Does predation risk influence habitat use by northern redbelly dace *Phoxinus eos* at different spatial scales?

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This study investigated the relationship between spatial variations in predation risk and abundance of northern redbelly dace *Phoxinus eos* at both macroscale (littoral *v.* pelagic zones) and microscale (structured *v.* open water habitats in the littoral zone) of Canadian Shield lakes. Minnow traps were placed in both structured and open water habitats in the littoral zone of 13 Canadian Shield lakes, and estimates of the relative predation risk of *P. eos* in both the pelagic and the littoral zones were obtained from tethering experiments. Results showed that (1) the mean abundance of *P. eos* in the littoral zone was positively correlated with the relative predation risk in the pelagic zone, (2) *P. eos* preferentially used structured over open water habitats in the littoral zone and (3) this preference was not related to the relative predation risk in the littoral zone but decreased as the relative predation risk increased in the pelagic zone. At the lake level, these results support the hypothesis that *P. eos* enter the littoral zone to avoid pelagic piscivores. At the littoral zone level, the results do not necessarily contradict the widely accepted view that *P. eos* preferentially use structured over open habitats to reduce their predation risk, but suggest that flexibility in antipredator tactics (*e.g.* shelter use *v.* shoaling) could explain the spatial distribution of *P. eos* between structured and open water habitats.

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Key words: antipredator behaviour; diel horizontal migration; habitat selection; habitat structural complexity; shelter use; tethering experiment.

INTRODUCTION

Many studies have shown that prey fishes alter their habitat selection in order to reduce predation risk (Lima & Dill, 1990; Lima, 1998). Habitats differ in both biotic and abiotic characteristics (including predation risk), and spatial heterogeneity occurs at different scales. Kramer *et al.* (1997) suggested that habitat selection by fishes is a hierarchical process in which a general area is first selected (*e.g.* a lake or stream) followed by the selection of a macrohabitat

(*e.g.* nearshore, riffle and pool) and finally by progressively smaller scale decisions regarding local habitat characteristics (microhabitat; *e.g.* depth or structural complexity). This concept has been examined in birds and mammals (Orians & Wittenberger, 1991; Schaefer & Messier, 1995; Rolstad & Loken, 2000) but rarely in aquatic organisms (Bult *et al.*, 1998; Crook *et al.*, 2001). Yet, given that the spatial distribution of fishes is associated with a set of habitat characteristics that depends on spatial scale (Poizat & Pont, 1996; Bult *et al.*, 1998; Crook *et al.*, 2001; Brind'Amour *et al.*, 2005), it could be expected that habitat selection results from such a hierarchical decision-making process. Many studies have shown that prey fishes avoid predator-rich or refuge-poor habitats at the macroscale to decrease predation risk (*e.g.* pelagic zone of lakes; Lima, 1998; Brown, 2003). At the microscale, prey fishes increase the use of structurally complex habitats (such as submerged vegetation and woody structures) when predation risk is high (Lima & Dill, 1990; Lima, 1998).

Refuge habitat use is often associated with lost foraging opportunities and increased resource competition (Werner *et al.*, 1983; Sih, 1997). Consequently, it could be expected that threatened fishes adapt their habitat use to the level of predation risk (Helfman, 1989; Krause *et al.*, 1998, 2000) in an attempt to maximize their fitness (Lima & Dill, 1990; Lima, 1998). The use of refuge habitats was also found to be related to prey size (Krause *et al.*, 1998; Dowling & Godin, 2002; Mirza & Chivers, 2003). Because the vulnerability of prey decreases as their body size increases (Sogard, 1997), prey fishes of different sizes respond differently to the same level of predation risk (Krause *et al.*, 1998, 2000; Dowling & Godin, 2002).

