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Salvelinus namaycush spawning substratum attracts egg predators and opportunists through chemosensory cues

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Two separate field experiments were conducted in a series of small boreal lakes to test for the attraction of egg predators to lake trout *Salvelinus namaycush* spawning shoals and subsequently to determine whether chemosensory cues attract egg predators to these sites. In the first experiment, minnow traps set on spawning sites captured significantly more egg predators than those set on structurally similar non-spawning sites. Captures of slimy sculpin *Cottus cognatus*, common shiner *Luxilus cornutus*, blacknose shiner *Notropis heterolepis* and virile crayfish *Orconectes virilis* were more than double on spawning sites relative to non-spawning sites for the two study lakes. To test whether chemosensory cues could attract egg predators to *S. namaycush* spawning sites, paired minnow traps were placed on eight to 10 sites in each of the three study lakes; one trap contained visually concealed *S. namaycush* spawning substratum and the other with visually concealed non-spawning substratum. Traps containing spawning substratum consistently captured more fish and had higher mean daily catches than those that contained non-spawning substratum. The combined results demonstrate a greater prevalence of egg predators on *S. namaycush* spawning shoals that appears to be the result of chemosensory attraction to spawning substratum.

Key words: *Cottus cognatus*; egg predation; olfaction; *Pimephales promelas*.

INTRODUCTION

In aquatic environments, chemical cues mediate many fundamental ecological interactions across taxa, including recognizing conspecifics, evaluating predation risk, finding food and establishing social status (Hara, 1994; Kats & Dill, 1998; Krieger & Breer, 1999; Huertas *et al.*, 2007). Chemosensory cues allow aquatic organisms to gain valuable information about and interpret their environment (Ache & Young, 2005). The olfactory system of fishes responds to an array of diverse molecules including amino acids (Hara, 2006), bile acids (Døving & Stabell, 2003, Zhang & Hara, 2009), peptides (Hara, 1992) and steroidal compounds (Sorensen *et al.*, 2005). The reception and interpretation of these compounds can help co-ordinate different actions for different

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members of the aquatic community. For example, spawning sites are spatiotemporally unique locations used during the breeding season that contain chemical cues that can be interpreted as either spawning cues to conspecifics or food cues to egg predators.

Organisms in the aquatic environment are able to distinguish, mark and recall areas that are significant to them (Odling-Smee & Braithwaite, 2003). In many species, spawning locations are recognized annually by olfactory cues (Johnsen & Hasler, 1980; Horrall, 1981; Miller *et al.*, 2001; Døving *et al.*, 2006). Salmonids in particular are able to migrate hundreds of km to their natal streams using olfactory cues (Dittman & Quinn, 1996). In many instances, salmonids that have had their olfactory systems occluded are unable to locate spawning sites (Wisby & Hasler, 1954; Hansen *et al.*, 1987). The ability to locate these areas using olfaction can help to limit the amount of time spent searching for suitable spawning locations and help to co-ordinate the reproducing population (Goodenough *et al.*, 2009).

Lake trout *Salvelinus namaycush* (Walbaum 1792), specifically, use the same spawning sites annually even though there may be other structurally similar sites available (Gunn, 1995). Foster (1985) hypothesized that spawning *S. namaycush* are attracted to the accumulation of juvenile faeces and discarded egg membranes that are found on successful reproductive sites. Recently, field experiments have demonstrated the preferential attraction of *S. namaycush* to concealed spawning substratum, thereby supporting the role of chemical cues in the selection of spawning sites (Wasylenko *et al.*, 2013). Typically, these sites are on rocky, windswept shoals that are at the end of the lake fetch, where fertilized eggs are deposited into the interstices of cobble substratum and develop here for several months before hatching (Martin & Olver, 1980; Gunn, 1995). These locations are ideal for *S. namaycush* to successfully express their negatively buoyant eggs and keep them well oxygenated during incubation. Although these sites generally have characteristics that aid in the development of the embryos, they do not offer complete protection from egg predators.

