had increased following the round goby invasion. Second, shifts in diet to prey of different energy density may have altered growth rate, so we compared the mean energy density of prey consumed during the 1975-1977 and 1999-2001 simulations. Finally, because we did not have temperature data for 1975-1977, the temperatures used in our simulation may have resulted in erroneous model output. Therefore, we ran 1975-1977 simulations with different temperatures (± 5ºC from the 1980-2001 daily averages) to test the sensitivity of the model to temperature.

RESULTS

Smallmouth bass growth

In their first summer, smallmouth bass in Lake Erie grew more rapidly during 1999-2001 than previously documented (Figure 30). We found a significant decade by day-of-year interaction ($F_{3,77}$=18.84, p<0.0001), indicating differences in growth rate among sample periods. Upon closer examination, growth was higher in 1999-2001 (1.2 mm/d) than in the 1940's (0.58 mm/d; t = 6.81, p < 0.001), the 1950's (0.73 mm/d; t = 2.62, p =

0.01), or the 1970's (0.85 mm/d; $t = 4.67$, $p < 0.001$). While long-term preservation may

have affected our growth estimates, we corrected for the average shrinkage of samples

preserved in EtOH (DiStefano et al. 1994; Johnson and Swanson 1974), and most of the

1970's measurements (75% of fish) were on fresh fish. Differential hatch timing could

have influenced these results. Fish hatched later in the season start growing later but

likely faced warmer water temperatures and, thus, a more favorable growth environment.

By including multiple years of data in each decade, we reduced the possibility that inter-

annual variability in hatch times drove our results.

Smallmouth bass diet

Historically, young-of-the-year smallmouth bass (21-100 mm TL) in Lake Erie

consumed zooplankton, amphipods (Gammarus), mayflies (Ephemeroptera),

chironomids, and fish (Hair 1979; Wickliff 1920). During 1999-2001, YOY smallmouth

bass diets contained more fish, especially round goby, and fewer amphipods and mayflies

than during 1975-1976 (Figure 31; $G^2 = 23.6$, $df = 6$, $p=0.0006$). The frequency of

amphipods and mayflies in smallmouth bass diets during 1999-2001 (18% and 2%,

respectively) and 1919 (0% and 16%) was lower than in 1975 (64% and 42%). Not only

was the weight of fish consumed greater during 1999-2001 than 1975-76, but the

frequency of fish in diets also was higher than in previous decades. During 1999-2001,

54% of all smallmouth bass (21-100 mm) consumed fish, but only 23% in 1919 and 20%

in 1975 contained fish. Fish dominated the diets of smallmouth bass with TL >50 mm

during the current study: for all but the smallest YOY (21-35 mm), smallmouth bass ate

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fish more frequently during 1999-2001 than in 1975 (Figure 32; $W_{16,16} = 185.5$, $p = 0.003$) or in 1919 ($W_{16,11} = 111.0$, $p = 0.036$). Of fish consumed, 75% (by weight) were round goby during 1999-2001.

Bioenergetic analyses

To match observed first-summer growth during 1999-2001, YOY smallmouth bass consumed more prey (by weight) than during 1975-77 (Figure 33). In fact, model simulations predicted that prey consumption from June 9 through September 10 during 1999-2001 (49.9 g) was nearly double that of the mid 1970's (26.2 g). For smallmouth bass >5-g wet weight, round goby was the dominant prey item (by weight) during 1999-2001 (Figure 33). Consumption of invertebrate prey also differed in the simulations: in the 1970's YOY smallmouth bass consumed more Diptera, Gammarus, and crayfish, while during 1999-2001 smallmouth bass consumed more Ephemeroptera.

A confounding factor for these results was that smallmouth bass grew more during 1999-2001 than in the 1970's and, therefore, consumption had to increase to meet metabolic demands of the larger fish during 1999-2001. Therefore, we compared consumption data for YOY smallmouth bass < 9.1 g (the average size on September 10 in the 1970's). Average consumption (g/d) of YOY smallmouth bass was 15% higher during 1999-2001 (0.22 g/d) than in the 1970's (0.19 g/d) when considering only the period when fish were of the same size (Figure 34). Daily consumption of prey during 1999-2001 exceeded that of the 1970's once round gobies became the most dominant

prey. When YOY smallmouth bass were of the same sizes, they consumed more invertebrate prey in the 1970's (16.4 g) than during 1999-2001 (4.9 g).

