RESEARCH PAPER

Altered Prey Responses in Round Goby from Contaminated Sites

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Abstract

Although prey must move to forage, escape predation or gain information about predation risk, movement itself enhances the risk of predation by increasing visibility of prey and encounter rates with predators. Animals subjected to stressors often show altered behaviour; a widely cited effect of contaminant exposure is an increase in vulnerability to predation, which may be mediated by an increase in risky behaviour. Round goby are invasive fish that typically rely on crypsis and sheltering (low-activity behaviours) to avoid predators. We collected round goby from contaminated sites and tested whether they showed signs of altered risk-taking compared with fish from a less contaminated reference site. We subjected the fish to a simulated predation event (a motor-operated model bass) under both diurnal and nocturnal conditions. Fish from contaminated sites showed lower overall activity levels, but also failed to reduce activity following an attack, unlike fish from the reference site. The intensity of effects varied with diel period. Males, but not females, from contaminated sites showed reduced likelihood of darting during an attack, while females, but not males, from contaminated sites were less likely to approach the predator. Sex differences in round goby risk-taking may reflect sex-specific selection pressures on activities promoting predation risk. With the exception of post-attack activity, round goby from contaminated sites generally showed signs of reduced risk-taking. If contaminant exposure increases goby vulnerability to predators, it may be occurring through behavioural mechanisms other than impacts on risky prey responses.

Introduction

Moving is risky. Increased activity levels, measured as either the duration or speed of locomotion, will make encountering predators more likely, and predators are more apt to notice and direct attacks towards prey that move (Lima & Dill 1990; Werner & Anholt 1993). For this reason, a decrease in activity following an increase in predation risk (e.g. a recent predator attack or predator-associated sensory stimuli) is a widely reported phenomenon across taxa (Lima 1998).

Prey movement and responses can be altered by a variety of stressors. The extent to which individuals are willing to trade off the costs of movement with its benefits (e.g. foraging success) will vary with condition or energetic state. Hungry or otherwise metaboli-cally taxed animals are more apt to exhibit risky behaviour such as greater activity, faster recovery of baseline levels of activity following an attack to find food (Lima 1998). Prey are also more likely to engage in inspection behaviour, approaching a predator to assess its chances of attack. Although inspection confers information benefits to prey, it also comes with a price – elevated mortality (Dugatkin & Godin 1992).

Anthropogenic stressors such as pollutants may also modify normal behaviour, which may indirectly impair movement, reproduction and survival (Del-l'omo 2002; Sloman & Wilson 2006). Most often studied in fishes, a wide variety of contaminants reduce the ability of exposed individuals to react to predators. Contaminants may impair sensory systems such as olfaction (Scholz et al. 2000) or lateral line detection (Faucher et al. 2006), by increasing reaction times

(McGee et al. 2009) or by promoting risky behaviour such as a reduction in schooling, increase in activity or increased time spent in open locations after an attack (Nakayama et al. 2005; Bell 2004). However, many contaminants often decrease activity in general (reviewed in Little & Finger 1990; Bayley 2002), which may reduce visibility to predators.

We examined contaminant impacts on prey behaviour in the round goby (*Neogobius melanostomus*), a small-bodied, cryptically coloured benthic fish that, like many species, relies on sheltering and burial in loose substrates to avoid predators (Belanger & Corkum 2003). This invasive species serves as prey for many piscivores, is exposed to contaminants through its diet of filter-feeding dreissenid mussels and has long been recognized as a potential vector for mobilizing contaminants in Great Lakes foodwebs (Jude et al. 1995). If contaminant exposure deleteriously impacts the ability of round goby to evade predators, this process of contaminant transfer could be accelerated locally, in regions where contaminants pose a problem (Marentette et al. 2010). One way in which round goby predator vulnerability could be affected by contaminant exposure is through an increase in risky behaviour. In our study, we tested the prey responses of round goby from areas of high and low contamination in Hamilton Harbour, a Lake Ontario embayment contaminated by polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), wastewater treatment plant effluents and metals such as cadmium, arsenic, zinc, mercury, iron and lead (Hamilton Harbour Remedial Action Plan (RAP) 1992; 2003).