Northern redbelly dace *Phoxinus eos* (Cope) exhibit diel onshore–offshore migrations in Canadian Shield lakes (Naud & Magnan, 1988; Gauthier *et al.*, 1997). They form shoals in the littoral zone during the day, disperse in the pelagic zone at sunset to feed on zooplankton and then return to the littoral zone at sunrise. There is variability around this general pattern, with a small number of *P. eos* being observed outside the littoral zone during daytime (Naud & Magnan, 1988; Comeau & Boisclair, 1998; Gaudreau & Boisclair, 1998). Naud & Magnan (1988) suggested that *P. eos* use the littoral zone during daytime to reduce their predation risk by brook trout *Salvelinus fontinalis* (Mitchill), a visual predator (Power, 1980). In agreement with this hypothesis, tethering experiments have shown that the relative predation risk of *P. eos* was significantly higher during daytime than during the night (A. Dupuch, A. Bertolo, P. Magnan & L. M. Dill, unpubl. data). Also, Gaudreau & Boisclair (1998) showed that the presence of pelagic piscivores such as *S. fontinalis* significantly reduced the number of *P. eos* present outside the littoral zone. Furthermore, *P. eos* preferentially use structured habitats that include vegetation and woody structures in the littoral zone of lakes (Naud & Magnan, 1988; He & Lodge, 1990; MacRae & Jackson, 2001; Jacobus & Ivan, 2005). Because many studies have shown that fish density in the littoral zone is generally higher in more structurally complex habitats (Lewin *et al.*, 2004), the results described above suggest that predation risk is the causal mechanism of this pattern. This has seldom been the subject of a specific test in the field, however, due to the difficulties of estimating predation risk in nature (Rozas & Odum, 1988). In the laboratory, the use of structured habitats allowed *P. eos* to significantly reduce the number of attacks and captures by *S. fontinalis* (East & Magnan,

1991), supporting the predation risk hypothesis. Furthermore, *P. eos* are able to adapt the intensity of their antipredator response with the level of predation risk (Dupuch *et al.*, 2004). Thus, this system is a good model to test the effect of predation risk level on habitat use of prey fishes at both the macroscale and the microscale.

Previous studies showed that *S. fontinalis* prey upon *P. eos* (East & Magnan, 1991; Lacasse & Magnan, 1992). Furthermore, the occurrence of *P. eos* in the diet of *S. fontinalis* was higher in lakes containing white sucker *Catostomus commersonii* (Lacépède) and creek chub *Semotilus atromaculatus* (Mitchill) than in lakes containing only *S. fontinalis* (East & Magnan, 1991; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992). *Salvelinus fontinalis* shift their diet from benthic invertebrates to zooplankton and prey fishes when living in sympatry with *S. atromaculatus* and *C. commersonii* because these two species are better adapted to feeding on benthic invertebrates than are *S. fontinalis* (Magnan & Fitzgerald, 1982, 1984; Tremblay & Magnan, 1991; Bourke *et al.*, 1999). This result suggests that the predation risk of *P. eos* is higher in lakes containing *C. commersonii* and *S. atromaculatus* than in lakes containing only *S. fontinalis* (lakes 'with competitors' and 'without competitors,' respectively).

The goal of this study was to test whether habitat selection by *P. eos* is a hierarchical process associated with spatial scale (from macrohabitat to microhabitat). In this context, if *P. eos* use the littoral zone to avoid pelagic piscivores, predictions were that (1) their abundance in the littoral zone will be positively related with relative predation risk in the pelagic zone at the lake level and (2) their abundance in structured habitats (compared to open water habitats) in the littoral zone will be positively related to the relative predation risk at the littoral zone level. The relationship between *P. eos* total length (L_T) and their microhabitat use in the littoral zone was also analysed. The abundance of *P. eos* in both structured and open water habitats of the littoral zone was estimated as well as their relative predation risk in the littoral and pelagic zones of lakes with and without competitors.

