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RESEARCH ARTICLE

Indirect effects of asymmetrical competition among top predators determine spatial patterns of predation risk for prey

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Abstract Asymmetrical interspecific competition among top predators can indirectly affect the predation risk for their prey by altering the abundance, diet, and habitat use of inferior competitors. However, the indirect effects of such biological interactions are poorly known because of the difficulties in measuring predation risk in nature. We addressed this issue by assessing the effect of asymmetrical competition among brook trout (*Salvelinus fontinalis*) and two superior non-piscivorous competitors, creek chub (*Semotilus atromaculatus*) and white sucker (*Catostomus commersonii*), on the predation risk of a brook trout prey, northern redbelly dace (*Chrosomus eos*). We determined the spatio-temporal patterns of relative predation risk of dace with tethering experiments in 11 lakes containing either only brook trout and dace (n = 5), or brook trout, dace, chub, and sucker (n = 6). The diel pattern of the relative predation risk and the overall relative predation risk of dace were not significantly different in lakes with or without brook trout competitors. However, we observed a significant shift in the relative predation risk from the lower pelagic to the upper pelagic and littoral zones in the presence of brook trout

competitors. This study highlights the fact that the outcome of interactions can vary in space and that care should be used when extrapolating the results of small-scale experiments or coarse-scale estimates to the whole ecosystem.

Keywords Brook trout · Competition · Trophic interactions · Spatial scale · Tethering experiment

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Introduction

Asymmetrical competition has a great potential to shape communities (Amarasekare 2003; Persson and de Roos 2013) since it is often associated with decreases in the abundance as well as niche shifts of inferior competitors (e.g., Robertson 1996; Persson and Hansson 1999). Asymmetrical interactions can also change the feeding activity pattern of inferior competitors (Kronfeld-Schor and Dayan 2003), with potential consequences for their food resources. Thus, superior competitors may indirectly affect the level of predation risk in both space and time for the prey upon which the inferior competitors feed. Given the high occurrence of asymmetrical competition in nature at both intra—(e.g., between different ontogenetic stages; Persson and de Roos 2013) and inter-specific levels (Werner and Hall 1977; Schoener 1983), these indirect effects of competition on predation risk should be relatively common. However, most experimental studies focus on the effects of predation on competitive interactions among prey (Chase et al. 2002). It is thus important to investigate the effects of asymmetric competition on predator–prey interactions, such as spatio-temporal variations in predation risk. These indirect effects are poorly documented in nature because of the difficulties in measuring predation risk.

The effects of spatial scale on trophic interactions have been reported in several studies (e.g., Skelly 2002; Taylor et al. 2002). Given that most estimates of interspecific interactions in nature are derived from relatively small-scale experiments (Wootton and Emmerson 2005), extrapolation to a whole ecosystem may be misleading (Englund and Cooper 2003). Therefore, fine-scale experimental studies conducted at the scale of the entire ecosystem (i.e., coupling high spatial resolution with large spatial extent) should help to elucidate these interactions. By minimizing the chances of missing key aspects concerning the outcome of these interactions, such approaches would allow a more detailed picture of the indirect effects of interspecific competition, from the local to the whole-ecosystem scale.

Species-poor fish communities found in boreal lakes provide good models to investigate the effects of asymmetrical interspecific competition at the top of the food web on the spatial and temporal patterns of predation risk of prey. Previous studies in Canadian Shield lakes showed that brook trout (*Salvelinus fontinalis*) feed preferentially on benthic prey and to a lesser extent on alternative prey such as zooplankton and fish, notably northern redbelly dace (*Chrosomus eos*, formerly *Phoxinus eos*; Strange and Mayden 2009) (Magnan 1988; East and Magnan 1991; Lacasse and Magnan 1992; Bourke et al. 1999). Furthermore, these studies showed that this omnivorous predator shifts its diet from benthic invertebrates to more open-water prey such as zooplankton and dace in response to interspecific competition with creek chub (*Semotilus atromaculatus*) and white sucker (*Catostomus commersonii*), two species that are better adapted to feeding on benthic invertebrates than are brook trout (Magnan and FitzGerald 1982, 1984a; Tremblay and Magnan 1991). This diet change was associated with a shift in the brook trout's spatial distribution from the bottom to the upper part of the water column. This suggests that asymmetrical competition among brook trout, white sucker, and/or creek chub could indirectly influence the predator–prey interaction between brook trout and dace by increasing the level of brook trout piscivory and spatial overlap with dace.

