

Round goby *Neogobius melanostomus* attraction to conspecific and heterospecific egg odours

S. YAVNO* AND L. D. CORKUM

Department of Biological Sciences, University of Windsor, Windsor, Ontario, N9B 3P4
Canada

(Received 14 September 2010, Accepted 23 February 2011)

In this study, cannibalistic and predatory responses of juvenile *Neogobius melanostomus* (either fed or deprived of food and caught during the reproductive summer or non-reproductive winter season) to water washings of fertilized eggs from conspecifics (*N. melanostomus*), heterospecifics (rainbow trout *Oncorhynchus mykiss*) and control lake water were tested. Fed juveniles (summer season) spent significantly more time on the side of the flume containing stimuli from conspecific eggs over control water, while significantly preferring control water to heterospecific stimuli. In addition, fish showed a significant preference towards stimuli from conspecific eggs over heterospecific stimuli by associating near conspecific egg odours 1.5 times longer [Correction added after online publication 28 April 2011, text changed]. Fish that were deprived of food, regardless of whether caught during the summer or winter season, did not show any preference towards either conspecific or heterospecific stimuli. These findings show that conspecific egg odours attract fed juveniles and that there is a potential to lure fish to odour traps as a means of control.

© 2011 The Authors

Journal of Fish Biology © 2011 The Fisheries Society of the British Isles

Key words: food limitation; invasive fish; non-kin intercohort cannibalism; rainbow trout.

INTRODUCTION

Food availability in an aquatic environment can have a significant effect on the behaviour of fishes. When the density of a population increases, food can become scarce, which leads to high levels of intraspecific competition among individuals (Elgar & Creps, 1992) [Correction added after online publication 28 April 2011, text changed]. In such cases, cannibalism may be an adaptive behavioural response wherein fish prey on conspecifics to survive (Wootton, 1971; Amundsen, 1994). Rather than consuming fully developed fry, eggs and embryos are usually eaten (*i.e.* non-kin intercohort cannibalism) because they are easier to handle (Smith & Reay, 1991; Acha *et al.*, 2002). In fact, freshwater fishes from several taxa consume eggs (through cannibalism or otherwise) (Roseman *et al.*, 2006; Frommen *et al.*, 2007; Johnson *et al.*, 2009a). Some species guard their nests to increase offspring survival (Cheney, 2008), but eggs are still lost to conspecifics because individuals are usually in very close proximity to one another (*e.g.* in a colony)

*Author to whom correspondence should be addressed at present address: Environmental & Life Sciences, Trent University, 1600 West Bank Drive, Peterborough, Ontario, K9J 7B8 Canada. Tel.: +1 705 748 1011 ext. 7256; email: stanyavno@trentu.ca

(Slotte *et al.*, 2006; Meunier *et al.*, 2009). Interestingly, feeding on conspecific eggs contributes to an overall reduction in intraspecific competition (Kinzler *et al.*, 2009), and this could be a useful strategy for any invasive species with a high population density.

In the Laurentian Great Lakes of North America, the round goby *Neogobius melanostomus* (Pallas 1814) is a colonial fish in which females spawn repeatedly between May and September (Wickett & Corkum, 1998). Males nest in cavities, under stones or artificial substrata, found on natural reefs or shipwrecks (Charlebois *et al.*, 1997; Wickett & Corkum, 1998) at a density of approximately one nest per m² (Wolfe, 2002). Males and females aggregate in colonies. Once a nest is established, males become territorial, interacting aggressively towards intruders. Interestingly, males in adjacent nests avoid interacting with one another as long as each male remains within his own nest. The nest opening is aggressively guarded, but the male still allows up to 15 reproductive females to enter and spawn (MacInnis & Corkum, 2000; Meunier *et al.*, 2009). During this period, numerous observations have been made of non-reproductive conspecifics attempting to enter parental nests (Wickett & Corkum, 1998), and in most cases to consume the eggs that have been deposited inside (Meunier *et al.*, 2009). Several types of heterospecific [*e.g.* rainbow trout *Oncorhynchus mykiss* (Walbaum 1792)] eggs are also consumed by *N. melanostomus* (Fitzsimons *et al.*, 2006), but no particular species is targeted. *Neogobius melanostomus* have not evolved in North American waters, thereby making this invader unfamiliar with any species of fish from the Laurentian Great Lakes. To further support this idea, field studies conducted in Lake Erie have described *N. melanostomus* as a generalist when it comes to egg predation (Nichols *et al.*, 2003; Steinhart *et al.*, 2004).