We evaluated baseline levels of activity, shelter use, post-attack activity changes (the *post-attack response*), predator inspection and escape by darting in round goby from sites of varying contamination. We predicted that if contaminant exposure impairs the ability of individuals to produce appropriate responses to predators as discussed above, round goby from our contaminated sites might exhibit more risky behaviour such as faster recovery to baseline levels of activity after a simulated predation event, more high-visibility darting (vs. hiding) and more predator inspection, than fish from our low-contamination reference site.

Methods

Study Site

Round goby were collected in Hamilton Harbour, Lake Ontario, Canada (43°17′N 79°50′W). We exam-

ined fish from three locations: a low-contamination site (LCS) that served as a within-harbour reference site, LaSalle Park; and two highly contaminated sites (HCS) to examine the effects of chronic exposure pollutants, the mouth of Sherman Inlet, or HCS1; and Pier 27 or HCS2 (Fig. 1). Fish from areas of high contamination are smaller, show evidence of fin erosion, gonadal intersex, genital feminization and hepatic expression of vitellogenin by males, elevated 7-ethoxyresorufin-o-deethylase (EROD) activity, and greater body burdens of copper and cadmium (Bowley et al. 2010; Marentette et al. 2010). Fish from more contaminated areas have reduced activity levels (spontaneous locomotion) in novel environments (Marentette et al. 2012) and take longer to assess opponents in shelter resource contests (Sopinka et al. 2010).

Animal Collection and Housing

Round goby were collected in commercially available minnow traps baited with 30 g frozen corn, deployed in <1 m of water for 24 h up to 7 m from shore. Upon capture, round goby were transported to the laboratory and sorted by sex and site of capture into 60-l housing aquaria at McMaster University. Round goby are easily sexed by the shape of the urogenital papilla, which is pointed in males and blunt in females. Housing aquaria were maintained at 20–23°C under a light schedule of 16L:8D, and fish were provided with several centimetres of aquarium gravel substrate and
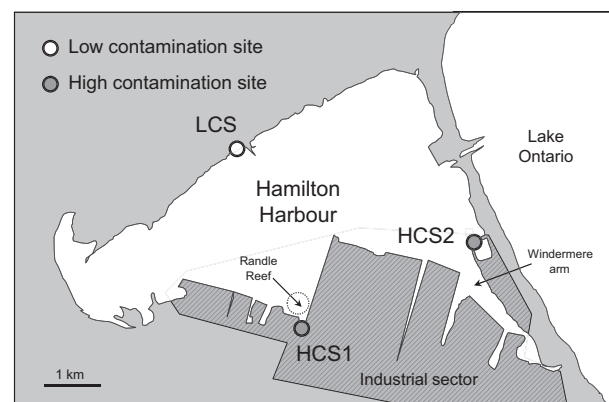

Fig. 1: Map of Hamilton Harbour with the round goby collection sites indicated as a site of low contamination (LCS; white circle) or high contamination (HCS1 and HCS2; grey circles). Sites were selected based on published sediment contaminant distribution patterns. Windermere Arm is a region known to be contaminated with PCBs and many metals; Randle Reef is a coal tar dump rich in PAHs and metals (Hamilton Harbour RAP 2003; Zeman 2009).

10-cm sections of black PVC tubing for shelter. Fish were fed with Nutrafin Basic fish flakes *ad libitum* once per day except on the day of behavioural tests. All round goby used in behavioural trials were allowed to acclimate to the laboratory for at least 48 h after capture and tested before 7 d in captivity had elapsed.