MATERIALS AND METHODS

STUDY SITES

The study was carried out in 13 lakes of the Mastigouche Reserve (Québec, Canada; 46°40′ N; 73°20′ W) from June to September 1989 and from July to August 2003. These lakes are oligotrophic and typical of the Canadian Shield but differ in their fish assemblages. The study lakes have comparable morphologies (with shallow littoral zones continuously distributed around each lake) and structured habitats in the littoral zones. Therefore, *P. eos* density was assumed to be comparable among lakes. The main characteristics and fish assemblages of the study lakes are shown in Table I. Apart from *S. fontinalis*, potential piscivores were considered negligible in the study lakes. *Semotilus atromaculatus* is a generalist feeder (Scott & Crossman, 1974), with large individuals (>135 mm L_T) feeding on small fishes (Gilliam & Fraser, 1987). Given that (1) gillnet fishing showed that the abundance of large *S. atromaculatus* was low in the study lakes (A. Dupuch, A. Bertolo, P. Magnan & L. M. Dill, unpubl. data) and (2) small fishes were absent in stomach contents of large *S. atromaculatus* captured in lakes similar to the study lakes (Magnan & Fitzgerald, 1982, 1984), *S. atromaculatus* was assumed to be a negligible predator on *P. eos*. Moreover, piscivorous birds (common loon,

TABLE I. Lake area, mean depth, study year, fish species composition and mean relative predation risk (obtained from tethering experiments) in the littoral and pelagic zones of the study lakes

| Lake name | Area (ha) | Mean depth (m) | Study year | | Fish assemblage | | | | | Mean ± S.D. predation (%) | |
			1989	2003	Sf	Pe	Cc	Sa	Sm	Littoral zone	Pelagic zone
Without competitors											
Bondi	25·7	8·1		x	x	x				0 ± 0	38 ± 5
Charme	22·0	3·2	x		x	x					
Cerné	13·2	4·4		x	x	x				23 ± 9	42 ± 20
Diablos	9·1	3·5	x		x	x					
Lafond	46·7	7·9		x	x	x				6 ± 10	20 ± 2
Osborn	10·8	4·8	x	x	x	x				7 ± 12	40 ± 10
Vautour	7·2	4·8	x		x	x					
With competitors											
Gauthier	36·9	n.d.		x	x	x		x	x	20 ± 28	15 ± 15
Grignon	29·6	7·9	x	x	x	x	x	x		18 ± 17	62 ± 20
Grosse	8·0	6·2		x	x	x	x	x		75 ± 25	48 ± 35
Joe	23·3	n.d.	x		x	x	x				
Sauterelle	8·1	5·4	x		x	x	x		x		
Vert	17·1	8·7	x		x	x	x	x			

Cc, *Catostomus commersonii*; n.d., not determined; Pe, *Phoxinus eos*; Sa, *Semotilus atromaculatus;* Sf, *Salvelinus fontinalis*; Sm, *Semotilus margarita*; X, year samples are taken.

kingfisher and great blue heron) were rarely observed on the study lakes. Therefore, their effect on the relative predation risk of *P. eos* was also considered negligible compared to *S. fontinalis*.

STUDY DESIGN

In 1989, eight lakes were sampled three times between June and September. In 2003, seven lakes were sampled three times over 1 week in July or August. To estimate *P. eos* abundance, minnow traps (420 mm long by 2250 mm in diameter, 10 mm mesh and 25 mm diameter opening) baited with constant quantities of bread were placed in the shallow littoral zone (water depth <1 m) from 1800 to 0800 hours in 1989 and from 1100 to 1300 hours in 2003. He & Lodge (1990) found that catch per unit effort (CPUE) obtained from minnow traps provided an accurate index of *P. eos* abundance. The 1989 and 2003 experiments were part of projects having different logistical constraints, which is why the fishing periods were different. Despite the different fishing periods, the two sampling years were assumed to yield similar information regarding *P. eos* abundance in the littoral zone during the day because both covered at least 2 h of the daylight period (in 1989, traps sampled fish for *c.* 2 h before sunset and 2 h after sunrise, based on sunrise and sunset tables provided by the National Research Council of Canada for Trois-Rivières, Québec, Canada). Furthermore, *P. eos* probably entered the traps during daylight in 1989 given that *P. eos* are rarely found in the littoral zone at night in these small boreal lakes (Naud & Magnan, 1988; Gauthier & Boisclair, 1997). Traps were randomly placed at a distance of 20 m from each other in two types of habitat (15 and 10 traps in each habitat type in 1989 and 2003, respectively). The structured habitat was characterized either by numerous rigid and tangled stems of *Cassandra*

