Management and Ecological Note

Reproductive investment drives capture probability in fish: an interspecific comparison

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Sustainable use of fisheries resources requires knowledge of how exploitation interacts with life history. Often, life history characteristics within a species can change across latitudes, resulting in population-dependent variations in growth rates, maturation schedules, reproductive effort, parental care and mortality (Winemiller & Rose 1992; Yamahira & Conover 2002). Despite this interpopulation variation, species and species complexes with wide geographic ranges are often managed with common approaches, ignoring life history variation (Quinn 2002). Recently, proposals to liberalise spring fishing for *Micropterus* at the northern extent of their natural range have gained interest with regulatory agencies (Jackson & Brooking 2004; Pearson 2008; Ontario Ministry of Natural Resources 2012). Year-round fishing for *Micropterus* is common in southern jurisdictions, while northern jurisdictions often restrict spring fishing to protect spawning individuals (Quinn 2002). In an effort to understand better potential consequences for homogenising regulations across broad spatial scales through liberalising fishing regulations, the present study compared how reproductive characteristics influence vulnerability to angling during parental care in largemouth bass, *Micropterus salmoides* Lacépède, and Florida bass, *Micropterus floridanus* (Lesueur), two phylogenetically related species (Near *et al.* 2003) inhabiting different latitudes.

Brood size and nest defence behaviour were compared between nest-guarding male Florida bass from northern Florida [Lake Susan (30° N, 82° W) and Devil's Hole (30° N, 82° W)] and largemouth bass from south-eastern Ontario [Lake Opinicon (45° N, 76° W) and Elbow Lake (44° N, 76° W)] sampled at the beginning of the spawning season (early March, 2011 at Florida sites, mid-May, 2011 at Ontario sites). All four populations inhabited lakes with similar trophic states previously described as oligotrophic to mesotrophic (Carlson 1977; Canfield & Hoyer 1992) and had similar angling history (D. Philipp and M. Allen, personal observation). Nests with brood-guarding males were located by snorkel surveys in the littoral zone and marked with individually numbered plastic tags. Male total length (TL) was visually estimated under water as described by Suski and Philipp (2004). Following nest detection, the number of

potential egg predators in a 2-m circumference around the nest was assessed using a cumulative predator count over 2 min, similar to Gravel and Cooke (2009). Vulnerability to angling, a metric indicative of brood defence (Suski & Philipp 2004), was quantified by anglers in a boat who presented three fishing lures to an area within 2 m of each male's nest (12-cm black/silver floating minnow bait, 6-cm white jig, 15-cm black plastic worm, in this order). Each lure was cast five times (15 casts in total) and the number of strikes recorded. Following the presentation of the lures, egg number (i.e. brood size) was quantified using a transparent 1-m^2 acrylic gridded sheet (Landsman *et al.* 2011). All activities were approved by the Institutional Animal Care and Use Committee of the University of Illinois at Urbana-Champaign (protocol #11036). Male TL, predator count and brood size were compared using a nested analysis of variance with *lake* nested within *latitude* (Wagner *et al.* 2006). The proportion of fish that struck the minnow bait on the first cast and the proportion of fish that hit any of the three lures during the 15 casts were compared using a nominal logistic model with the same hierarchical design described previously (Blanchette *et al.* 2002). Means were separated using a Tukey–Kramer test when the nested term [i.e. *lake* (*latitude*)] was significant (Zar 1999). Statistical analyses were performed with JMP 9.0.2 (SAS Institute, Cary, NC, USA).

Both males and brood sizes were significantly larger in Ontario compared to Florida, and brood sizes varied significantly between Ontario lakes (Table 1). Only bass from Ontario struck the minnow bait on the first cast (nominal logistic model: $\chi^2 = 14.65$, d.f. = 1, $P = <0.001$,