Simulated Predation Experiment

Between 16 Jun. and 6 Aug. 2009, round goby (n = 216) were collected in the field as described above, brought into the laboratory and housed in sex- and site-specific groups of three fish for 2–7 d. Goby were tested in groups of three as triads are more active than single fish, and the presence of conspecifics more closely approximates a natural social environment (Marentette et al. 2011; Marentette et al. 2012). Twelve groups were formed for each of three sites and two sexes, or 72 groups in total. Fish were acclimated to a 16L:8D light cycle with the nocturnal phase running from 0500 to 1300 h (facilitating observations during the day and the night). The three individuals in a group were of varying sizes and marked in different body locations with two subcutaneous visible implant elastomer (VIE) tags per fish, so that fish size (small, medium or large), supplemented by VIE tag location, could be used by the observer to identify individuals during the experiment. Fish were allowed to recover from VIE injection for at least 24 h before testing. The order of trial presentation was randomized across groups, and all trials were videotaped.

Round goby are active and forage throughout the diel cycle, but are most active at night, when they can be observed under red light (Dubs & Corkum 1996). For this reason, round goby may be at risk of predation by both diurnal and nocturnal predators. Groups of fish were subjected to a simulated predation event twice, once under diurnal conditions (1300–1900 h) and once under nocturnal (red light) conditions (0700–1300 h), on consecutive days. The order of trial presentation was balanced and randomized across groups.

Each trial had three phases: acclimation, attack and recovery. In the acclimation phase, round goby groups were introduced to a large open environment (1 m long, 0.75 m wide, filled to a depth of 0.15 m, with 1 cm of sandy substrate, three shelters in the middle and two external box filters placed along the back; Fig. 2). An observer, blind to the sex and site of origin of the fish, was positioned behind a blind 0.5 m away. Fish were allowed to acclimate to the apparatus for 60 min, and then each was observed for 1 min, every 3-min interval, for five observations. Fish were
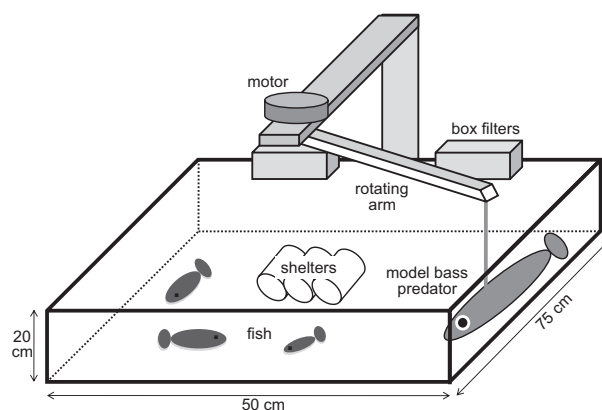

Fig. 2: Schematic representation of the experimental set-up. Objects are not to scale. Round goby were placed in the apparatus in groups of three. The model bass predator was first inserted and moved in a circle to simulate an attack; the model was then removed to evaluate post-attack responses. The movement of the model was controlled by a motor remotely operated by the observer.

observed in randomized order, and the number of baseline behaviours per minute was counted. Fish that did not move were designated as 'inactive' for that observation minute. The baseline observation period lasted 15 min in total.

The predator stimulus used in this experiment was a model bass (*Micropterus* spp.), adapted from a commercially available muskellunge lure (30 cm in length) attached to a transparent swivel, anchored to a wooden frame over the testing environment and powered by a remotely operated electric motor (Fig. 2). Smallmouth and largemouth bass (*Micropterus dolomieu* and *Micropterus salmoides*) are known round goby predators and are present in Hamilton Harbour (Brousseau & Randall 2008). The swivel moved the lure in a circle around the perimeter of the testing environment. The observer could operate the speed and direction of the swivel from behind the blind.

The attack phase began when the observer placed the model bass on the swivel, lowering the model into the water, simulating a predator appearance. The model was stationary for a 3-min period, and the observer would record whether any fish approached the model predator. The model was then manipulated to move in three short bursts at a rapid speed (1 m/s) around the perimeter of the environment to simulate an attack and quickly removed from the testing environment (approximately 30 s). The observer noted which fish darted in response to the model entry or movement and later confirmed these observations through videotape analyses. The observer then immediately began a sequence of 1-min observations on

each fish in turn, every 3-min interval, for five observations per fish. This recovery phase, lasting 15 min in total, evaluated round goby responses (and designated 'active' vs. 'inactive' fish for each minute) during a period when a predator appeared to have left the area.