Salvelinus namaycush eggs are especially vulnerable to predation because, unlike all other salmonine species, females do not construct and bury eggs in a redd (nest) for protection (Martin & Olver, 1980). As such, predators can consume up to 80% of eggs found on spawning sites (Fitzsimons *et al.*, 2002). *Salvelinus namaycush* eggs are a protein-rich, highly abundant prey item for predators such as slimy sculpin *Cottus cognatus* Richardson 1836, crayfish *Orconectes* spp. and common white sucker *Catostomus commersoni* (Lacépède 1803) (Savino *et al.*, 1999; Wasylenko *et al.*, 2013). Densities of egg predators on spawning sites are known to increase as eggs become abundant (Fitzsimons *et al.*, 2002). While there is evidence that different sculpin species (Cottidae) are attracted to salmonid eggs, it is not known whether these egg predators are attracted directly to spawning sites (Dittman *et al.*, 1998; Mirza & Chivers, 2002). Because the spawning season of *S. namaycush* is typically brief, 10 days on average (Martin, 1957), presumably egg predators have developed ways through which spawning sites can be quickly located.

This experiment examined whether egg predators are attracted by olfactory cues to *S. namaycush* spawning shoals in small boreal lakes. Two main predictions of the olfactory hypothesis are as follows: (1) egg predator density is higher on spawning reefs than on structurally similar adjacent habitats and (2) egg predators preferentially choose spawning substratum over non-spawning substratum, when provided with a choice between these habitat types. A separate field experiment was conducted to test each prediction. The first study directly compared the catches of egg predators on spawning sites to structurally similar non-spawning sites. If habitat selection alone influenced site choice, then similar catches would be observed at all sites, whereas greater abundance on natural spawning shoals *v*. habitat-matched control sites would indicate site preference by egg predators. In the second study, the abundance of egg predators in traps with visually concealed spawning substratum were compared to paired traps with visually concealed non-spawning (control) substratum.

Greater abundance of egg predators in visually concealed spawning substratum would suggest the role of olfaction in the attraction to spawning sites (Wasylenko *et al.*, 2013).

MATERIALS AND METHODS

STUDY 1: ATTRACTION TO SPAWNING SHOALS

Egg predator attraction to spawning sites and structurally similar non-spawning sites were examined at two lakes; L020 (49° 07′ N; 92° 08′ W) and L042 (49° 05′ N; 92° 09′ W) within the Coldwater Lakes Area (CLA) north of Atikokan, ON, Canada, from September to November 2011 (Fig. 1). The lakes were chosen based on the known location of *S. namaycush* spawning sites from previous long-term research on these lakes related to deforestation (Steedman, 2000; Steedman & Kushneriuk, 2000).

Lakes 020 and 042 have similar fish species compositions, with *S. namaycush* and *C. commersoni*, as the only large fish species present (Table I). Both lakes contain common egg predators such as *C. cognatus*, *C. commersoni* and crayfish species. Three sites were chosen on each lake: one *S. namaycush* spawning site and two structurally similar non-spawning sites (based on previous netting data during *S. namaycush* spawn and no presence of eggs). Non-spawning sites were chosen based on published cobble size criteria of known spawning sites (Martin, 1955; Martin & Olver, 1980; Gunn, 1995) and on the lack of spawning *S. namaycush* captured during previous netting programmes. The evidence that these sites were not used for spawning was further confirmed with the lack of eggs on non-spawning sites during *S. namaycush* spawning. Each lake had one predominant *S. namaycush* spawning location, which was used for this study. The spawning site in Lake 042 was located *c.* 6–8 m offshore on a shoal that was *c.* 2–3 m in depth. All other sites in both lakes were located in the littoral zone, in *c.* 1–2 m of water and adjacent to shore. The non-spawning sites in both lakes were *c.* 100–200 m away from the spawning site.

Once sites were selected, five standard wire mesh, unbaited, minnow traps (6·4 mm mesh, 42 cm L × 23 cm W with a 22 mm opening) were placed on each of the three sites at each lake.

TABLE I. Physical characteristics and littoral fish species of the study lakes

	Lake				
Lake characteristics	020	042	224	260	468
Lake area (ha)	57	28	26	34	292 (100*)
Maximum lake depth (m)	32	19	27	14	29
Littoral fish species	1–9	1,2,5–7,9	1,2,5–7,9	1,2,5,6,9,11	1,2,4,6,9,10,12, 13

*Size of basin used for study (see Fig. 1).
1, *Catostomus commersoni*; 2, *Chrosomus eos* and *Phoxinus neogaeus*; 3, *Luxilus cornutus*; 4, *Notropis heterolepis*; 5, *Pimephales promelas*; 6, *Margariscus margarita*; 7, *Culaea inconstans*; 8, *Etheostoma exile*; 9, *Cottus cognatus*; 10, *Perca flavescens*; 11, *Couesius plumbeus*; 12, *Pimephales notatus*; 13, *Rhinichthys cataractae*.