Although the occurrence and frequency of prey in stomachs have often been used as indexes of predation risk (e.g., Brewer et al. 1995), this approach may give a biased picture of predator–prey interactions since it does not take into account variations in the abundance of predators. Experiments involving tethered prey have been shown to be an effective approach for measuring the combined effect of predator abundance, the size-dependent propensity for piscivory, and the intensity of their foraging activity (Aronson and Heck 1995; Post et al. 1998). However, it is important to remember that this technique measures relative predation rates 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 relative predation risk in comparative studies (Aronson et al. 2001).

The objective of our study was to estimate the relative predation risk of dace in lakes containing either brook trout and dace (hereafter "without competitors"), or brook trout and dace plus white sucker and/or creek chub (hereafter "with competitors"). We conducted tethering experiments in 11 oligotrophic Canadian Shield lakes during two consecutive summers to test the following three predictions:

1. *Among-lake scale* the relative predation risk of dace will be higher in lakes with competitors than without because brook trout shift from benthic invertebrates to fish and zooplankton when living in sympatry with chub and sucker (Magnan 1988; East and Magnan 1991; Lacasse and Magnan 1992). Even though brook trout are overall less abundant in lakes with competitors (Magnan et al. 2005), their higher occurrence in the pelagic zone relative to the littoral zone in these lakes (Magnan and FitzGerald 1982; Tremblay and Magnan 1991) should increase their spatial overlap with dace and thus the overall relative predation risk of dace;

2. *Within-lake scale* the relative predation risk of dace will shift from the bottom to the upper part of the water column in lakes with competitors given that brook trout shift their spatial distribution from the littoral to the pelagic zone in the presence of creek chub and/or white sucker (Magnan and FitzGerald 1982; Tremblay and Magnan 1991);

3. *Temporal pattern* Brook trout is a visual predator (Power 1980), thus the relative predation risk of dace should be higher in daylight periods than during the night. However, it was suggested that (i) temporal partitioning on the diel scale may facilitate coexistence between competitors (Kronfeld-Schor and Dayan 2003) and (ii) brook trout can show variation in the expression of its diel behaviour (Bertolo et al. 2011; Goyer et al. 2014). Thus we predict that the diel patterns of relative predation risk of dace will differ between lakes with and without competitors because asymmetric interspecific competition can affect the daily feeding activity pattern of inferior competitors (Kronfeld-Schor and Dayan 2003).

Materials and methods

Study sites

The experiments took place in 11 lakes located in the Mastigouche Reserve, Québec, Canada (46°40′N,

Table 1 General characteristics, fish composition, and sampling frequency of the study lakes

Lake	Surface area (ha)	Maximum depth (m)	Secchi depth (m)	Fish composition				Sampling frequency	
				Ce	Sf	Cc	Sa	2002	2003
Bondi	25.7	29.3	4.3	x	x			2	3
Cerné	13.2	9.3	3.5	x	x			2	3
Diablos	9.8	16.5	4.9	x	x			2	
Lafond	46.7	23.3	5.5	x	x			2	3
Osborn	10.8	12.8	5.8	x	x			2	3
Joe	25.6	13.0	5.8	x	x	x		2	
Gauthier	36.9	21.4	4.2	x	x		x	2	2
Lafleur	21.8	19.0	7.0	x	x		x	2	
Grignon	29.6	21.0	6.3	x	x	x	x	2	3
Grosse	8.0	17.0	3.5	x	x	x	x	2	3
Tête	23.1	18.0	4.1	x	x	x	x	2	

Ce, *Chrosomus eos*; Sf, *Salvelinus fontinalis*; Cc, *Catostomus commersonii*; Sa, *Semotilus atromaculatus*; "x" indicates the presence of a species

73°20′W), from 3 July to 27 August 2002 and from 25 June to 22 August 2003. These are typical small oligotrophic Canadian Shield lakes with respect to surface area, maximum depth, and Secchi depth transparency (Table 1). We considered that potential piscivores (fish and birds) other than brook trout were negligible in the study lakes. Creek chub is a generalist feeder (Scott and Crossman 1974), with large individuals (total length >135 mm) feeding on small fish (e.g., Gilliam and Fraser 1987). Given that gillnet fishing showed no such large creek chub in the study lakes except in Lake de la Grosse, where few individuals >135 mm were captured in the littoral zone (A. Dupuch, unpubl. data), we assumed that this species was a negligible predator on dace (but see "Discussion" section). Furthermore, piscivorous birds (common loon, kingfisher, and great heron) were rarely observed on the study lakes. The abundance and spatial distribution of brook trout were not estimated in our study lakes (1) because of logistical reasons and (2) because experiments involving tethered prey provide a measure of predation risk that incorporates spatial and temporal variations in predator density and foraging activity as well as the size-dependent propensity for piscivory within and among predator populations (Aronson and Heck 1995; Post et al. 1998).