calyculata (L.) and *Sparganium* sp. (L.) (large patches of vegetation, >15 m of length, were regularly dispersed in littoral zone) or by immersed wood (trees or branches randomly distributed in the littoral zone); the open water habitat had no structures. Traps in open water habitats were placed at a minimum distance of 5 m from structured habitats. For both years, *P. eos* captured in each trap were counted. In 2003, 20 randomly sampled individuals per trap were sacrificed with an overdose of MS-222 and preserved in 95% alcohol for further laboratory analyses (L_T for the present study).

In 2003, predation risk was estimated in parallel to *P. eos* abundance using chronographic tethers (Danilowicz & Sale, 1999). Once the potential artefacts due to this approach are taken into account, tethering experiments are an effective approach for measuring the combined effect of predator abundance and the intensity of their foraging activity (Aronson & Heck, 1995; Post *et al.*, 1998). It is important to take into account, however, that this technique measures relative predation rates rather than natural ones because tethers may increase prey susceptibility to predation by restricting their ability to escape or by inducing attention-attracting behaviour. Despite such limitations, tethering experiments offer a valuable measure of predation potential in comparative studies (Aronson *et al.*, 2001). In each lake, 30 tethered *P. eos* were set at different combinations of depth × water column isobath (isobaths = 1, 2, 3, 4 and 5 m; depths = 0·5, 1·5, 2·5, 3·5 and 4·5 m). During daytime, *P. eos* were rarely observed outside the areas used for tethering in lakes containing *S. fontinalis* (Naud & Magnan, 1988; Gaudreau & Boisclair, 1998). Fish were attached to the tethers with fishing wire inserted into the musculature under the dorsal fin, allowing them to swim freely. The length of *P. eos* used for the tethering experiment was standardized among lakes (mean ± S.D. = 60 ± 3 mm in 2003). *Phoxinus eos* were maintained in a given location by an anchored float and placed in an open area (*i.e.* without vegetation or woody debris) to avoid entanglement and at a minimum distance of 20 m from each other. The positions of chronographic tethers were changed randomly each sampling day within a given lake to take into account spatial variations in predator density and activity, thus giving a better estimate of the relative predation risk. The relative predation risk was estimated in both the littoral and the pelagic zones based on *P. eos* tethered at the ≤2 and >2 m isobaths, respectively (submerged vegetation was rare beyond the 2 m isobath). The relative predation risk was estimated as the proportion of missing *P. eos* after a given period of time (here 17 h). The mean relative predation risks in the littoral and pelagic zones of each lake are given in Table I.

STATISTICAL ANALYSES

The 1989 and 2003 data were analysed separately in order to validate the results of 2003 with those of 1989. For each sampling year, a mixed model approach (MIXED procedure of SAS 9.1.3; 2002 SAS package; www.sas.com) with repeated measures and nested designs (lake was nested into fish assemblage) was used to model *P. eos* CPUE (mean number of fish trap^{-1} habitat^{-1}day^{-1}). The effects of habitat type (0 = open water habitat and 1 = structured habitat), fish assemblage (0 = without competitors and 1 = with competitors) and their interaction were tested for both sampling years. In addition to these variables, the effects of both littoral and pelagic relative predation risk and their interactions with habitat type (*i.e.* littoral predation risk × habitat type and pelagic predation risk × habitat type) on the CPUE of 2003 were also tested. Given that a preliminary analysis showed that (1) the average relative predation risk of *P. eos* was not significantly higher in lakes with competitors than without (A. Dupuch, A. Bertolo, P. Magnan & L. M. Dill, unpubl. data) and that (2) fish assemblage and the relative predation risks in the littoral and pelagic zones were not co-linear, all these variables were tested in the same analysis. Consequently, the variable 'fish assemblage' was interpreted as an effect of fish assemblage independent of predation risk.