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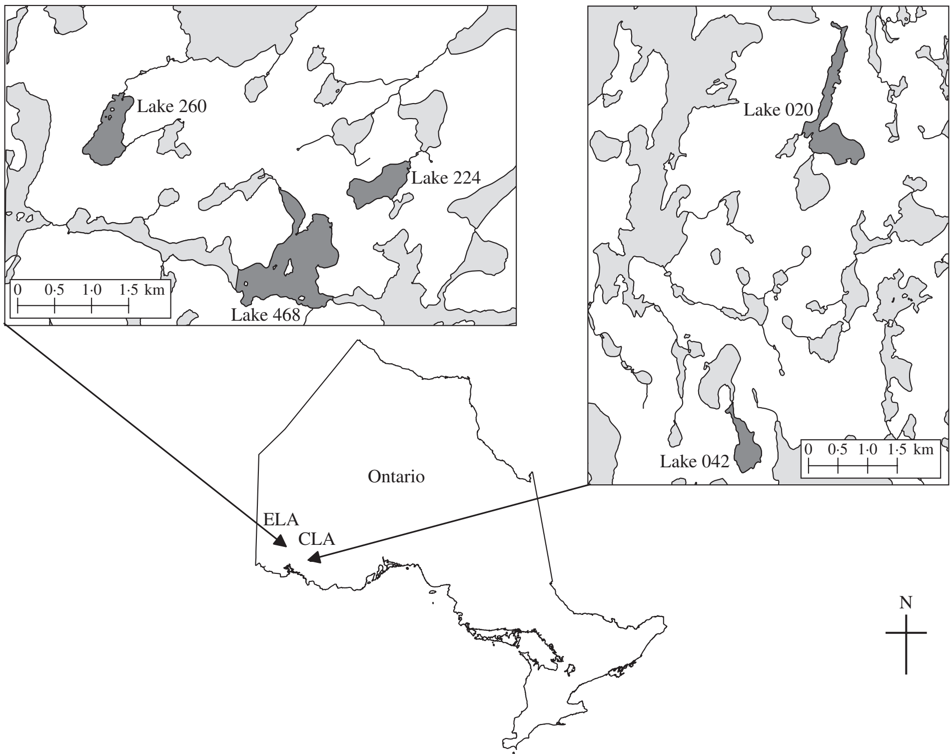

Fig. 1. Locations of study lakes. Lake 042 and Lake 020 located in the Coldwater Lakes Area (CLA) were used to examine the abundance of egg predators on natural spawning shoals. Lakes 224, 260 and 468, in the Experimental Lakes Area (ELA), were used to test for egg predator attraction to spawning substratum.

Sampling was conducted on nine different occasions for each lake from 3 October to 23 November 2011. During each sampling event, species abundance was recorded and traps were placed back on the site. All fishes captured were released *c.* 10 m from the sampling site.

STUDY 2: ATTRACTION TO SPAWNING SUBSTRATUM

The second study determined whether egg predators were attracted to spawning sites by chemosensory cues in three lakes at the Experimental Lakes Area (ELA) 50 km east south-east of Kenora, ON, Canada. The ELA is a pristine area that encompasses 58 lakes that have been set aside for research purposes (Blanchfield *et al.*, 2009). Lakes 260 (49° 41′ N; 93° 46′ W), 224 (49° 41′ N; 93° 43′ W) and the north-eastern basin of 468 (49° 40′ N; 94° 45″ W) (Fig. 1) were chosen based on the known locations of *S. namaycush* spawning sites. *Salvelinus namaycush* is the top predator in all lakes and is supported by a littoral fish community of six to eight species, of which all lakes contained common egg predators such as *C. cognatus* and *C. commersoni* (Table I). All lakes have natural reproducing population of *S. namaycush* that have not been stocked.