Sampling design

During the summer of 2002, predation risk in each lake was estimated once in both July and August in the same sequence. In each lake, 72 northern redbelly dace were attached individually to chronographic tethers (Danilowicz and Sale 1999). Chronographic tethers are stopwatches set in waterproof resin (see Fig. 1 in Danilowicz and Sale 1999). A removable steel plate was held in place on the timer surface by magnets set into the resin. Removing the plate tripped a reed-switch and stopped the stopwatch, allowing us to record the amount of time elapsed until a prey item had been removed by a predator. Chronographic tethers were placed at seven different depths in the water column (0.2, 1.0, 2.0, 3.0, 4.0, 5.0, and 6.0 m) at locations above five different isobaths (0.5, 1.0, 2.0, 4.0, and 8.0 m). In total, 1,584 individuals were attached to chronographic tethers in 2002 (11 lakes × 2 sampling dates × 18 depth–isobath combinations × 4 prey per combination [Fig. 1]).

During the summer of 2003, we sampled a subset of seven lakes (Table 1). Each lake was sampled three times during the summer except for Lake Gauthier, which was sampled only twice; sampling on a lake was completed within 1 week. Thirty northern redbelly dace were attached to chronographic tethers in each lake at five different depths in the water column (0.5, 1.5, 2.5, 3.5, and 4.5 m) and above the 1, 2, 3, 4, and 5 m isobaths. Six hundred dace were attached to chronographic tethers in 2003 (7 lakes × 3 sampling dates × 15 depth–isobath combinations × 2 prey per combination [Fig. 1]; Lake Gauthier was sampled only twice). Gillnet fishing performed in 2002 in the study lakes showed no dace below 5 m depth and that only 16 % of dace were captured beyond the 5 m isobath (unpublished data). Based on a preliminary analysis of the 2002 data, we concluded that predator–prey interactions between brook trout and dace occurred mainly between the 1 and 5 m isobaths. We thus concentrated our efforts in this zone in 2003, so the prey depth–isobath combinations were different between the 2 years. We analyzed these data separately and used the 2003 results to validate those from 2002.

Fish were collected in each lake with minnow traps set in the littoral zone between 08:00 and 14:00. They were attached to chronographic tethers with 6 lb test monofilament fishing line (length = 15 cm) inserted into the muscle under the dorsal fin, allowing individuals to swim freely. The length of dace used for the tethering experiment was standardized among lakes for both summers (5.3 ± 0.1 cm in 2002 and 6.0 ± 0.3 cm in 2003). Dace were maintained in a given location by an anchored float and placed at a minimum distance of 20 m from each other in an open area (i.e., without vegetation or woody debris) to avoid entanglement. This leads to an overestimation of the predation risk in the littoral zone compared to the pelagic zone because dace use submerged vegetation to reduce their predation risk by brook trout (East and Magnan 1991). Although this bias prevented a comparison of the relative predation risk between the littoral and pelagic