The inclusion of round goby in the diet, combined with increased consumption of Ephemeroptera, raised the mean energy density of prey consumed during 1999-2001 compared to the 1970's (Figure 35). When YOY smallmouth bass were of similar size (< 9.1 g), the average prey energy density was 8% higher during 1999-2001 (3,745 J/g) than in the 1970's (3,473 J/g). Increased prey energy density was attributable to a shift in diet to include more round gobies and Ephemeroptera. Round gobies have a higher energy density (3,766 J/g) than many of the benthic invertebrates common in diets during the 1970's: crayfish (3000 cal/g), Diptera (2,600 cal/g), and zooplankton (1,000-3,000 cal/g; Cummins and Wuycheck 1971); however, round gobies are lower in energy density than other common fish prey, such as sculpins (4,500 J/g), bluegill (*Lepomis macrochirus*, 5,500 J/g), shiners (*Notropis* spp., 5,000 J/g), rainbow smelt (*Osmerus mordax*; 5,700 J/g), and alewife (*Alosa pseudoharengus*; 5,000 J/g; Cummins and Wuycheck 1971; Hartman and Margraf 1992; Hanson et al. 1997; Kershner 1998). In addition, mean energy density of prey was higher during 1999-2001 because more Ephemeroptera (5,400 cal/g) were consumed than in the 1970's when lower energy density crayfish, Diptera, and amphipods (4,800 cal/g; Cummins and Wuycheck 1971) were common prey. When the consumption and prey energy differences were combined, YOY smallmouth bass consumed 21% more energy during 1999-2001 (800 J·g body weight^{-1}·d^{-1}) than during the 1970's (660 J·g body weight^{-1}·d^{-1}).

Differences in YOY smallmouth bass growth could not be explained by an error in our estimate of daily temperatures for the 1970's bioenergetic simulation. Although we only

had temperature data from 1980-2001, there was no trend for increasing or decreasing temperatures during that span and average June 9 - September 10 temperatures only fluctuated −1.5 to +2.2ºC from the 21-year mean, suggesting that our use of the mean daily temperatures in our bioenergetic simulations was acceptable. In addition, we used multiple years of growth data for each simulation, so year-to-year variation in temperature, and its effect on growth, would have been accounted for. Even if temperatures were quite different during the 1970's, bioenergetic simulations using temperatures ± 5ºC from the 1980-2001 daily averages, while holding consumption constant, only produced a ± 2 g difference in end weight. Therefore, unless consumption dramatically changed under different temperatures, a slight error in our estimate of daily temperatures would not have produced the more than twofold increase in end weight observed between the 1970's and during 1999-2001.

DISCUSSION

   Young-of-the-year smallmouth bass as small as 45 mm TL fed on round goby, with this prey becoming dominant for smallmouth bass > 60 mm TL. Not notably rich in calories, round gobies do provide a more energy dense prey source than some traditional macro-invertebrate prey. But bioenergetic simulations suggest that both mean prey energy density and total consumption by YOY smallmouth bass increased after the establishment of round gobies in Lake Erie. High densities of round gobies (> 100/m^2) provide a hyper-abundant prey source for smallmouth bass (Charlebois et al. 1997). With these prey densities, search costs may be very low (Adams et al. 1982; MacKinnon

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1972). Round goby and juvenile smallmouth bass are both abundant in shallow, rocky

habitats (Charlebois et al. 1997; Gross and Kapuscinski 1997; Jude and DeBoe 1996).

Further, because fecund round goby begin spawning early and produce multiple clutches

during the summer (Charlebois et al. 1997; Corkum et al. 1998), ample numbers and

sizes of round goby are available throughout spring and summer. Thus, fast smallmouth

bass growth derived from increased consumption of the round goby, an extremely

abundant and relatively high energy density prey.