For the analysis performed on the 1989 data, the sampling period (1 = beginning of summer; 2 = middle of summer and 3 = end of summer) was introduced into the model only to control for its effect on CPUE and so was not used in the interactions with the

other variables. The same procedure to model repeated measures was applied in 2003. Based on the Akaïke information criterion (AIC; Burnham & Anderson, 2002), however, the model that does not include the parameter for repeated measures better explained the CPUE, suggesting a low degree of temporal autocorrelation in the data. Because removing this parameter from the model did not qualitatively change the results, only the more parsimonious model that includes the nested design is presented. CPUE was $\log_{10} (x + 1)$ transformed to normalize the residuals and reduce their heteroscedasticity.

RESULTS

The analysis performed on the 1989 data showed that the average *P. eos* abundance in the littoral zone was significantly higher (1) in lakes with competitors than without and (2) in structured than in open water habitats (Table II). Moreover, *P. eos* abundance in structured habitats was significantly higher in lakes with competitors than without [the (fish assemblage × habitat type) term was significant; Table II], leading to a higher proportion of *P. eos* in structured habitats in these lakes (*i.e.* with competitors; Fig. 1).

The analysis of the 2003 data gave qualitatively the same results (Table II and Fig. 1). Furthermore, this analysis showed that, on average, the *P. eos* abundance in the littoral zone was significantly and positively correlated with the relative pelagic predation risk and negatively correlated with the relative littoral predation risk. The positive correlation between *P. eos* abundance in the littoral zone and the relative pelagic predation risk, however, was higher in

TABLE II. Results of the mixed models performed on the 1989 and 2003 data to predict *Phoxinus eos* catch per unit effort in structured and open water habitats in the littoral zone of study lakes

| Variables	Estimates ± S.E.	d.f.	*F*-value	*P*
1989				
Intercept	+2·20 ± 0·30			
Time 1	+1·56 ± 0·30	235·3	26·03	<0·001
Time 2	−0·37 ± 0·30			
Time 3	0·00			
Habitat type	−1·08 ± 0·33	134·5	6·52	<0·05
Fish assemblage	−0·70 ± 0·35	16·31	21·56	<0·01
Habitat type × fish assemblage	+0·95 ± 0·47	124·5	4·04	>0·05
2003				
Intercept	+1·67 ± 0·45			
Habitat type	−0·56 ± 0·19	127·9	5·87	<0·05
Fish assemblage	−1·37 ± 0·55	15·18	9·43	<0·05
Habitat type × fish assemblage	+0·55 ± 0·24	127·9	4·98	<0·05
Littoral predation risk	−0·30 ± 0·13	132·9	4·75	<0·05
Pelagic predation risk	+0·56 ± 0·11	131·8	5·98	<0·05
Pelagic predation risk × habitat type	+0·67 ± 0·12	127·9	30·68	<0·001
Littoral predation risk × habitat type	+0·04 ± 0·16	126·9	0·06	>0·05
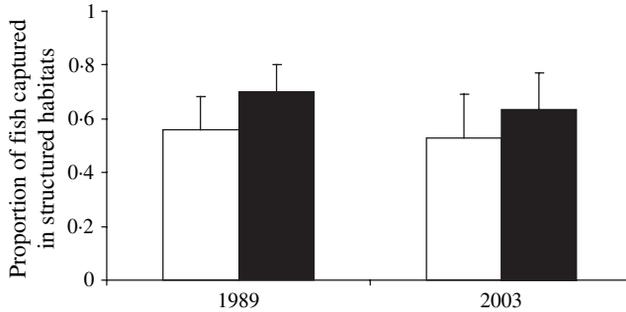
FIG. 1. Mean ± S.E. proportion of *Phoxinus eos* captured in structured habitats of the littoral zone of lakes according to fish assemblage (□, without competitors; ■, with competitors) for 1989 and 2003.