The reproductive behaviours of some *N. melanostomus* may promote cannibalistic behaviours in others. Nest-holding parental males fan inside their nests, using caudal and paired fins, to increase the amount of oxygen available for developing embryos (Meunier *et al.*, 2009). Unfortunately, this may have an inadvertent secondary effect, wherein the presence of eggs is actually advertised to the surrounding colony through the dispersal of egg odours. During the development of aquatic embryos, odourants released from eggs can be detected by other organisms (Mirza & Chivers, 2002), and in aquatic invertebrates or fishes, these compounds may be in the form of single amino acids (Ferrari & Targett, 2003; Hara, 2006). Following exposure to chemical cues from eggs, fishes engage in species-specific searching behaviours to locate this potential (egg) food source (Hara, 2006). Because *N. melanostomus* dwells in waters that are turbid, limiting visual communication, the use of olfaction to detect cues becomes important. Thus, *N. melanostomus* is believed to be capable of locating fertilized conspecific and heterospecific eggs using only odourants (Meunier *et al.*, 2009).

In this study, the behavioural responses of juvenile *N. melanostomus*, a life stage capable of exhibiting non-kin intercohort cannibalism (L. D. Corkum, pers. obs.), were examined in response to water washings of fertilized eggs from conspecifics (*N. melanostomus*), heterospecifics (*O. mykiss*) and control lake water. Fish were caught during the reproductive or non-reproductive season and were either fed or deprived of food (for 36 h) in the laboratory under flow-through conditions. *Neogobius melanostomus* were hypothesized to engage in opportunistic feeding behaviours, with the prediction that juveniles should exhibit a higher attraction to water washings of eggs than

to control lake water. Second, if juveniles had been recently exposed to conspecific egg odours in the wild, such as those dispersed by conspecific males engaged in egg fanning, they might readily associate conspecific egg odours with a potential source of food. Therefore, fish caught during the reproductive season should be more attracted to washings of conspecific rather than heterospecific eggs. If a preference towards conspecific eggs is maintained when food is provided, it may indicate that *N. melanostomus* are opportunist predators. Lastly, because a recent pre-exposure to egg odours in nature is unlikely during the non-reproductive season, fish that are caught during this period should not exhibit a preference to either conspecific or heterospecific egg odours (*i.e.* fish may not readily identify conspecific egg odours with food).

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS AND FISH EGGS

Juvenile *N. melanostomus* were collected along the Detroit River at Windsor, ON, Canada (42° 18' N; 83° 04' W) using a seine [9.1 m long × 1.8 m deep (mesh-size = 6.4 mm) containing a 1.8 m long × 1.8 m deep bag (mesh-size = 3.2 mm)]. Fish were collected during the reproductive [from June to August (2009) and May (2010)] and non-reproductive (November 2009) seasons and transported to the University of Windsor laboratory holding facility. Fish were held in 90 l flow-through equipped tanks containing 15–20 individuals per tank and continuously supplied with *c.* 1 l of fresh dechlorinated water per min. Each tank was under a constant 16L:8D cycle, 22° C temperature, and fish were fed daily with Nutrafin flakes (www.hagen.com). All fish caught during the winter season were held in identical tanks, and the water temperature was gradually raised from 11 to 22° C over a 24 h period.

Fertilized *N. melanostomus* eggs were collected using artificial nests. Seven sets of nests were constructed, with each set containing five polyvinyl chloride (PVC) cylindrical tubes (7.5 cm diameter, 29 cm length). The PVC tubes were secured together through two plastic plates, with one end of the PVC tubes sealed. The other end of each tube contained a removable cap with a circular opening (3 cm diameter) for fish entry. An acetate sheet was inserted into each PVC tube to serve as a substratum for egg deposition, enabling the removal of any eggs from the tube, while preventing damage to the egg membrane. A new acetate sheet was inserted into each nest before nests were redeployed.