Increased YOY smallmouth bass growth is significant because recruitment of many

YOY fishes in Lake Erie can be limited by competition for food (Gopalan et al. 1998;

Tyson and Knight 2001). With the addition of round goby, more fish are competing for

food in rocky, littoral habitats favored by smallmouth bass (Jude and DeBoe 1996). But,

concurrent with increases in potential competitors, phosphorous reductions and habitat

alteration by exotic zebra mussels (*Dreissena polymorpha*) have increased biomass of

amphipods, mayflies, and other benthic invertebrates by providing additional substrate

and food (Hayward and Margraf 1987; Krieger et al. 1996). Fish are now more common

in YOY smallmouth bass diets, but the total weight of invertebrate prey consumed was

higher in the 1970's and during 1999-2001. While smallmouth bass consumed fewer

amphipods and crayfish during 1999-2001 than in the 1970's, they consumed more

mayflies (by weight) after the round goby invaded Lake Erie. Observed changes in the

amount and type of invertebrate prey in smallmouth bass diets could have resulted either

from competition, or a preference for round gobies as prey. Our bioenergetic simulations

suggest that juvenile smallmouth bass have increased their total consumption by

including round goby in their diet, and because round goby are more energetically rich

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than many invertebrate prey, we believe that YOY smallmouth bass are selecting round goby over invertebrate prey shared with competing fishes.

Although smallmouth bass historically grew faster in Lake Erie than in other systems (Doan 1940), growing even faster may increase survival to adulthood. For the closely related largemouth bass (*M. salmoides*), rapid juvenile growth improves overwinter survival, especially the survival of late-hatched offspring (Ludsin and DeVries 1997; Post et al. 1998). First summer temperatures, a correlate of growth, strongly predict smallmouth bass recruitment to adulthood (Casselman et al. 2002; Clady 1975; Serns 1984). Rapid growth also may improve survival because fast-growing fish reduce their risk of predation more quickly than slow growing fish (Crowder et al. 1987; Miller et al. 1988).

Growth rate and survival have been shown to affect age, size, and fecundity of first reproduction (Stearns 1992; Wootton 1990). Faster growth of YOY smallmouth bass may alter the reproductive dynamics and nest success of smallmouth bass, especially if high growth continues due to adult consumption of round gobies. Rapidly growing individuals may mature earlier than slow-growing individuals (Stearns 1992) and, in Lake Erie, with its high fishing related mortality, early maturation may afford smallmouth bass a higher probability of reproducing before being captured by an angler. In addition, fast-growing fish may produce more offspring at the same age than slower growing individuals in their cohort because smallmouth bass fecundity increases with size (Hair 1979) and large male smallmouth bass tend to receive more eggs than small males (Baylis et al. 1993). Large size is also an advantage because substantial energy reserves are required for nest-guarding male smallmouth bass (Mackereth et al. 1999);

thus, individuals with low energy reserves may abandon nests prematurely (Ridgway and

Shuter 1994). Male smallmouth bass may benefit from consuming round gobies while

defending their offspring; however, nest-guarding males eat very little while providing

parental care (Mackereth et al. 1999, Chapter 3).

Despite the benefits of increased growth for YOY smallmouth bass, and possibly other

native piscivores, adding round goby to Lake Erie poses many potential problems.

Round gobies are competitors and predators of many native species (Charlebois et al.

1997; Chotkowski and Marsden 1999; Janssen and Jude 2001). Although competition

with YOY smallmouth bass (20-155 mm TL) was not proven in our study, round gobies

may reduce prey availability for various age of smallmouth bass, or for other native

fishes. By preying on benthic invertebrates, zebra and quagga mussels (*D. bugensis*),

round goby may indirectly alter prey abundance for native species and act as a conduit

from the benthos to the pelagia for harmful toxins, such as PCB's and mercury (Morrison

et al. 1997). Indeed, bioaccumulation of toxins poses a risk to native fauna, as well as

humans who consume Lake Erie fishes. Round gobies also may prey on native fishes

and, given such high round goby densities, they could have profound effects as predators

(Steinhart et al. 2004).