At the conclusion of the trial, round goby groups were collected and either returned to their housing tank (if this was the first of two trials), or euthanized and dissected for body morphometrics (total length, total mass and body condition, measured as Fulton's K = total mass/total length^3 × 100 and also as the residuals of a regression of log-transformed mass against log-transformed total length) and to confirm sex. Females were classed as gravid if their gonadosomatic index (GSI; gonad mass/somatic mass × 100%) exceeded 8%, while males were classed as reproductive if their GSI exceeded 1%. Because of the size of the apparatus, water in the testing arena was changed once per day, filtered throughout the course of the experiment and thoroughly mixed between trials to minimize the effect of odours on fish behaviour. A maximum of two groups would occupy each testing environment in between water changes.

Data and Statistical Analyses

Statistics were performed using JMP 8 (SAS Institute 2008) and IBM SPSS Statistics 19 (IBM 2010). Morphometric data were transformed to meet the requirements of parametric tests where possible; otherwise, nonparametric tests were used. We evaluated five types of behaviour in round goby: baseline activity, sheltering (in the shelters provided or by self-burial in substrate), attack response (change in activity following an attack), approaching the model predator and the immediate escape response (darting vs. freezing) to the simulated attack. Each fish was given an activity score (the number of 'active' minutes, out of five) for two 5-min time periods before and after an attack. There were four times and thus four activity scores altogether (i.e. before and after both a diurnal and nocturnal attack). As these data were repeated-measures and counts, they were analysed with a generalized estimating equation (GEE) model, with a Poisson distribution and log link function. Factor effects were evaluated with Wald tests (χ^2).

Fish were also given a single binary score as to whether they ever approached the predator model and whether they darted as an immediate response to either the entry or movement of the model predator. Round goby were considered to have approached the predator if the fish made at least two movements

directly towards the stationary model. Fish would approach the model with a stereotypical posture, with all fins held erect and away from the body during pauses in between movements. These data were analysed with generalized linear models (GLM), using a binomial distribution and logit link function.

Models were first constructed using site as a factor and log-transformed total length as a covariate. A second more complex model was constructed incorporating the additional factor of sex. Interaction terms in all models were considered non-significant when p > 0.10; otherwise, main effects were explored within each interaction because p values < 0.10 but >0.05 were considered to represent trends. Covariates and covariate-main effect interaction terms were removed when non-significant. Estimated marginal means were contrasted with least significant difference *post-hoc* pairwise comparisons (LSD), among all possible pairs, to identify differences among groups while controlling for family-wise type I error.

Results

Baseline Patterns of Activity and Sheltering

Overall, round goby from LCS were more active than fish from contaminated sites, fish were also more active during the night than during the day, and smaller fish were more active than larger fish (Table 1). Within individuals, day and night activity scores were correlated (Spearman rho, r_s = 0.40, p < 0.0001).

Site effects varied with sex (Table 2), but in general, contamination was associated with reduced round goby baseline activity (Fig. 3). There was no difference in tendency to hide in shelter among sites (GEE, Wald χ^2 = 4.30, p = 0.12), diel period (Wald

Table 1: Summary of statistical models (generalized estimating equation and generalized linear models) and their effect tests (Wald tests) for round goby risk-taking behaviour, accounting for differences in fish size and site of origin. 'Time' as an effect refers to the four times at which activity was assessed (both before and after a diurnal and nocturnal attack). TL = total length

Behaviour	Effect	df	Wald χ^2	p
Activity (Baseline and attack response)	Log TL	1	38.22	0.000
	Site	2	28.89	0.000
	Time	3	53.78	0.000
	Site × Time	6	6.71	0.349
Approach	Log TL	1	26.78	0.000
	Site	2	4.43	0.109
Darting	Log TL	1	27.57	0.000
	Site	2	10.60	0.005

Table 2: Summary of statistical models (generalized estimating equation and generalized linear models) and their effect tests (Wald tests) for round goby risk-taking behaviour, accounting for differences in fish size, site of origin and sex. 'Time' as an effect refers to the four times at which activity was assessed (both before and after a diurnal and nocturnal attack). TL = total length