Nests were deployed on 5 June 2009 at a depth of 7–8 m along the north shore of the central basin of Lake Erie at Eriean, ON (42° 15' N; 81° 54' W) and retrieved on 29 June 2009. Acetate sheets containing developing *N. melanostomus* eggs (eggs with clearly visible embryos) were removed from the artificial nests. The eggs were gently removed from the surface of the sheet and transferred to 50 ml sterile Cellstar test tubes (www.vwrs.com) containing fresh lake water. This method also mixed all the eggs, thereby preventing the selection of 'adjacent-only' eggs from any single nest (*i.e.* during the creation of water washings of eggs). Tubes were immediately frozen on site in dry ice, thereby killing the embryos but maintaining the integrity of the egg membrane. Chemical stimuli that have previously been frozen have still been known to elicit behavioural responses in *N. melanostomus* (Yavno & Corkum, 2010). Because *N. melanostomus* is an invasive species that has not evolved with any fishes from the Laurentian Great Lakes, fertilized eggs from any co-occurring species could have been used as the source for collecting egg odours. *Oncorhynchus mykiss* eggs were elected for use because previous studies have demonstrated that *N. melanostomus* consume *O. mykiss* eggs (Fitzsimons *et al.*, 2006; Sreedharan *et al.*, 2009), and these eggs could be conveniently obtained (Ringwood Fish Culture Station, Whitchurch-Stouffville, ON, Canada). *Oncorhynchus mykiss* eggs were also frozen until needed.

WATER WASHINGS OF EGGS

The present protocol follows that of Mirza & Chivers (2002) used to create water washings of eggs. In the laboratory, five random Cellstar test tubes were selected, with each tube

containing a mixture of all the eggs obtained from a single nest. Eggs (4 g) were removed from each tube, pooled (20 g total) and then placed in 2 l of lake water that had been previously collected where nests were deployed. The eggs were aerated in the water for 15 min, after which the supernatant was poured off into individual 50 ml aliquots to be used for stimuli. All aliquots were stored at -20°C until needed. Similarly, 20 g of *O. mykiss* eggs were placed in 2 l of lake water and then aerated for 15 min. The supernatant was also poured off into individual 50 ml aliquots to be used for stimuli and stored at -20°C . Lake water was selected as a control and a carrier for egg odours because the developing eggs were collected from and frozen in lake water. Control lake water was poured into individual 50 ml aliquots and stored at -20°C until needed.

BEHAVIOURAL EXPERIMENTS

Tests were conducted to examine the attraction of *N. melanostomus* juveniles to randomly paired chemical stimuli from eggs of conspecifics (*N. melanostomus*; RG), heterospecifics (*O. mykiss*; RT) and lake water (control; CNT). Experiments were conducted during the reproductive (*i.e.* summer) and non-reproductive (*i.e.* winter) seasons, using fish that were either fed or withheld from receiving food for 36 h. *Neogobius melanostomus* held under laboratory conditions are often observed exhibiting 'food-begging' behaviours (*e.g.* anticipating food drops by following hand motions) *c.* 36 h after a previous feeding (S. Yavno, pers. obs.). Odour pairings consisted of RG + CNT (food provided, summer season, $n = 12$), RT + CNT (food provided, summer season, $n = 12$), RG + RT (food provided, summer season, $n = 12$), RG + RT (food withheld, summer season, $n = 12$) and RG + RT (food withheld, winter season, $n = 12$). At the end of each trial, fish were sacrificed (with clove oil) to determine the mass of their gonads, expressed as a percentage of total body mass (the gonado-somatic index; I_G). I_G values $<1.3\%$ in males and $<8\%$ in females are indicative of non-reproductive status in *N. melanostomus* (Belanger *et al.*, 2006). Fish were used within 7 days of capture and only once for each trial. All protocols followed guidelines set by the University of Windsor Animal Care Committee (AUPP #09-03).