Because round gobies are beneficial to YOY smallmouth bass growth, the

consequences of a round goby population crash also must be considered. Like many

invaders, round goby numbers may peak, then subside to more sustainable levels

(Bachmann et al. 2001). Indeed, initial data suggest that round goby abundance has

declined in some areas of Lake Erie (personal communication, C. Knight, Ohio

Department of Natural Resources, Fairport, May 2003). The reduction or removal of

introduced species can have far-reaching consequences for the ecosystem (Zavaleta et al. 2001). Although round goby compete with some native fishes (Janssen and Jude 2001; Jude and DeBoe 1996), a rapid decline in round goby numbers may or may not be accompanied by a corresponding, immediate increase in depressed native species owing to the myriad of interactions in the food web. But if, as our results suggest, smallmouth bass growth benefits when round gobies are abundant, future growth, and possibly survival, may be lower if round goby populations decline. Therefore, although some fast-growing year-classes may attract attention of anglers, current growth rates may not be sustainable, so managers must be prepared to lower expectations of anglers in the future (Gale 1987).

We observed higher YOY smallmouth bass growth associated with the introduction of the round goby. Although round gobies have the potential to compete with YOY smallmouth bass, we found that smallmouth bass ate nearly as much invertebrate prey as in the past (by weight) and supplemented their diet by consuming many round gobies. As we realize the full range of interactions between round goby and native fauna, we will be better prepared to limit or compensate for the impact of round goby, as well as better understand how the Lake Erie ecosystem may change following a rapid change in round goby abundance. What is clear, however, is that the round goby represent only one of a series of successful invaders in the Great Lakes that have had dramatic effects throughout the food web (Mills et al. 1993; Ricciardi and MacIsaac 2000).

Figure 30. Change in smallmouth bass total length during their first summer of life in the

Bass Islands, Lake Erie. Growth rate was higher in 1999-2001 (1.2 mm/d) than in the

1940's (0.58 mm/d; t = 6.81, $p < 0.001$), the 1950's (0.73 mm/d; t = 2.62, $p < 0.01$), or

the 1970's (0.85 mm/d; t = 4.67, $p < 0.001$).
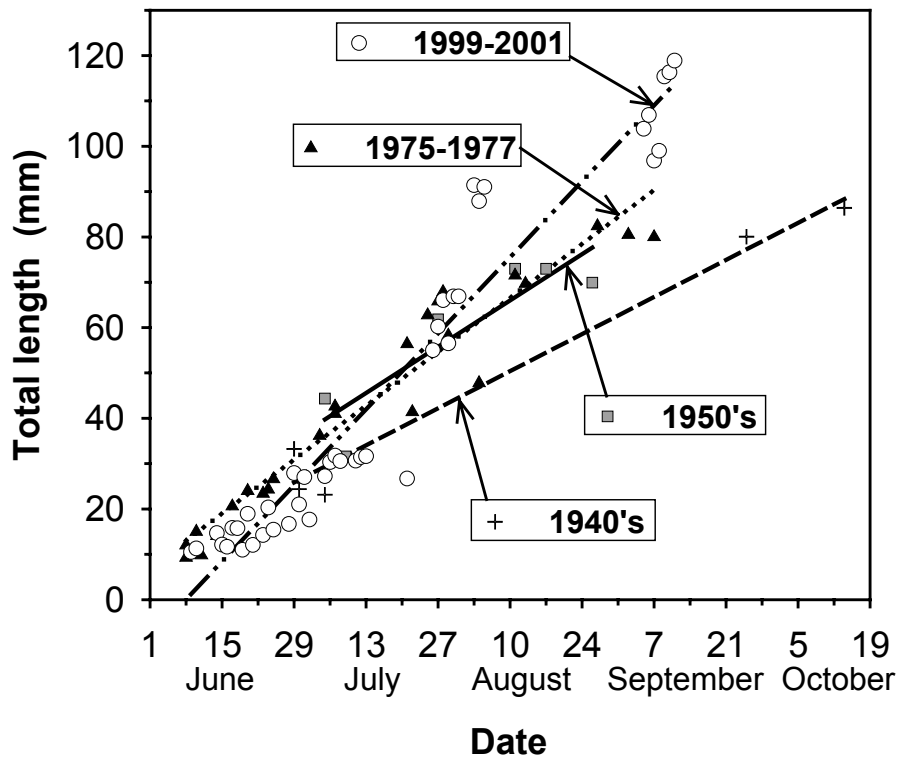
Figure 30.