The experimental design compared pairs of traps that contained either a bag of spawning substratum or a bag of non-spawning substratum types (control). Spawning substratum was collected from known *S. namaycush* spawning locations (during *S. namaycush* spawning) in each lake and separated into 0·25 kg units (approximately five to eight pieces of substratum per unit). Each substratum sample was wrapped in fine mesh netting to allow water to infiltrate the sample but visually conceal the substratum (Wasylenko *et al.*, 2013). This method was repeated with the

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control substratum from a structurally similar non-spawning site. Spawning was confirmed by the presence of *S. namaycush* and eggs on the spawning location. Two minnow traps (same trap types as used in study 1) were placed at each sampling site *c.* 2–3 m apart with the trap opening facing the other trap. Each trap contained a fine mesh bag of either spawning substratum or the control. Traps were checked daily between 0900 and 1200 hours. Species, quantity and total length (L_T) were recorded for each individual captured in each trap and returned to the lake *c.* 15 m from the original capture location. Once each trap was sampled at a particular site, trap position was switched with the position of the paired treatment (*i.e.* if spawning substratum was on the right, the next night it would be on the left, and *vice versa*). The same substratum was used continuously throughout the experiment and remained within the same trap throughout. Sampling continued for 7 days, with the exception of Lake 468, which was sampled for 10 days due to low catch numbers.

STATISTICAL ANALYSIS

Catches from unbaited traps on spawning and non-spawning shoals (study 1) were highly variable resulting in data that failed to meet parametric statistical assumptions, despite data transformations intended to reclaim such assumptions. Consequently, non-parametric analysis (Pearson χ^2) was used to examine whether there was any difference between the catches at non-spawning sites and the spawning site on each lake. *Chrosomus eos* Cope 1861 and *Phoxinus neogaeus* Cope 1867 were grouped as *Phoxinus* spp. due to the common hybridization of the two species in these lakes.

Similarly, catches to assess the attraction to spawning substratum (study 2) were also highly variable within each lake, such that parametric statistical assumptions could not be met. Therefore, non-parametric analysis (Pearson χ^2) was used to examine the data for individual lakes. Parametric assumptions were reclaimed from pooled-lake total catch data using a $\log_{10}(x+1)$ data transformation.

RESULTS

STUDY 1: ATTRACTION TO SPAWNING SHOALS

In Lake 042, there were significantly more *C. cognatus* and virile crayfish *Orconectes virilis* caught on the spawning site compared to non-spawning sites (*C. cognatus*: $\chi^2 = 20{\cdot}83$, d.f. = 2, $P < 0{\cdot}001$; *O. virilis*: $\chi^2 = 8{\cdot}91$, d.f. = 2, $P < 0{\cdot}01$) [Fig. 2(a)]. More *Phoxinus* spp. were captured on non-spawning sites than the spawning site ($\chi^2 = 90{\cdot}63$, d.f. = 2, $P < 0{\cdot}001$) [Fig. 2(a)]. There was no difference in catch of *C. inconstans* between spawning and non-spawning sites ($\chi^2 = 5{\cdot}47$, d.f. = 2, $P > 0{\cdot}05$) [Fig. 2(a)].

In Lake 020, *C. cognatus*, *Notropis heterolepis* Eigenmann & Eigenmann 1893 and *Luxilus cornutus* (Mitchill 1817) were more abundant on the spawning site than on the non-spawning sites (*C. cognatus*: $\chi^2 = 46{\cdot}97$, d.f. = 2, $P < 0{\cdot}001$; *N. heterolepis*: $\chi^2 = 96{\cdot}09$, d.f. = 2, $P < 0{\cdot}001$; *L. cornutus* $\chi^2 = 165{\cdot}7$, d.f. = 2, $P < 0{\cdot}001$) [Fig. 2(b)]. The number of *Phoxinus* spp. caught did not differ between the spawning site and non-spawning sites [$\chi^2 = 4{\cdot}23$, d.f. = 2, $P > 0{\cdot}05$; Fig. 2(b)].

STUDY 2: ATTRACTION TO SPAWNING SUBSTRATUM

In Lake 468, traps containing spawning substratum captured more *Perca flavescens* (Mitchill 1814) than control traps ($\chi^2 = 15{\cdot}21$, d.f. = 1, $P < 0{\cdot}001$; Fig. 3). *Cottus cognatus*, *N. heterolepis* and *Margariscus margarita* (Cope 1867) were not caught in sufficient numbers for meaningful interpretation.