Fig. 1 Mean percent predation on northern redbelly dace (represented by *circle* diameter) in lakes with (**a** and **c**) and without (**b** and **d**) competitors for each prey depth—isobath combination for the summers of 2002 (**a** and **b**) and 2003 (**c** and **d**). *White circles*: littoral zone; *light grey circles*: upper pelagic; *dark grey circles*: lower pelagic. The *dotted-line rectangle* defines the surface layer area whereas the *dashed-line rectangle* defines the pelagic zone area. Percent predation was estimated as the mean percent of missing dace after one sampling day [mean for lakes without competitors is based on six (2002) or four (2003) lakes; mean for lakes with competitors is based on five (2002) or three (2003) lakes]
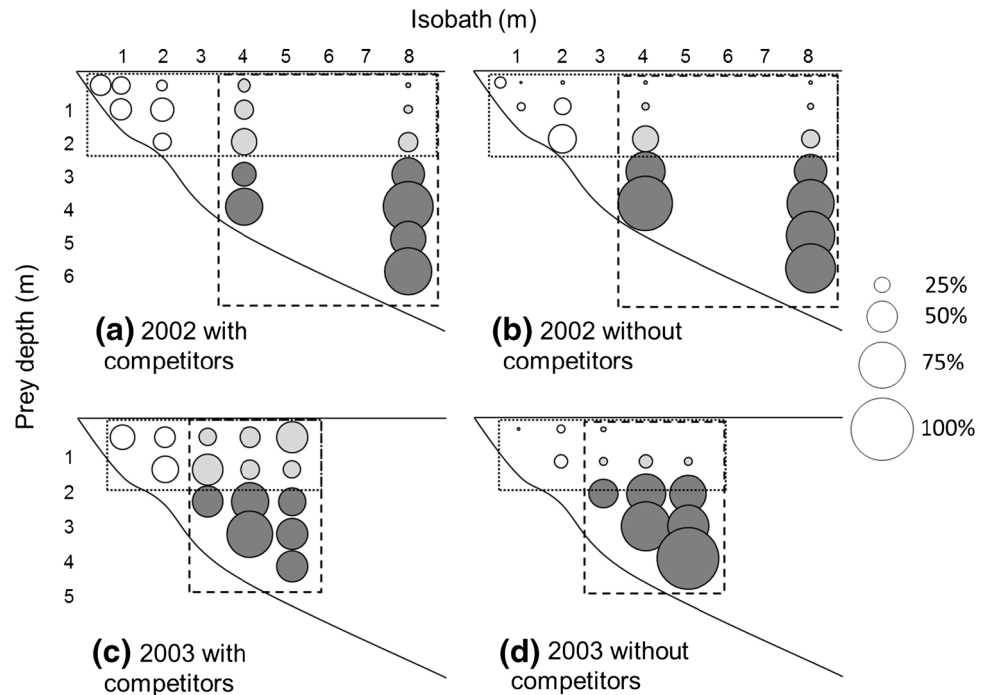
zones, it did not prevent us from testing the effects of asymmetrical competition on predation risk of dace. The chronographic tethers were set between 14:00 and 15:30 and removed between 07:30 and 09:00 the next morning because a previous study had shown that adult brook trout are mainly active at sunset, night, and sunrise while very few are active around midday (Bourke et al. 1996). The positions of the chronographic tethers were changed randomly each sampling day within a given lake to account for the spatial variation in predator density and activity. A predation event starts the chronometer, thus allowing us to determine the time elapsed between the beginning of an experiment and the predation event (hereafter "survival time"). Before the experiment, we verified in the laboratory that dace (n = 10) cannot escape from the tethering wire or start the chronometer device by struggling.

Lake thermal profiles (measurements taken at each metre in the water column) were made each day of the experiments in both years. The state of all dace remaining at the end of the experiment (dead or alive) was also noted. A significant proportion of fish were dead at the end of an experiment (see "Results" section). To determine when this mortality occurred during the experiment and if a predation event was affected by the state of dace (dead or alive), we conducted an additional experiment (hereafter "validation experiment") in 2002, in Lake Lafond. This experiment consisted of checking the chronographic tethers (n = 72 placed at the same depth–isobath combinations tested in 2002) every three hours from 16:00 to 07:00 by pulling them up and noting (1) the time at which predation

events occurred, when applicable, and (2) the state (dead or alive) of uneaten dace attached to the chronographic tether. This manipulation required <1 min per tether, and we assumed that it did not affect prey or predator behaviour.

Statistical analyses

Survival times were analyzed using Cox Proportional Hazards (CPH) regressions (Cox and Oakes 1984); this is a semi-parametric model commonly used in survival analysis that allows one to study the occurrence and timing of mortality or predation events. The CPH model takes into account censored data and the non-normal distribution usually observed with survival times (Cox and Oakes 1984). In our study, censored data were obtained when a fish was still alive at the end of an experiment (i.e., the fish survived the length of the experiment, so the exact survival time was not known). We used the CPH regression model to assess the effects of independent variables on the survival time of dace. In our analysis, the independent variables used were isobath, prey depth, sampling day, and fish assemblage (lakes with competitors vs. without competitors).