Figure 31. Young-of-the-year smallmouth bass diet during 1975-1976 (**A**) and during 1999-2001 (**B**) in the Bass Islands, Lake Erie. Diet composition during 1975-1976 was estimated using the points method for estimating percent of the total diet of each prey (Hair 1979). During 1999-2001, percent composition was calculated from dry weight of prey in the diet. Samples were collected during mid-June through early-September for 1975-1976, and 23 June - 11 September for 1999-2001.

A) 1975-1976
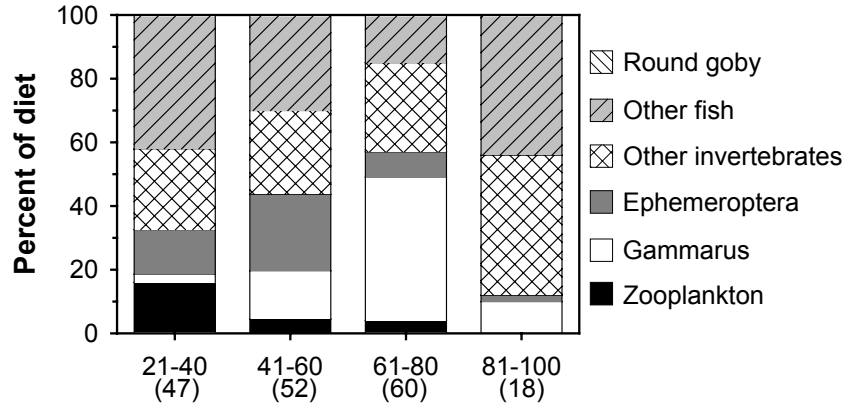
B) 1999-2001
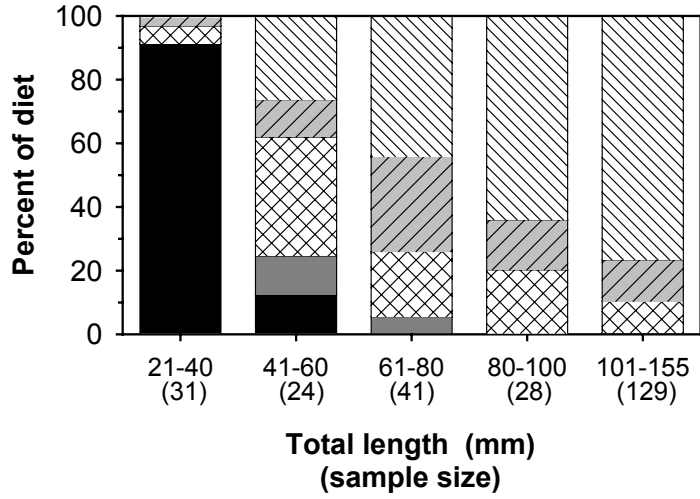
Figure 31.

Figure 32. Frequency of fish in the diet of young-of-the-year smallmouth bass in the

Bass Islands, Lake Erie in 1919 (Wickliff 1920), 1975 (Hair 1979), and during 1999-

2001. Sample size for each size class is shown above each bar. Frequency of fish in the

diet of smallmouth bass differed little within the length range 96-155 mm TL, so these