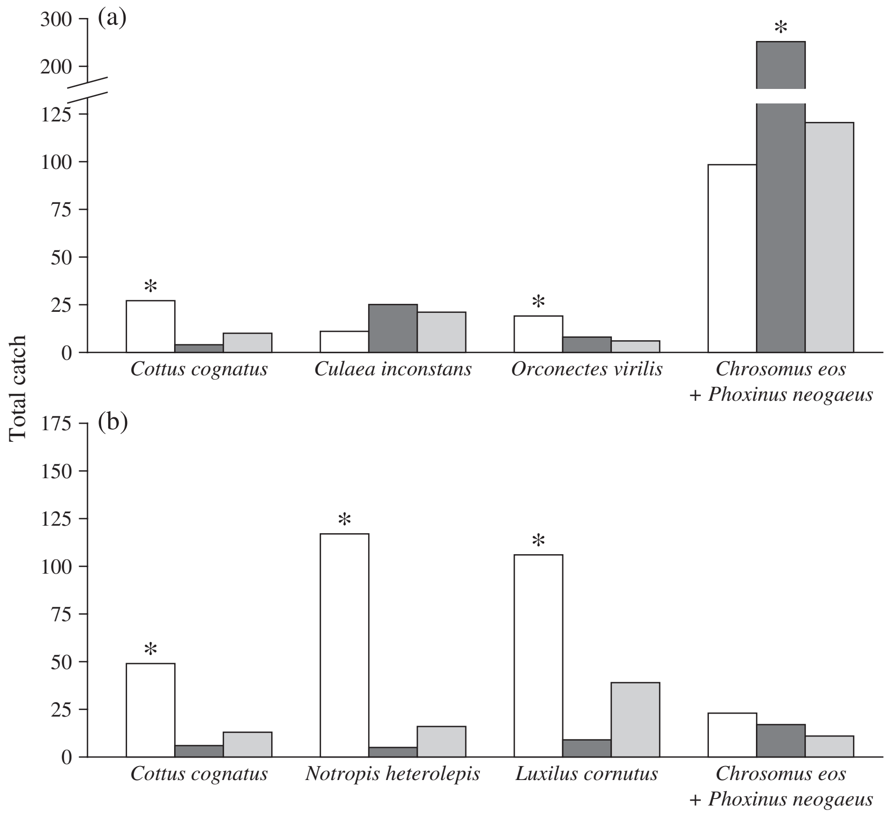

Fig. 2. Total catches from non-baited minnow traps for *Salvelinus namaycush* egg predators in (a) Lake 042 and (b) Lake 020. Traps were placed on three sites in each lake: a known spawning site (□) and two structurally similar non-spawning sites (■ and □) located *c.* 200 m away. *, a significant difference (P>0·05) in catch among sites.

In Lake 260, significantly higher catches of *C. cognatus*, *Pimephales promelas* Rafinesque 1820 and *M. margarita* were observed in spawning substratum-containing traps than control traps (*P. promelas*: $\chi^2 = 23{\cdot}75$, d.f. = 1, $P < 0{\cdot}001$; *C. cognatus* $\chi^2 = 11{\cdot}84$, d.f. = 1, $P < 0{\cdot}001$; *M. margarita*: $\chi^2 = 6{\cdot}76$, d.f. = 1, $P < 0{\cdot}01$; Fig. 4).

In Lake 224, significantly higher catches were observed for *M. margarita* in spawning substratum-containing traps than in control traps ($\chi^2 = 11{\cdot}67$, d.f. = 1, $P < 0{\cdot}001$; Fig. 5). There was no difference catches between the spawning and control traps for *C. inconstans* ($\chi^2 = 0{\cdot}64$, d.f. = 1, $P > 0{\cdot}05$; Fig. 5) and *P. promelas* ($\chi^2 = 11{\cdot}67$, d.f. = 1, $P > 0{\cdot}05$; Fig. 5). *Cottus cognatus* were not captured in significant numbers for meaningful interpretation.