Behaviour	Effect	df	Wald χ^2	p
Activity (Baseline and attack response)	Log TL	1	44.57	0.000
	Site	2	30.75	0.000
	Sex	1	10.37	0.001
	Time	3	52.22	0.000
	Site × Sex	2	1.71	0.425
	Site × Time	6	6.28	0.393
	Sex × Time	3	3.24	0.350
	Site × Sex × Time	6	12.83	0.046
Approach	Log TL	1	26.23	0.000
	Site	2	4.61	0.100
	Sex	1	4.89	0.027
	Site × Sex	2	5.00	0.082
Darting	Log TL	1	32.00	0.000
	Site	2	11.61	0.003
	Sex	1	8.42	0.004
	Site × Sex	2	6.05	0.049

Fig. 3: Estimated marginal means (±SE) of round goby activity levels, scored as the number of minutes active out of 5, before and after a simulated predator attack. The upper panels (a–c) represent diurnal activity, and the lower panels (d–f) represent nocturnal activity. (a) Variation in diurnal activity and post-attack response (reduction in activity) across sites; (b) in males only; and (c) in females only. (d) Variation in nocturnal activity and response to attack across sites; (e) in males only; and (f) in females only. Letters indicate significant differences among means within each panel (LSD tests, p < 0.05).

$\chi^2 = 0.39$, p = 0.53) or by sex (Wald $\chi^2 = 1.86$, p = 0.17).

Post-Attack Response

As expected, a post-attack response (a reduction in activity from baseline levels following an attack) was displayed in both diurnal and nocturnal conditions by fish in the low-contamination reference site (Table 1; Fig. 3a,d). Contaminated-site fish only displayed a post-attack response during the night. This was generally true for both males and females, although females from contaminated sites were somewhat less likely than males to show a post-attack response at all (Table 2, Fig. 3).

Approaching the Model Predator

Only 18% of fish ever approached the stationary model bass. Smaller fish in general were more likely to inspect the simulated predator, and there was no overall effect of site on the probability of predator approach (Table 1, Fig. 4a). When sex was taken into account, males were more likely to inspect than females, but this tended to vary with site (p = 0.08; Table 2). Males showed no variation across sites, while females from HCS2 were less likely to approach than fish from LCS (Fig. 4a–c). There was no significant difference in the GSI of females that approached
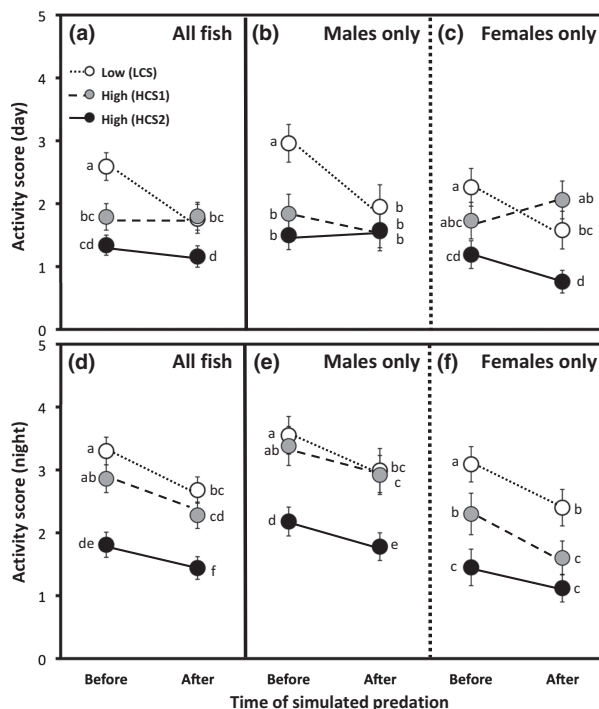
the predator or not (Wilcoxon rank-sum, Z = 1.41, p = 0.16).

Darting as Escape Response to Simulated Attack

Nearly 40% of round goby darted in response to either the appearance or the movement of the model bass predator. Overall, fish from HCS2 were less likely to dart, and smaller fish in general were more likely to dart than larger fish (Table 1, Fig. 4d). When sex was taken into consideration, there were no site differences among females, but males showed a lower propensity to dart with site contamination (Table 2, Fig. 4e,f).