Fig. 1). In addition, 84% of Ontario males struck at least one of the 15 casts presented, compared with 43% recorded for nest-guarding Florida bass (nominal logistic model: $\chi^2 = 12.18$, d.f. = 1, $P = 0.001$, Fig. 1). Males from the same species had similar probabilities of striking the first or any of the 15 casts, making differences between lakes within latitudes not statistically significant (nominal logistic model: $\chi^2 = 1.96$, d.f. = 2, $P = 0.56$ and $\chi^2 = 1.40$, d.f. = 2, $P = 0.56$, Fig. 1). Finally, predator densities showed a high variability across lakes within a latitude but not between latitudes (Table 1).
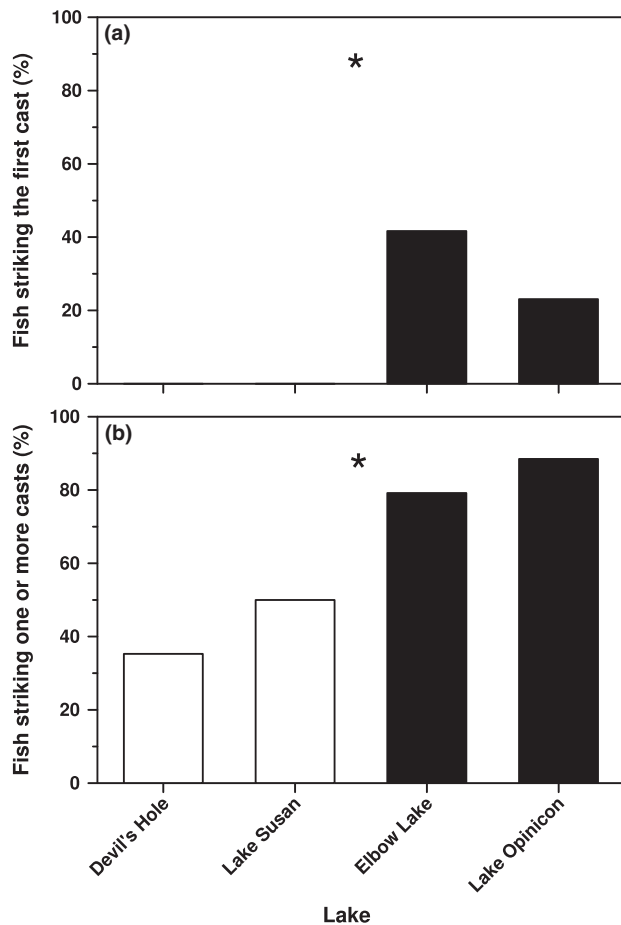
Results from the current study indicate pronounced differences in the response to angling across latitudes, with nest-guarding bass from Ontario much more likely to strike a lure than fish from Florida. Often, vertebrate populations from high latitudes show increased investment per brood, coupled with fewer reproductive events per year, resulting in large broods and high brood defence relative to low-latitude populations (Spencer & Steinhoff 1968; Leggett & Carscadden 1978; Chalfoun & Martin 2007). Multiple reproductive events per year have been reported for bass stocked into tropical reservoirs and for one of the Florida populations investigated here (Waters & Noble 2004; Rogers & Allen 2010; Shaw & Allen 2014), while northern bass populations often only achieve a single spawning event per season (Ridgway 1989). Besides a potential latitude/site effect, a number of additional factors have previously been shown to influence angling vulnerability for brood-guarding bass. For example, larger nesting male bass, typically with larger broods, are more aggressive nest defenders than smaller males, likely due to increased potential fitness returns, or

Table 1. Male size, brood size and number of predators near nests of brood-guarding largemouth bass (Lake Opinicon; $N = 27$, Elbow Lake; $N = 24$) and Florida bass (Devil's Lake; $N = 17$, Lake Susan; $N = 28$) with results of the statistical tests comparing variables across lakes and latitudes

Dependent variable	Measured variables		Statistical analyses			
	Lake	Mean (SE)*	Independent variable	d.f.	$F^{\dagger}$	P
Male size (mm)	Lake Opinicon	355 (6)a	Latitude	1	52.23	<0.0001
	Elbow Lake	338 (24)a				
	Devil's Hole	286 (10)b	Lake (Latitude)	2	2.00	0.14
	Lake Susan	299 (8)b				
Brood size	Lake Opinicon	6759 (623)a	Latitude	1	22.87	<0.0001
	Elbow Lake	4168 (930)b				
	Devil's Hole	1831 (290)bc	Lake (Latitude)	2	4.71	<0.01
	Lake Susan	1682 (267)c				
Predators at nest	Lake Opinicon	4 (1)ab	Latitude	1	3.07	0.08
	Elbow Lake	0 (0)a				
	Devil's Hole	7 (2)c	Lake (Latitude)	2	7.811	<0.001
	Lake Susan	3 (0)bc				

* Dissimilar letters indicate significant differences between parameters at $\alpha = 0.05$ level (Tukey–Kramer HSD).

† F ratios for analyses of variance (male size, brood size and predators at nest).

Figure 1. Proportion of brood-guarding bass striking at lures on the first cast (a) and percentage of males striking at lures one or more times within the 15 casts (b) for largemouth bass at Ontario sites (filled bars) and Florida bass at Florida sites (open bars). Asterisks denote significant differences across geographical locations.

breeding season length (Keast & Eadie 1985; Winemiller & Rose 1992; Suski & Philipp 2004). Species-specific differences and/or past angling history (i.e. harvest) across latitudes may have also played a role. Thus, while the exact mechanism for elevated aggression during the spawning period was not defined, results demonstrate that brood-guarding bass from Ontario were significantly more vulnerable to angling lures than were fish from Florida.