open than in structured habitats [the (pelagic predation risk × habitat type) term was significant; Table II]. This led to a negative correlation between the proportion of *P. eos* captured in structured habitats and the relative pelagic predation risk (Fig. 2). Moreover, the effect of the relative littoral predation risk was not significantly different between habitat types [the (littoral predation risk × habitat type) term was not significant; Table II].

The mean ± S.D. and range of L_T of *P. eos* captured in minnow traps in 2003 were $54·3 ± 6·8$ and $40·1–76·7$ mm, respectively. No significant differences were observed in the mean L_T of *P. eos* between structured and open water habitats (Kolmogorov–Smirnov test, $P > 0·05$ in all lakes).

DISCUSSION

Habitat selection by *P. eos* was related to both structural complexity and predation risk. The fact that the average abundance of *P. eos* in the littoral zone (depth <1 m) was significantly and positively correlated with the relative pelagic predation risk supports the hypothesis that at the lake level, *P. eos* enter
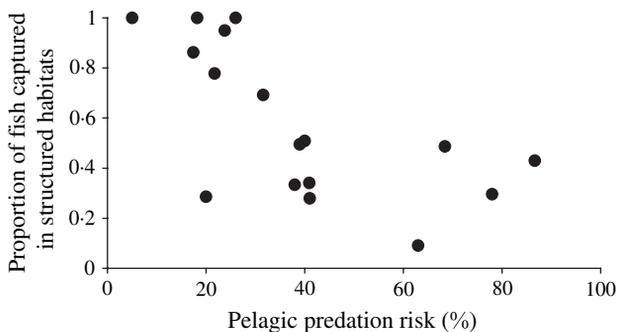

FIG. 2. Variations in the proportion of *Phoxinus eos* captured in structured habitats of the littoral zone of lakes according to the relative predation risk in the pelagic zone (2003 data) (generalized linear model with a repeated measures design, $P^2 = 0·42$, $F_{1,16}$, $P < 0·01$).

the littoral zone to reduce their predation risk by pelagic piscivores. The proximity of structured habitats and the rare presence of *S. fontinalis* in the warm waters (Bourke *et al.*, 1996) make the littoral zone a safer habitat for *P. eos* than deeper areas.

At the littoral zone level, *P. eos* were on average more numerous in structured than in open water habitats, a distribution pattern that has been observed in other studies (Naud & Magnan, 1988; He & Lodge, 1990; MacRae & Jackson, 2001; Jacobus & Ivan, 2005). This preference for the structured habitats compared to the open water habitat was not related to *P. eos* L_T, probably partly because the L_T range of *P. eos* captured in minnow traps was small.