Although darting is considered risky because it increases prey visibility, darting may be beneficial if it enables the fish to become inaccessible to predators, either by moving to shelter or by self-burial in substrate. We addressed this by examining the tendency to take shelter while darting; however, there were no
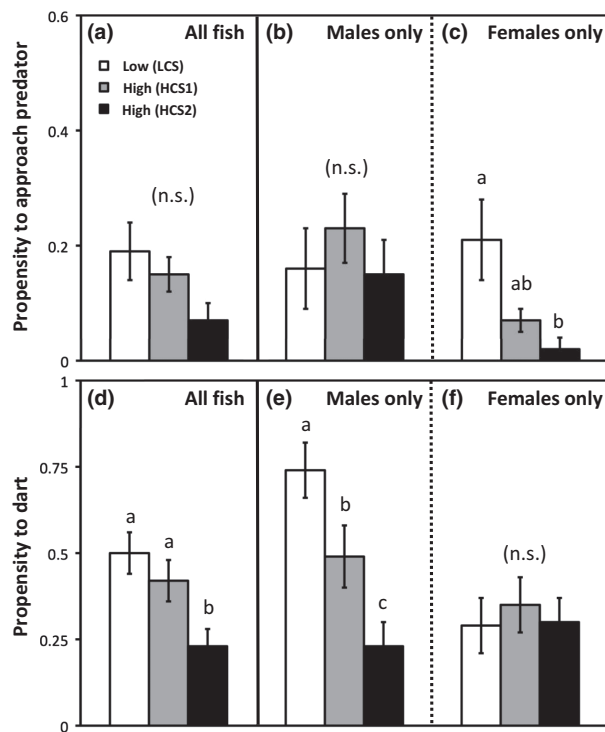
Fig. 4: (a–c) Estimated marginal mean (±SE) probability of round goby approach to a stationary predator model. (a) Sites did not vary in probability of approach. (b) Male approach probability did not vary across sites. (c) Female approach probability was reduced with site contamination. (d–f) Estimated marginal mean (±SE) probability of darting in response to predator model. (d) Contaminant exposure lowered the likelihood of darting across sites. (e) Male darting was lower in fish from contaminated sites. (f) Female darting probability did not vary across sites. Letters indicate significant differences among means within each panel (LSD tests, p < 0.05). n.s., not significant.

Discussion

Round goby from contaminated sites did not reduce their activity levels in response to a simulated attack, unlike goby from a low-contamination reference site. Effects of site contamination varied with sex. Females from contaminated sites responded with less predator inspection, which can confer benefits about the risk of an attack (Dugatkin & Godin 1992). Males from contaminated sites responded with a reduced propensity to dart. Failure to reduce activity after a predator attack has also been observed in pentachlorophenol-exposed rotifers (*Brachionus calyciflorus*; Preston et al. 1998), mercury-exposed golden shiners (*Notemigonus crysoleucas*; Webber & Haines 2003), tributyltin oxide (TBTO)–exposed sticklebacks *(Gasterosteus aculeatus*; Wibe et al. 2001), dichlorodiphenyltrichloroethane (DDT)-exposed goldfish (*Carassius auratus*, Weis & Weis 1974) and EE$_2$-exposed sticklebacks (Bell 2004). TBTO-exposed sticklebacks also displayed the same reduced tendency to dart during attack (Wibe et al. 2001) as did fish in this study.