Total catches were compared for all lakes over the duration of the study (7–10 days); 327 fishes were captured in spawning substratum-containing traps *v.* 206 fishes captured in paired control traps. Mean daily catch in minnow traps with spawning substratum (mean was significantly higher ($t = -2{\cdot}12$, d.f. = 44·45, $P < 0{\cdot}05$) than traps with non-spawning substratum [Fig. 6(a)]. Significant differences were also observed in mean daily catch among the three lakes (ANOVA, d.f. = 2·42, $P < 0{\cdot}001$). Catches

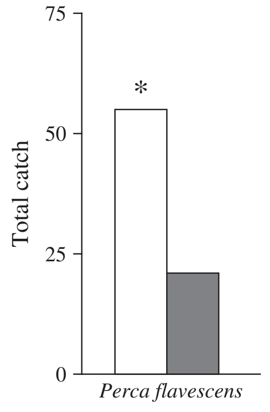

FIG. 3. Total catches for *Perca flavescens* in Lake 468. *, a significant difference ($P<0{\cdot}05$) in catch between minnow traps containing concealed spawning substratum (□) and structurally similar non-spawning substrate (■).

in Lake 224 (primarily *M. margarita* and *C. inconstans*) were twice that of Lake 260 (primarily *P. promelas*) and *c.* four-fold higher than Lake 468 (primarily *P. flavescens*) [Fig. 6(b)].

DISCUSSION

Overall, there was a higher abundance of egg predators on *S. namaycush* spawning shoals compared to nearby lake areas of similar structure, as well as higher catches of egg predators in traps with visually concealed *S. namaycush* spawning substratum. This study is the first field test of the olfactory attraction hypothesis by egg predators and is the first to document the potential for chemical attraction to *S. namaycush* spawning

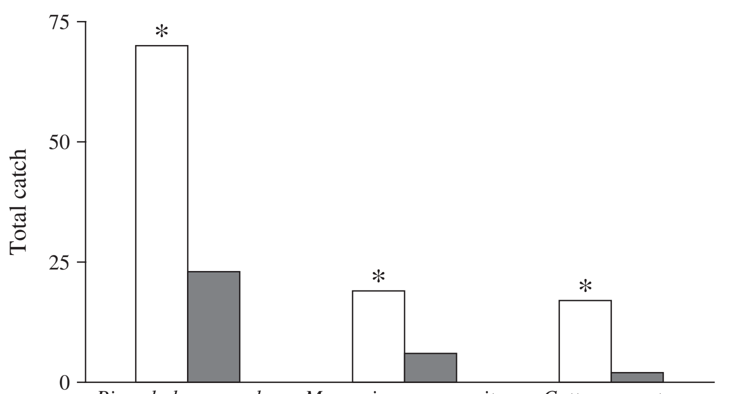

FIG. 4. Total catches for *Pimephales promelas*, *Cottus cognatus* and *Margariscus margarita* in Lake 260. *, a significant difference ($P<0{\cdot}05$) in catch between minnow traps containing concealed spawning substratum (□) and structurally similar non-spawning substratum (■).

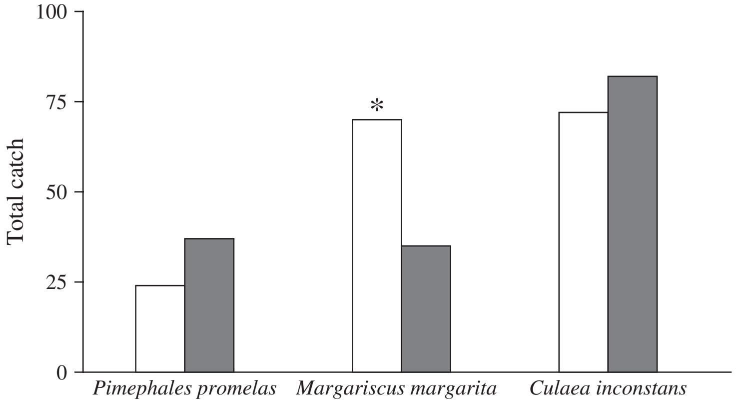

FIG. 5. Total catches for *Margariscus margarita*, *Pimephales promelas* and *Culaea inconstans* in Lake 224. *, a significant difference ($P<0{\cdot}05$) catch between minnow traps containing concealed spawning substratum (□) and structurally similar non-spawning substratum (■).

sites by a suite of predators. These findings support that cues associated with spawning sites are received and interpreted by various littoral fish species, including known *S. namaycush* egg predators (*C. cognatus*) as well as other species (*Phoxinus* spp. and *P. promelas*). While this study shows that egg predators are attracted to spawning shoals, the exact cues used by each species remain to be determined.