Contrary to expectations, the abundance of *P. eos* in structured habitats (compared to the open water habitat) was not positively correlated to the relative predation risk in the littoral zone. This does not contradict the widely accepted view that *P. eos* use these habitats to reduce their predation risk (Naud & Magnan, 1988). Although the use of structured habitats to avoid predation is common in aquatic species (Lima & Dill, 1990; Lima, 1998), prey fishes do not always shift to structured habitats in the presence of predators (Jacobsen & Berg, 1998; Pink *et al.*, 2007). Several, not mutually exclusive, hypotheses could explain this unexpected result. First, the availability of structured habitats limits prey abundance in these habitats (Rangeley & Kramer, 1998). Given that submerged vegetation and woody debris were abundant in the littoral zones of the study lakes (A. Dupuch, pers. obs.), there is no reason to raise this hypothesis for the study system. Second, shallow habitats in the littoral zone are also refuge habitats for prey fishes (Lima, 1998), whatever the availability of structured habitats they offer. He (1986) observed that *P. eos* aggregate in the very shallow water in the littoral zone in the presence of predators. The use of an alternative refuge habitat by *P. eos* could thus explain the absence of a positive correlation between *P. eos* abundance in structured habitats and relative predation risk in the littoral zone. Furthermore, sheltering is often associated with a reduction of the prey's activity level (Lima, 1998), which could explain the reduced *P. eos* CPUE as the relative littoral predation risk increased. Third, *P. eos* shoal when in the littoral zone (Naud & Magnan, 1988; Pink *et al.*, 2007): a preference for shoaling over refuge use in response to predation risk, as has been observed in other fish species (Brown & Warburton, 1997; Rangeley & Kramer, 1998), could explain the results of this study. Such a preference for shoaling over sheltering behaviour has been observed in *P. eos* (Pink *et al.*, 2007). These authors showed that after the introduction of *S. fontinalis* to lakes, *P. eos* did not increase their use of structured habitats but significantly increased their shoal size. Ashley *et al.* (1993) also showed that *P. eos* were less sensible of the presence of a nearby predator when their shoal size was >10 individuals: the larger the group size, the greater the benefits from the dilution and confusion effects (Pitcher, 1986; Godin, 1997; Krause & Ruxton, 2002). Shoaling behaviour also has the advantage of allowing individuals to search for food by switching among habitats while reducing predation risk (Pitcher & Parrish, 1993; Eklov & Persson, 1995; Godin, 1997), whereas sheltering is often associated with lost foraging opportunities and increased resource competition within the refuge habitat (Werner *et al.*, 1983; Sih, 1997).

Layman & Smith (2001) showed that *Fundulus heteroclitus* (L.) are attracted to minnow traps due to structure, perhaps as a behavioural adaptation to minimize predation risk. Furthermore, Robichaud *et al.* (2000) suggested that a trap in open water habitats is more attractive than in structured habitats. Consequently, it could be expected that *P. eos* used minnow traps as refuges, particularly in open water habitats of the littoral zone, and that their attraction to traps increased with predation risk. Thus, this sampling technique could also explain the higher CPUE in open water than in structured habitats of the littoral zone as the relative pelagic predation risk increases, a counterintuitive result if *P. eos* use structured habitats as refuges. Laboratory experiments showed that *P. eos* were attracted to traps, but that this attraction decreased as predation risk increased (A. Dupuch, A. Bertolo, P. Magnan & L. M. Dill, unpubl. data). In fact, *P. eos* increased their shoaling behaviour when predation risk was high rather than searching for a structure (*i.e.* the trap) to hide (A. Dupuch, pers. obs.). Shoaling behaviour thus appears to be an important antipredator strategy in *P. eos*. All these results combined suggest that *P. eos* use several different antipredator tactics, leading to an unexpected spatial distribution of *P. eos* in the littoral zone of lakes.

For both years, the fish assemblage significantly influenced the spatial distribution of *P. eos*. Abundance of the fish in the littoral zone was higher in lakes with competitors than without, especially in structured habitats. Based on previous studies, the presence of competitors in lakes was considered to be a factor that indirectly increased predation risk of *P. eos*. Given (1) that the relative predation risk was similar in both fish assemblages (A. Dupuch, A. Bertolo, P. Magnan & L. M. Dill, unpubl. data), (2) that the effect of fish assemblage was estimated after controlling for the effects of the relative littoral and pelagic predation risk and (3) that *S. atromaculatus*, *C. commersonii* and *Margariscus margarita* (Cope) shared the littoral zone with *P. eos*, the higher abundance of *P. eos* in structured habitats in lakes with competitors than without could be a response to interspecific competitive interactions rather than to predation risk. Such interactions have been shown to directly affect the use of structured habitats by fishes (Werner & Hall, 1977; Schofield, 2003). In the presence of competitors, the use of structured habitats by *P. eos* probably results from a combination of both interspecific competition and predation risk.

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