The more aggressive response to angling lures observed in largemouth bass relative to Florida bass highlights the potential for increased risk of angling-related disturbances for northern bass populations. Even short-term removal of a nest-guarding male (e.g. catch and release) can negatively affect reproductive success due to egg predation (Philipp *et al.* 1997). By contrast, the longer breeding seasons and potential for multiple broods in a year for Florida bass could be a partial explanation as to why decades of angling during the spring may have imparted little population-level impairment on southern populations of *Micropterus* (Gwinn & Allen 2010). Relationships between reproductive success and recruitment have not been well defined for *Micropterus* spp. and should be the subject of future investigations, ideally across broad latitudinal ranges.

Results from the current study emphasise that management needs to consider the long-term, evolutionary impacts of regulations. A number of recent studies have highlighted the potentially negative population-level consequences that can arise through harvest or improper management of fish and wildlife resources, resulting either from evolutionary or plastic changes to populations (Olsen *et al.* 2004; Darimont *et al.* 2009; Stenseth & Dunlop 2009; Sutter *et al.* 2012). Together, these studies, coupled with the present results, emphasise the need to consider potential population-dependent evolutionary responses to human resource use, and the need for a precautionary approach to reduce the risk of undesirable evolutionary population changes. The current study shows that populations of *Micropterus* can express significant differences in vulnerability to angling during brood defence, potentially as a result of local adaptation, which could be partially mediated by climatic factors, spawning duration or human influences. Due to the potentially negative impacts that may result, even under catch-and-release regulations (e.g. Philipp *et al.* 1997), managers should acknowledge population-dependent differences. Despite differences in male sizes, high-latitude environments offering limited reproductive opportunities could potentially result in more aggressive nest-guarding behaviour and, thus, more vulnerable bass populations; southern populations may be less vulnerable due to more reproductive opportunities per year. Because the current

a breeding event closer to the end of their reproductive lifetime (Suski & Philipp 2004; Steinhart *et al.* 2008). In addition, past harvest in heavily fished populations may remove vulnerable individuals and result in reduced response to angling (Philipp *et al.* 2009). To minimise the latter, effort was taken to standardise angling history across latitudes to the best extent possible (i.e. both Florida lakes and Elbow lake were private access and limited fishing, whereas in Lake Opinicon, fishing is not permitted during spring). Despite differences in angling history and predator abundances across lakes within a latitude, responses to angling did not differ across lakes within a latitude, suggesting only a minor influence of angling history and predator abundance on nest defence behaviour. Therefore, elevated angling vulnerability of Ontario fish may be due to a suite of factors related to larger (older) male sizes, coupled with larger broods and/or fewer reproductive opportunities per year, mediated by reduced

study only examined individuals residing at the extreme ends of their natural range with a limited sample size, additional work needs to quantify population differences in reproductive tactics and their role in defining vulnerability to angling, ideally at mid-latitudes. Together, the findings of this study suggest managers should be cautious when extrapolating population-level trends across environments and species.

Acknowledgments

References

Blanchette C.A., Miner B.G. & Gaines S.D. (2002) Geographic variability in form, size and survival of *Egregia menziesii* around Point Conception, California. *Marine Ecology Progress Series* **239**, 69–82.

Canfield D.E. & Hoyer M.V. (1992) *Aquatic Macrophytes and their Relation to the Limnology of Florida Lakes*. Final Report. Bureau of Aquatic Plant Management, Florida Department of Natural Resources, Tallahassee, FL. Available from: University of Florida, Gainesville, FL.

Carlson R.E. (1977) A trophic state index for lakes. *Limnology and Oceanography* **22**, 361–369.

Chalfoun A.D. & Martin T.E. (2007) Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis. *Animal Behaviour* **73**, 579–585.

Darimont C.T., Carlson S.M., Kinnison M.T., Paquet P.C., Reimchen T.E. & Wilmers C.C. (2009) Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences* **106**, 952–954.

Gravel M.-A. & Cooke S.J. (2009) Influence of inter-lake variation in natural nest predation pressure on the parental care behaviour of smallmouth bass (*Micropterus dolomieu*). *Ethology* **115**, 608–616.

Gwinn D.C. & Allen M.S. (2010) Exploring population-level effects of fishery closures during spawning: an example using largemouth bass. *Transactions of the American Fisheries Society* **139**, 626–634.