Each trial was conducted in a 1 m long flow-through flume with an inflow valve on each side and one outflow valve located on the bottom in the centre of the flume. For every treatment, the order for introducing each pair of stimuli was randomized, along with the side of the flume each individual stimulus was to be released; that is, no single type (*i.e.* RG, RT or CNT) of egg odour stimuli was released on any one side of the flume more than any other type of egg odour. Trials consisted of a 1 h acclimation period, following previous laboratory-based behavioural studies on *N. melanostomus* (Yavno & Corkum, 2010). A 15 min stimulus period (based on dye trials, taking *c.* 3 min to reach the outflow from either inflow) followed directly after the acclimation period. Dechlorinated water flowing into the flume from each side, during both the acclimation and stimulus periods, was introduced at a rate of 25 ml min^{-1} and was controlled with a Masterflex L/S variable-speed modular drive (Cole-Parmer; www.coleparmer.com). The single outflow valve was connected to another pump, removing water at 50 ml min^{-1} ; a rate twice that of the inflow ends in order to maintain a constant water level in the flume. Stimuli were introduced directly into tubing that carried dechlorinated water over the course of the stimulus period. For each trial, a fish was held in the centre quarter of the flume by transparent gates during the acclimation period. Each gate contained two rows of small holes located below the water line, allowing water to flow through during the acclimation period. Immediately following the introduction of stimuli, the two gates were simultaneously lifted using a remote pulley system, limiting any physical disturbance to the fish. Fish were observed for the amount of time spent in left and right three eighths of the flume (stimulus areas) using a video camera (Hitachi VKC-370; www.hitachi.com) mounted above the flume (Fig. 1), and simultaneously recorded onto DVD for analysis using FishTracker software (Shen, 2005) [Correction added after online publication 28 April 2011, text removed]. In a few trials, females were observed moving directly after the gates were lifted. The first 3 min of the stimulus period, however, were not discounted because none of those fish spent the first 180 s in any single particular area of the flume. In those trials, females continued to traverse from one end of the flume to another. Data were $\log_{10}(x + 1.1)$ transformed to meet the assumption of normality and were analysed using a paired *t*-test.

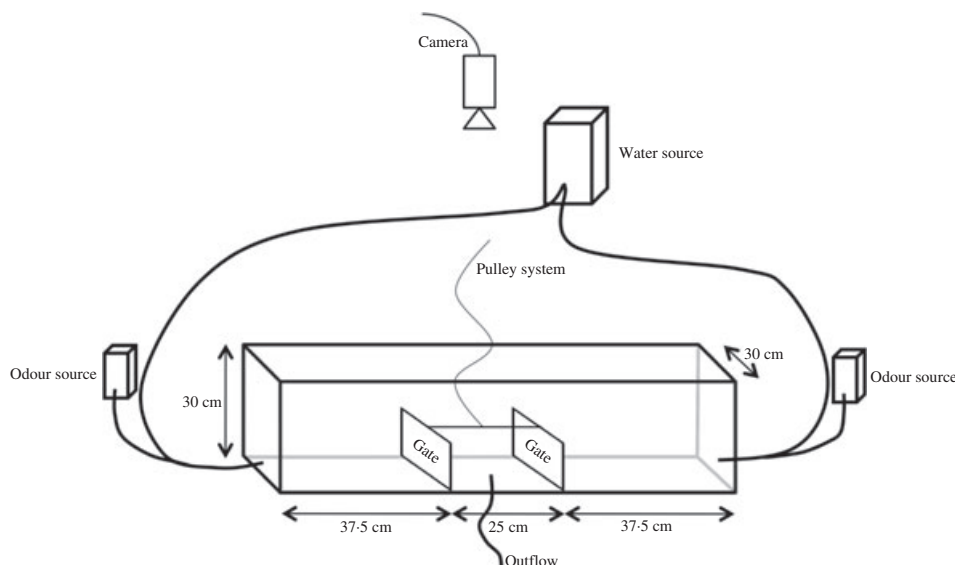


FIG. 1. Schematic representation of flume used in behavioural experiments. Paired stimulus odours (conspecific eggs, heterospecific eggs or control lake water) were introduced into tubing carrying dechlorinated water at the ends of the flume.

RESULTS

Juvenile *N. melanostomus* had a mean \pm s.e. total length (L_T) of 7.31 ± 0.11 cm, with equal numbers of males ($n = 24$; $I_G = 0.17 \pm 0.04$) and females ($n = 24$; $I_G = 2.02 \pm 0.41$). During the summer season, fed juveniles spent significantly more time (paired t -test, $n = 12$, $P < 0.05$) on the side of the flume containing stimuli from RG eggs *v.* CNT water and significantly preferred (paired t -test, $n = 12$, $P < 0.01$) CNT water *v.* RT stimuli. In addition, fish showed a significant preference (paired t -test, $n = 12$, $P < 0.05$) towards stimuli from RG eggs *v.* RT stimuli. The mean time spent associated with the RG egg odours was 1.5 times that spent with RT egg odours. Fish that had food withheld, regardless if caught during the reproductive (summer) or non-reproductive (winter) season, did not show any significant preference (winter season, paired t -test, $n = 12$, $P > 0.05$; summer season, paired t -test, $n = 12$, $P > 0.05$) towards either RG or RT stimuli (Fig. 2).