In the first study, replicated in two lakes, it was observed that there were significantly greater numbers of egg predators on *S. namaycush* spawning shoals than at the closely situated sites of similar substratum where spawning did not occur. These results suggest that an egg predator is attracted to something other than the physical structure

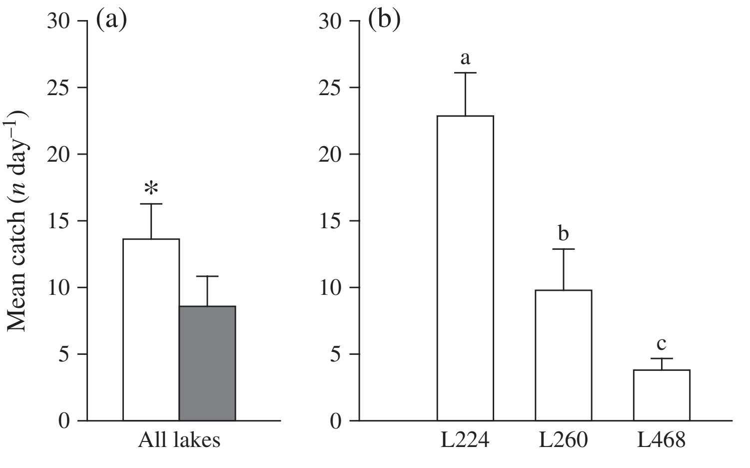

FIG. 6. Mean + S.E. daily catch at Experimental Lakes Area study lakes (see Fig. 1) of fishes captured in minnow traps (a) containing concealed spawning substratum (□) *v*. structurally similar non-spawning substratum (■) and (b) among study lakes. * and different lower case letters, significant difference ($P<0{\cdot}05$) in catches between substratum type and lakes.

of spawning sites. Recognition of the fact that that egg predator species could potentially be attracted to these sites by other means, such as visual cues, prompted the second field experiment. Using a replicated, paired design that allowed littoral fishes a choice between spawning *v*. non-spawning site substratum, egg predator species were determined to be preferentially attracted to *S. namaycush* spawning substratum. These results are significant due to the fact that there was no food source concealed within the substratum samples and the sampling sites were located away from active spawning locations. Most studies to date have looked at an egg predator's attraction to eggs but not its attraction to the spawning substratum (Dittman *et al.*, 1998; Mirza & Chivers, 2002). This study shows an attraction by egg predators to spawning substratum, suggesting that species are not only attracted to *S. namaycush* eggs but also attracted to substratum that is associated with the annual presence of these eggs. Collectively, data from both field studies lend support for role of chemical cues in the attraction of egg predators to *S. namaycush* spawning shoals.

Cottus cognatus, a known *S. namaycush* egg predator (Stauffer & Wagner, 1979; Martin & Olver, 1980), were not only significantly more abundant on spawning sites when compared to structurally similar non-spawning sites but also attracted to *S. namaycush* spawning substratum in the absence of eggs. The highest catches of *C. cognatus* were in Lake 260 with the majority being captured in traps containing spawning substratum (89%, $n = 19$). Although *C. cognatus* have been shown to be attracted to olfactory cues released by salmonids and brook trout *Salvelinus fontinalis* (Mitchill 1814) eggs (Dittman *et al.*, 1998; Mirza & Chivers, 2002), the absence of eggs in this study illustrates that they can recognize chemically tagged spawning substratum. Fitzsimons *et al.* (2002) estimated that for a 30-day period after spawning (beginning from the peak spawning period), *C. cognatus* were able to consume up to 54% of the estimated *S. namaycush* egg abundance in Lake Ontario. In areas of low egg deposition, *C. cognatus* and northern Clearwater crayfish *Orconectes propinquus* were estimated to consume almost 100% of the eggs. This level of egg predation can have negative effects on *S. namaycush* recruitment, especially those with declining populations.