Jackson J.R. & Brooking T.E. (2004) GreatLakesBass.com: Early opening of black bass fishing seasons in New York State: a review of issues and available data. New York black bass early season white paper. GreatLakesBass.com, Lansing, MI. Available at: http://www.greatlakesbass.com/fishing/NewYork BlackBassWhitePaper.pdf. (accessed 12 April 2014)

Keast A. & Eadie J.M. (1985) Growth depensation in year-0 largemouth bass: the influence of diet. *Transactions of the American Fisheries Society* **114**, 204–213.

Landsman S.J., Gingerich A.J., Philipp D.P. & Suski C.D. (2011) The effects of temperature change on the hatching success and larval survival of largemouth bass *Micropterus salmoides* and smallmouth bass *Micropterus dolomieu*. *Journal of Fish Biology* **78**, 1200–1212.

Leggett W.C. & Carscadden J.E. (1978) Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. *Journal of the Fisheries Research Board of Canada* **35**, 1469–1478.

Near T.J., Kassler T.W., Koppelman J.B., Dillman C.B., Philipp D.P. & Orti G. (2003) Speciation in North American black basses, *Micropterus* (Actinopterygii: centrarchidae). *Evolution* **57**, 1610–1621.

Olsen E.M., Heino M., Lilly G.R., Morgan M.J., Brattey J., Ernande B. *et al.* (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932–935.

Ontario Ministry of Natural Resources. (2012) *Proposed Changes for Bass Seasons in Southern Ontario*. Peterborough ON: Ontario Ministry of Natural Resources. Available at: http://www.ofah.org/downloads/getfile.php?id=PDF/EBR/stdprod_095259_Bass_Season.pdf. (accessed 12 April 2014)

Pearson J. (2008) *Bass Fishing on the Beds: an Indiana Perspective*. Columbia City, IN: Indiana Division of Fish and Wildlife, 8 pp. Available at: http://www.in.gov/dnr/fishwild/files/Bass_on_Beds_Final.pdf. (accessed 12 April 2014)

Philipp D.P., Toline C.A., Kubacki M.F., Philipp D.B.F. & Phelan F.J.S. (1997) The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. *North American Journal of Fisheries Management* **17**, 557–567.

Philipp D.P., Cooke S.J., Claussen J.E., Koppelman J.B., Suski C.D. & Burkett D.P. (2009) Selection for vulnerability to angling in largemouth bass. *Transactions of the American Fisheries Society* **138**, 189–199.

Quinn S. (2002) Status of restrictions on black bass fisheries in Canada and the United States. In: D.P. Philipp & M.S. Ridgway (eds) *Black Bass: Ecology, Conservation, and Management*. Washington, DC: American Fisheries Society, pp 455–465.

Ridgway M.S. (1989) The parental response to brood size manipulation in smallmouth bass (*Micropterus dolomieui*). *Ethology* **80**, 47–54.

Rogers M.W. & Allen M.S. (2010) Simulated influences of hatching-date dependent survival on year class composition and abundance. *The Open Fish Science Journal* **3**, 169–179.

Shaw S. L. & Allen M. S. (2014) Localized spatial and temporal variation in reproductive effort of Florida bass. *Transactions of the American Fisheries Society* **143**, 85–96.

Spencer A.W. & Steinhoff H.W. (1968) An explanation of geographic variation in litter size. *Journal of Mammalogy* **49**, 281–286.

Steinhart G.B., Dunlop E.S., Ridgway M.S. & Marshall E.A. (2008) Should I stay or should I go? Optimal parental care decisions of a nest-guarding fish. *Evolutionary Ecology Research* **10**, 351–371.

Stenseth N.C. & Dunlop E.S. (2009) Evolution: unnatural selection. *Nature* **457**, 803–804.

Suski C.D. & Philipp D.P. (2004) Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. *Transactions of the American Fisheries Society* **133**, 1100–1106.

Sutter D.A.H., Suski C.D., Philipp D.P., Klefoth T., Wahl D.H., Kersten P. *et al.* (2012) Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences* **109**, 20960–20965.

Wagner T., Hayes D.B. & Bremigan M.T. (2006) Accounting for multilevel data structures in fisheries data using mixed models. *Fisheries* **31**, 180–187.

Waters D.S. & Noble R. (2004) Spawning season and nest fidelity of largemouth bass in a tropical reservoir. *North American Journal of Fisheries Management* **24**, 1240–1251.

Winemiller K.O. & Rose K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196–2218.

Yamahira K. & Conover D.O. (2002) Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? *Ecology* **83**, 1252–1262.

Zar J.H. (1999) *Biostatistical Analysis*, 4th edn. Upper Saddle River, NJ: Prentice Hall, pp. 208–222.