DISCUSSION

In this study, juvenile *N. melanostomus* were able to discriminate between odours from a conspecific and heterospecific species. When food was provided during the reproductive season, *N. melanostomus* were significantly attracted to conspecific egg odours over lake water. Meanwhile, juveniles that had food withheld, regardless of the season in which they were caught, did not significantly prefer one type of egg odour to another. This supports the hypothesis that *N. melanostomus* are opportunist

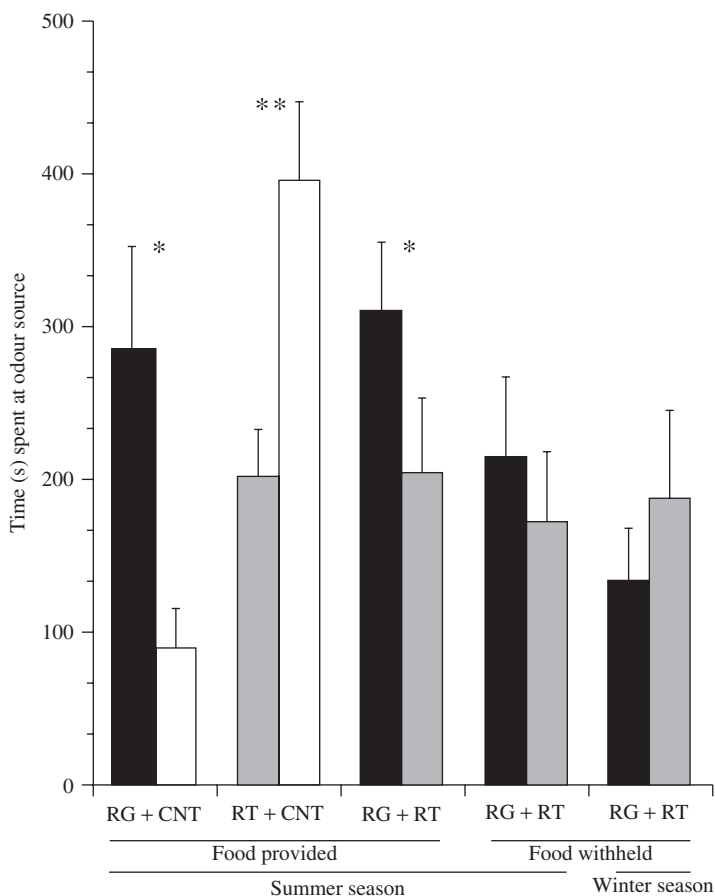


FIG. 2. Mean \pm S.E. time spent by juvenile fish, where food had either been provided or withheld, in the area of the flume containing an egg odour stimulus during each paired odour treatment. Trials were conducted during summer (*i.e.* reproductive) or winter (*i.e.* non-reproductive) seasons. ■, conspecific (*Neogobius melanostomus*; RG) egg odour stimuli; ▒, heterospecific (*Oncorhynchus mykiss*; RT) egg odour stimuli; □, lake water (control; CNT) stimuli. *, significant differences between preferences towards odour stimuli (* $P < 0.05$; ** $P < 0.01$).

predators, seeking out eggs from any species when food is limited, yet maintaining a strong attraction to conspecific eggs when food is available. Moreover, these findings provide the first evidence that *N. melanostomus* are able to discriminate between different species using only olfactory cues and that conspecific eggs may serve as a candidate for use in an odour-based trapping system.

High population densities, such as those experienced in a colony, often lead to decreases in food availability (Alexander, 1974; Tyler, 1995). In the case of *N. melanostomus*, colonies also contain nests that are guarded by parental males, with each male continuously removing nest debris and promoting egg oxygenation by pumping water in and out of the nest (Meunier, 2009; Meunier *et al.*, 2009). These combined factors suggest that when *N. melanostomus* experience food deprivation, they are simultaneously being exposed to odours from nearby developing embryos

(released into the colony through fanning) [Correction added after online publication 28 April 2011, text changed]. Consequently, juvenile *N. melanostomus* may engage in egg cannibalism and thereby learn to associate odours of conspecific eggs with an obtainable food source. Laboratory observations have confirmed that *N. melanostomus* do indeed sneak into the nests of males and cannibalize eggs (Meunier *et al.*, 2009). Furthermore, juveniles caught during the winter may require significantly more time to recall their association of conspecific egg odours with food.