Within Lake 468, *P. flavescens* were also caught in significantly higher numbers in spawning substratum-containing traps than non-spawning containing traps. *Perca flavescens* are not typically associated with *S. namaycush* egg predation but are known to prey on smaller walleye *Sander vitreus* (Mitchill 1818) eggs (Wolfert *et al.*, 1974; Roseman *et al.*, 2006). Previously, it was determined that large-bodied *C. commersoni* were also a major predator of *S. namaycush* eggs in Lake 468; apparently, small individuals of this species are not a major threat as none were captured by minnow traps (Wasylenko *et al.*, 2013).

Several fish species that are not normally associated with egg predation were captured in significant numbers in spawning site traps at the CLA and in traps containing spawning substratum at the ELA. In Lake 020, *N. heterolepis* and *L. cornutus* were more abundant on the spawning site as opposed to the non-spawning sites. In Lake 260, both *P. promelas* and *M. margarita* were attracted to spawning substratum over non-spawning substratum, but in Lake 224, only *M. margarita* was attracted to spawning substratum. Although not typically associated with egg predation [there are some instances of spottail shiners *Notropis hudsonius* (Clinton 1824) preying on fish eggs (Wolfert *et al.*, 1974; Roseman *et al.*, 2006)], cyprinids may be attracted to these sites for other non-egg food opportunities. *N. heterolepis*, *L. cornutus*, *P. promelas* and

M. margarita generally feed on small invertebrates and detritus (Scott & Crossman, 1973). Spawning *S. fontinalis* stir up detritus during reproductive activities, which may attract invertebrates and cyprinids to spawning sites. Although these species may not be preying on *S. namaycush* eggs (due to gape limitations), they may associate spawning substratum with other types of food sources.

During the substratum choice experiment, the most fish ($n = 156$) were captured at Lake 224, but the only species to show an attraction to spawning substratum was *M. margarita*, not known for *S. fontinalis* egg predation. Although *P. promelas* and *C. inconstans* were caught in Lake 224, there was not a significant difference in catches between the substratum types. For *P. promelas*, this finding is opposite to the greater attraction to spawning substratum that was observed in Lake 260. The lack of difference in *C. inconstans* catches was consistent with the findings from the first study where they were not more abundant on either spawning shoals *v.* structurally similar non-spawning shoals. This finding is somewhat surprising given that *C. inconstans* is known to consume eggs of other fishes as well as that of conspecifics (Stewart & Watkinson, 2004).

One interesting trade-off that has emerged from this study is the persistence of egg predators' attraction to spawning sites that have high predation risk. With *S. namaycush* being the top predator in the studied lakes, all the small-bodied fish species captured on the spawning sites are potential prey. Spawning sites can be associated with high rewards in the form of an abundance of food sources but can also be risky for egg predators owing to the presence of adult *S. namaycush* (Owens & Bergstedt, 1994). The attraction of small-bodied fishes to spawning shoals suggests that the reward associated with entering spawning sites outweighs the risk of predation. In all lakes, there were no juvenile *C. commersoni* captured in any of the traps. Small juvenile *C. commersoni* are common prey for *S. namaycush* (B. Wasylenko, pers. obs.) and in previous studies, mature *C. commersoni* were captured in significant numbers and were found to be attracted to visually concealed *S. namaycush* spawning substratum and predate on *S. namaycush* eggs (Wasylenko *et al.*, 2013). Juvenile *C. commersoni* may perceive the risk with foraging on eggs as too high due to their small body size and inability to find cover while feeding.

This study demonstrates that several species are attracted to visually concealed spawning substratum. Chemosensation allows an organism the ability to perceive and interpret the risk and reward of entering different habitats. In many instances, the ability to locate adequate food sources using olfaction limits the amount of energy expended on searching for food and maximizes energy gain (Goodenough *et al.*, 2009). The ability of an egg predator to evolve mechanisms to locate seasonal spawning areas, therefore, would be highly beneficial. Understanding how egg predators like *C. cognatus* recognize *S. namaycush* spawning sites is ecologically significant. From a management perspective, understanding the way that egg predators are attracted to these sites may allow for the fisheries managers to control or manage egg predation by creating alternative strategies to aid in recovery efforts.

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