data were grouped.
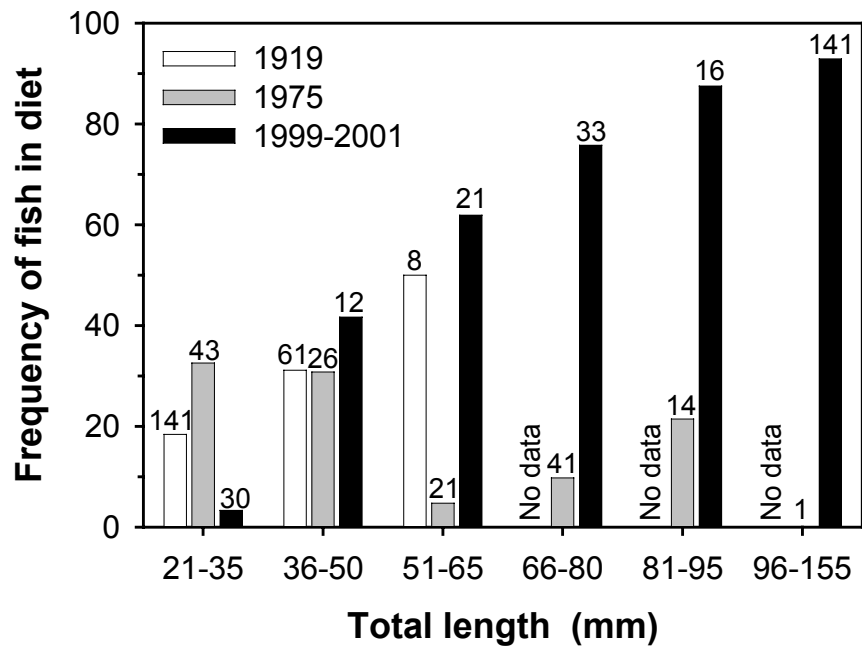
Figure 32.

Figure 33. Bioenergetic simulations of consumption (g wet weight/d) by prey type for young-of-the-year smallmouth bass in the Bass Islands, Lake Erie, in the 1970's (**A**) and during 1999-2001 (**B**). Simulations for both periods were run 93 d in duration (9 June-10 September), during which YOY smallmouth bass grew to more than double the weight during 1999-2001 than in the 1970's. Round gobies, which contributed >60% of smallmouth bass diets (by weight) during late July through early September, did not occur in Lake Erie during the 1970's.
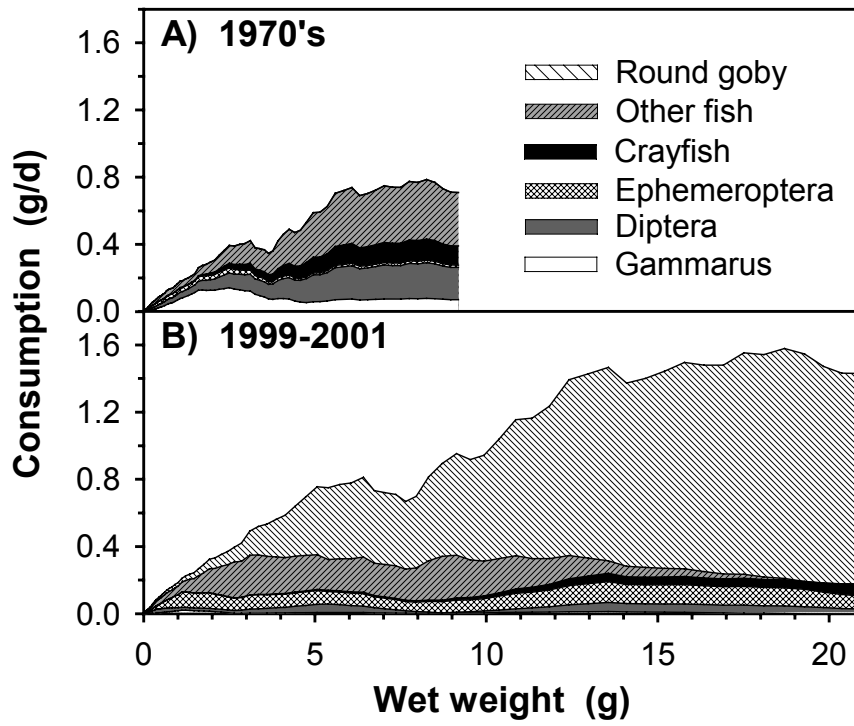
Figure 33.