Egg cannibalism has been well documented in several fish taxa (Skolbekken & Utne-Palm, 2001; Frommen *et al.*, 2007), but only recently have observations been made for *N. melanostomus*. Because high population densities lead to decreases in food availability, it is not uncommon to observe a simultaneous increase in cannibalistic behaviours (Elgar & Crepsi, 1992). In three-spined stickleback *Gasterosteus aculeatus* L. 1758, parental males improve their own body condition by partially cannibalizing their own egg clutches (*i.e.* filial cannibalism) (Mehlis *et al.*, 2009). *Neogobius melanostomus* engage in filial cannibalism, not only to improve body condition but also to remove diseased eggs.

Non-kin intercohort cannibalism of *N. melanostomus* eggs is a new behaviour that has only recently been confirmed in a laboratory study (Meunier *et al.*, 2009). The results from this study suggest that *N. melanostomus* egg odours are strong cues that lure non-kin juveniles, a life stage capable of cannibalizing younger cohorts, towards parental nests. Moreover, fed juveniles in this study were strongly attracted to conspecific egg odours, over both control and heterospecific odours. This suggests that cannibalism of eggs may occur not only when food is limiting and may be an attempt by juveniles to decrease future levels of intraspecific competition [Correction added after online publication 28 April 2011, text changed]. Hunter & Kimbrell (1980) suggest that cannibalism may actually help regulate population levels in fishes, and in some species, individuals are simply opportunist predators that prey on the eggs of nearby conspecifics (Pájaro *et al.*, 2007).

Because *N. melanostomus* entered into the Laurentian Great Lakes relatively recently (Jude *et al.*, 1992), the species has not had time to coevolve with any native fishes. Thus, it is possible that *N. melanostomus* do not immediately associate heterospecific egg odours with food, regardless of the species in question. *Oncorhynchus mykiss* and *N. melanostomus* are found in the same waterways (Kelch *et al.*, 2006); however, *N. melanostomus* are seldom exposed to odours from *O. mykiss* eggs. *Neogobius melanostomus* will consume *O. mykiss* eggs in the laboratory (Fitzsimons *et al.*, 2006), but few studies have demonstrated that individuals are directly attracted to odours from *O. mykiss* eggs. In one study, *N. melanostomus* were lured to minnow traps using food odours. Although conspecific eggs were not tested, Sreedharan *et al.* (2009) showed that traps baited with *O. mykiss* eggs attracted the fewest fish compared to traps baited with lake whitefish *Coregonus clupeaformis* (Mitchill 1818) tissue or crushed dreissenids. In this study, *O. mykiss* egg odours did not significantly attract juveniles over control lake water, indicating that juveniles may not completely associate this heterospecific odour with food. When simultaneously comparing both types of egg odours, juveniles continue to exhibit no significant preference towards heterospecific odours, regardless of food availability.

Juveniles were observed investigating both odour types, by means of fish repeatedly traversing the flume from one end to another, and eventually exhibiting a directional preference towards one egg odour over another (specifically towards

conspecific egg odour). The fact that juveniles significantly prefer lake water to *O. mykiss* odours does not necessarily suggest that fish are repelled by heterospecific egg odours. Every trial was conducted independently of the others, yet among all the treatments containing *O. mykiss* odours, juveniles appear to prefer *O. mykiss* egg odours for the same length of time (c. 190 s). In treatments where juveniles had been fed, fish preferred conspecific egg odours for a similar period of time (c. 300 s) in the two treatments (RG v. CNT and RG v. RT). The remaining (missing) time, equalling 900 s minus the total time spent on both sides during each treatment, represents the time spent by fish either in, or traversing, the central acclimation portion of the tank. Lastly, the increased variability observed in the treatments containing both types of fresh egg odours could be explained by interference created from two strong olfactory cues being released at once, thereby making it difficult for juvenile fish to distinguish one type of odour from another. In this study, odours were acquired from freshly collected eggs because they emit strong olfactory cues that elicit behavioural responses in fishes (Mirza & Chivers, 2002).

This study suggests that *N. melanostomus* clearly respond to odours that have been obtained from fertilized fish eggs. The specific egg components that elicit these behavioural responses, however, have not been identified. Some aquatic species have eggs containing proteins that can be detected by predators (Ferrari & Targett, 2003; Hara, 2006); other eggs contain steroidal compounds (Lucas *et al.*, 1979). This study demonstrated that odours from conspecific eggs attract juvenile *N. melanostomus*, indicating the presence of one or more chemoattractants being released by fertilized *N. melanostomus* eggs. Recent odour-based trapping systems deployed in waters of the Laurentian Great Lakes have successfully targeted and captured invasive sea lamprey *Petromyzon marinus* L. 1758 (Johnson *et al.*, 2009b). Ultimately, there is a potential to adapt this technique, using the attractants found in *N. melanostomus* eggs as a means to lure juveniles to traps, and thereby control the spread of this invasive fish.