Round goby from contaminated sites were also less active at baseline, something that has also been observed in other studies of fish chronically exposed to complex combinations of contaminants (Triebskorn et al. 1997; Candelmo et al. 2010). Why might round goby from contaminated sites have altered activity patterns? They may suffer from impaired physical mobility, because of toxic action, which may prevent fish from moving (Barron 2002). While this explanation may address a lower baseline level of activity or lower propensity to dart, it does not explain why round goby from contaminated sites fail to reduce activity even further after an attack. Instead, this altered activity pattern may reflect a cognitive or sensory impairment of mobility, preventing fish from modulating their activity adaptively in response to cues of predation risk (Sloman & Wilson 2006). Increased mortality from predation in contaminated sites may select for round goby of reduced activity and more shy, risk-averse personality traits (Huntingford 1982; Magnhagen & Borcherding 2008). The relationship of predation regime and personality is complex, however, as the opposite effect (increased boldness and activity relative to low-predation populations) can also occur (Brown et al. 2005; Harris et al. 2010). Differences in predation rates among sites in our study are unfortunately not clear. The high-contamination site HCS2 is located near a colony of double-crested cormorants (*Phalacrocorax auritus*) and other piscivorous birds (Somers et al. 2003). High levels of previous exposure to avian predators may modulate

site differences in this tendency within either males or females (GEE, site × sex interaction, Wald χ^2 = 5.28, p = 0.07; LSD tests, p > 0.05).

Morphological Differences among Sites

Round goby from LCS were larger than fish from the contaminated sites HCS1 and HCS2 (ANOVA on log total length, site $F_{2,210}$ = 9.26, p = 0.0001). However, fish from different sites did not differ in body condition (ANOVA on Fulton's K, site $F_{2,210}$ = 1.27, p = 0.28; ANOVA on residuals of mass against length, site $F_{2,210}$ = 1.22, p = 0.27). Nearly twice as many males were in reproductive condition at HCS1 (81%) vs. the LCS (44%) and HCS2 (47%; χ^2 = 11.9, p = 0.003). There were no differences across sites in the number of gravid females (χ^2 = 3.2, p = 0.21).

round goby behaviour. However, these visual hunters also forage many kilometres away from their nests and potentially affect many round goby populations, not just HCS2 (Stapanian et al. 2002). Round goby in stressed, contaminated sites may not show a post-attack response because they actually do not benefit from reducing their activity following an attack. This may be either because their baseline levels of activity may already be below a predator detection threshold (Strod et al. 2008) or because their energetic demands (possibly due to increased reproductive expenditures) are high enough that fish must continue to move and attempt to forage despite the increased risk (Lima 1998) as thought to be the case with stickleback exposed to EE_2 (Bell 2004).

Why were there sex differences in how round goby respond to predators? In LCS fish, there were no sex differences in inspection behaviour, but males darted more often than females. Females from contaminated sites displayed reduced inspection (Fig. 4–a–c). At the same time, males from contaminated sites were less likely to dart (Fig. 4–d–f). Although males from one high-contamination site (HCS1) were more likely to be in reproductive condition than male fish from the other sites, this pattern did not parallel darting behaviour. The overall reduction in male darting with habitat contamination (i.e. to female-typical levels) makes sense, particularly if movement increases the likelihood of predator detection and successful attack (Martel & Dill 1995). However, why might males, but not females, maintain relatively higher levels of inspection in contaminated sites? Inspecting fish gain information about predators, but at the price of being targeted more often (Dugatkin & Godin 1992). Females may be more susceptible to predators than males if an attack is initiated, possibly through impaired escape responses in gravid females swollen with eggs (Bauwens & Thoen 1981). However, we did not find a negative relationship between the relative size of the gonads (GSI) and inspection in females in this study.

We had predicted that fish from contaminant-stressed sites would show greater risk-taking. However, with the exception of failing to demonstrate a diurnal post-attack response (lowered activity relative to baseline), risk-taking was in all metrics highest in fish from the reference site LCS. It is possible that fish from LCS are able to obtain the benefits of increased movement (access to food resources, acquisition of predator information through inspection; Lima & Dill 1990; Lima 1998) while being able to compensate for their increased level of risk by having faster reaction times or better detection abilities than fish from

stressed sites. If round goby in contaminated sites are indeed more vulnerable to predators, it may be occurring through means other than risk-taking (e.g. slower reaction times, smaller startle responses, impaired sensory systems or cognitive responses to the threat of predation, reduced swimming performance; Barron 2002; Sloman & Wilson 2006). These are questions worthy of future attention.

Acknowledgements

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