Figure 34. Bioenergetic simulations of average daily consumption by young-of-the-year

smallmouth bass in the Bass Islands, Lake Erie, in the 1970's and during 1999-2001. For

the 1999-2001 simulation, consumption is split into all prey consumed and only

consumption of round gobies. Average daily consumption for YOY smallmouth bass of

the same weights (<9.1 g) was 15% higher during 1999-2001 than in the 1970's.
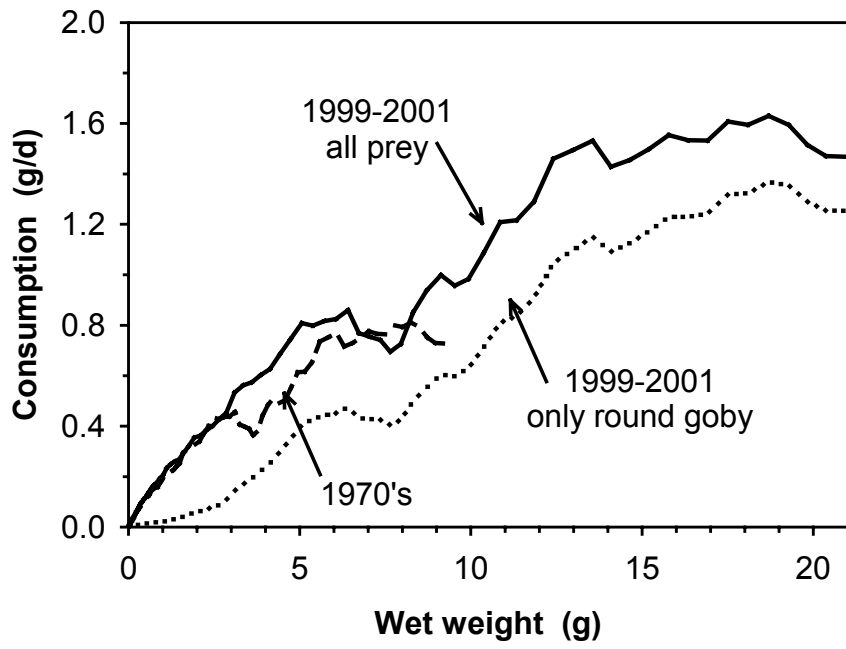
Figure 34.

Figure 35. Bioenergetic simulations of average prey energy density consumed by young-of-the-year smallmouth bass in the Bass Islands, Lake Erie, in the 1970's and during 1999-2001. Average energy density of prey consumed by YOY smallmouth bass of the same weights (<9.1 g) was 8% higher during 1999-2001 than in the 1970's.
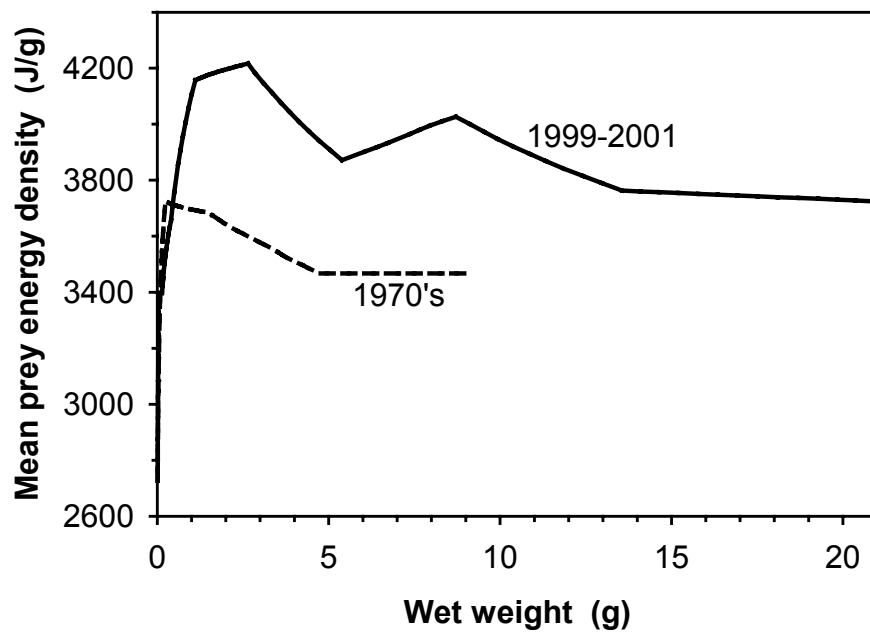
Figure 35.

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