We thank S. Ahmed, K. Cogliati, W. Glass and K. Lajevardi for field assistance. Funding was provided by the Ontario Ministry of Natural Resources (Canada Ontario Agreement) and the Natural Sciences and Engineering Research Council of Canada Discovery Grant to L.D.C. We also thank two anonymous reviewers for their constructive comments on an earlier draft of this paper.

References

- Acha, E. M., Bremec, C. & Lasta, C. (2002). Cannibalism on planktonic eggs by a non-filter feeding fish, *Micropogonias furnieri* (Sciaenidae). *Fisheries Research* **56**, 321–326.
- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology, Evolution and Systematics* **5**, 325–383.
- Amundsen, P. A. (1994). Piscivory and cannibalism in Arctic charr. *Journal of Fish Biology* **45**, 181–189.
- Belanger, R. M., Corkum, L. D., Li, W. & Zielinski, B. S. (2006). Olfactory sensory input increases gill ventilation in male round gobies (*Neogobius melanostomus*) during exposure to steroids. *Comparative Biochemistry and Physiology A* **144**, 196–202.
- Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolfe, R. K., Jude, D. J. & Rudnika, S. (1997). The round goby, *Neogobius melanostomus* (Pallas), a review of European and North American literature. *Illinois Natural History Survey Special Publication* **20**.
- Cheney, K. L. (2008). Non-kin egg cannibalism and group nest-raiding by Caribbean sergeant major damselfish (*Abudefduf saxatilis*). *Coral Reefs* **27**, 115.

- Elgar, M. A. & Crepsi, B. J. (1992). *Cannibalism: Ecology and Evolution Among Diverse Taxa*. New York, NY: Oxford University Press.
- Ferrari, K. M. & Targett, N. M. (2003). Chemical attractants in horseshoe crab, *Limulus polyphemus*, eggs: the potential for an artificial bait. *Journal of Chemical Ecology* **29**, 477–496.
- Fitzsimons, J., Williston, B., Williston, G., Bravener, G., Jonas, J. L., Claramunt, R. M., Marsden, J. E. & Ellrott, B. J. (2006). Laboratory estimates of salmonine egg predation by round gobies (*Neogobius melanostomus*), sculpins (*Cottus cognatus* and *C. bairdii*), and crayfish (*Orconectes propinquus*). *Journal of Great Lakes Research* **32**, 227–241.
- Frommen, J. G., Brendler, C. & Bakker, T. C. M. (2007). The tale of the bad stepfather: male three-spined sticklebacks *Gasterosteus aculeatus* L. recognize foreign eggs in their manipulated nest by egg cues alone. *Journal of Fish Biology* **70**, 1295–1301.
- Hara, T. J. (2006). Feeding behaviour in some teleosts is triggered by single amino acids primarily through olfaction. *Journal of Fish Biology* **68**, 810–825.
- Hunter, J. R. & Kimbrell, C. A. (1980). Egg cannibalism in the northern anchovy, *Engraulis mordax*. *Fishery Bulletin* **78**, 811–816.
- Johnson, J. H., Nack, C. C. & Chalupnicki, M. A. (2009a). Predation by Fallfish (*Semotilus corporalis*) on Pacific salmon eggs in the Salmon River, New York. *Journal of Great Lakes Research* **35**, 630–633.
- Johnson, N. S., Yun, S. S., Thompson, H. T., Brant, C. O. & Li, W. (2009b). A synthesized pheromone induces upstream movement in female sea lamprey and summons them into traps. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 1021–1026.
- Jude, D. J., Reider, R. H. & Smith, G. R. (1992). Establishment of Gobiidae in the Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 416–421.
- Kelch, D., Lichtkoppler, F., Sohngen, B. & Daigneault, A. (2006). The value of steelhead (*Oncorhynchus mykiss*) angling in Lake Erie tributaries. *Journal of Great Lakes Research* **32**, 424–433.
- Kinzler, W., Kley, A., Mayer, G., Waloszek, D. & Maier, G. (2009). Mutual predation between and cannibalism within several freshwater gammarids: *Dikerogammarus villosus* versus one native and three invasives. *Aquatic Ecology* **43**, 457–464.
- Lucas, J. S., Hart, R. J., Howden, M. E. & Salathe, R. (1979). Saponins in eggs and larvae of *Acanthaster planci* (L.) (Asteroidea) as chemical defenses against planktivorous fish. *Journal of Experimental Marine Biology and Ecology* **40**, 155–165.
- MacInnis, A. J. & Corkum, L. D. (2000). Fecundity and reproductive season of the round goby in the upper Detroit River. *Transactions of the American Fisheries Society* **129**, 136–144.
- Mehlis, M., Bakker, T. C. M. & Frommen, J. G. (2009). Nutritional benefits of filial cannibalism in three-spined sticklebacks (*Gasterosteus aculeatus*). *Naturwissenschaften* **96**, 399–403.
- Meunier, B. (2009). Reproductive behaviour and urinary signals in the round goby *Neogobius melanostomus*. MSc Thesis, University of Windsor, Windsor, ON, Canada.
- Meunier, B., Yavno, S., Ahmed, S. & Corkum, L. D. (2009). First documentation of spawning and nest guarding in the laboratory by the invasive fish, the round goby (*Neogobius melanostomus*). *Journal of Great Lakes Research* **35**, 608–612.
- Mirza, R. S. & Chivers, D. P. (2002). Attraction of slimy sculpins to chemical cues of brook charr eggs. *Journal of Fish Biology* **61**, 531–539.
- Nichols, S. J., Kennedy, G., Crawford, E., Allen, J., French, J., Black, G., Blouin, M., Hickey, J., Chernyák, S., Haas, R. & Thomas, M. (2003). Assessment of lake sturgeon (*Acipenser fulvescens*) spawning efforts in the lower St. Clair River, Michigan. *Journal of Great Lakes Research* **29**, 383–391.
- Pájaro, M., Curelovich, J. & Macchi, G. J. (2007). Egg cannibalism in the northern population of the Argentine anchovy, *Engraulis anchoita* (Clupeidae). *Fisheries Research* **83**, 253–262.
- Roseman, E. F., Taylor, W. W., Hayes, D. B., Jones, A. L. & Francis, J. T. (2006). Predation on Walleye eggs by fish on reefs in Western Lake Erie. *Journal of Great Lakes Research* **32**, 415–423.

- Shen, P. (2005). Real-time systems for moving objects detection and tracking using pixel difference methods. MSc Thesis, University of Windsor, Windsor, ON, Canada.
- Skolbekken, R. & Utne-Palm, A. C. (2001). Parental investment of male two-spotted goby, *Gobiusculus flavescens* (Fabricius). *Journal of Experimental Marine Biology and Ecology* **261**, 137–157.
- Slotte, A., Mikkelsen, N. & Gjøsæter, H. (2006). Egg cannibalism in Barents Sea capelin in relation to a narrow spawning distribution. *Journal of Fish Biology* **69**, 187–202.
- Smith, C. & Reay, P. (1991). Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries* **1**, 41–64.
- Sreedharan, G., Corkum, L. D. & Johnson, T. B. (2009). Response of the round goby, an invasive fish, to food odours. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie* **30**, 1275–1278.
- Steinhart, G. B., Marschall, E. A. & Stein, R. A. (2004). Round goby predation on small-mouth bass offspring in nests during simulated catch-and-release angling. *Transactions of the American Fisheries Society* **133**, 121–131.
- Tyler, W. A. (1995). The adaptive significance of colonial nesting in a coral-reef fish. *Animal Behaviour* **49**, 949–966.
- Wickett, R. G. & Corkum, L. D. (1998). Nest defense by the non-indigenous fish, the round goby, *Neogobius melanostomus* (Gobiidae), on a shipwreck in western Lake Erie. *Canadian Field-Naturalist* **122**, 245–249.
- Wolfe, R. K. (2002). Reproductive behavior of the round goby (*Neogobius melanostomus*): nest choice. MSc Thesis, Loyola University of Chicago, Chicago, IL, USA.
- Wootton, R. J. (1971). A note on the nest-raiding behaviour of male sticklebacks. *Canadian Journal of Zoology* **49**, 960–962.
- Yavno, S. & Corkum, L. D. (2010). Reproductive female round gobies (*Neogobius melanostomus*) are attracted to visual male models at a nest rather than to olfactory stimuli in urine of reproductive males. *Behaviour* **147**, 121–132.