In a first step, we looked at the average effect of fish assemblage on the overall relative predation risk of dace considering all the tethering data for each sampling year. In a second step, we looked at the effect of fish assemblage according to the spatial position of the tethered prey. Because of lake morphology, an increase in isobath was associated with an increase of depths at which tethered

prey could be positioned in the water column. Because isobaths and prey depth were thus confounded, we analyzed the effects of these variables separately. The effects of fish assemblage and isobath (representing essentially the distance from shore) were tested by using only the tethered prey located in the first 2 m of the water column (prey depth ≤ 2 m; hereafter "surface layer" analyses). The effects of fish assemblage and prey depth were tested by using only the tethered prey located in the pelagic zone (isobaths >2 m) but considering the entire water column (hereafter "pelagic zone" analyses). Data from the 4 and 8 m isobaths in 2002 and those from the 3, 4, and 5 m isobaths in 2003 were analyzed separately to test the effect of fish assemblage on relative predation risk at different depths.

The relative importance of the independent variables in determining predation risk for dace was determined by multimodel inference (Burnham and Anderson 2002) based on four CPH regression models. This approach allows one to acknowledge model uncertainty and focus on more than one plausible hypothesis to explain a given phenomenon. The models were built for each sampling year and separately for surface layer and pelagic zone data using one or more of the independent variables and interaction terms (data were nested in lakes). The models were based on hypotheses defined a priori: (1) only the spatial position of dace influenced their relative predation risk (independent variable: isobath or depth), (2) only fish assemblage influenced relative predation risk of dace (independent variable: fish assemblage), (3) both spatial position and fish assemblage influenced the relative predation risk of dace (independent variables: isobath or depth + fish assemblage), and (4) interactions between spatial position and fish assemblage influenced relative predation risk of dace (independent variables: isobath or depth + fish assemblage + isobath × fish assemblage or depth × fish assemblage). Because each lake was sampled three times over 1 week in either July or August 2003, sampling time was included as a covariable in the analysis to control for its potential effects. We removed sampling day from all the analyses in 2003 because this variable was not important in the explanation of the relative predation risk of dace ($p > 0.05$). In 2002, the sampling order of the study lakes was such that fish assemblages were sampled alternately in each sampling year. This allowed us to test the effect of fish assemblage without correcting for the sampling order, since this effect was controlled in the sampling design. Finally, prey depth and water temperature were highly correlated, so only prey depth was used in the models since the Akaïke Information Criteria (AIC; Burnham and Anderson 2002) showed that models including prey depth rather than water temperature better explained the relative predation risk of dace. Model-averaged estimates and unconditional standard error of the independent variables included in the four models were obtained by weighting the estimates and the standard error by their Akaïke weights, as shown in Burnham and Anderson (2002). Only models included in the "95 % confidence set of models" (sensu Burnham and Anderson 2002) were used for the multi-model inference. A practical way to assess which models should be included in the confidence set is to sum the Akaike weights of the ranked models (i.e., beginning from the best) until the sum is ≥ 0.95 (Burnham and Anderson 2002).

The strength of the relationship between each independent variable and the relative predation risk was assessed as a "risk ratio" (Cox and Oakes 1984). The risk ratio is defined as the change in the probability of a predation event as the variable x_i increases by one unit. The estimate and standard error were then used to compute the risk ratio of each independent variable and its 95 % CI. Positive and negative relationships are indicated by risk ratios larger or smaller than 1.0, respectively. When the unit value is not included within the risk ratio CI, the relationship is considered as significant (Quinn and Keough 2002). The further the risk ratio from the value 1.0, the greater the effect of that variable on the relative predation risk of dace.

To determine whether relative predation risk changed with period of the day, we estimated the mean relative predation risk (percentage of predation per hour per lake) at each period of the day [afternoon (14:00–19:15), sunset (19:16–21:15), night (21:16–04:30), sunrise (04:31–06:30 h), morning (06:31–07:30 h)] for both summers. The sunset and sunrise periods were defined as 1 h before to 1 h after sunset and sunrise (average times for July–August), respectively. Sunset and sunrise times were obtained from sunrise/sunset tables given by the National Research Council of Canada for Trois-Rivières (Québec, Canada). For each period, the number of prey potentially available was corrected for the number of predation events that occurred in the preceding period. We then performed a mixed model (MIXED procedure of SAS 9.1.3; 2002 SAS package) with repeated measures and nested designs (lake was nested into fish assemblage) on the mean relative predation risk of dace for each sampling year. We estimated the effect of period of the day and the interaction between fish assemblage (1 = with competitors; 0 = without competitors) and period of the day to determine whether the presence of competitors influenced the temporal pattern of predation risk of dace. We then compared mean relative predation risk among periods of the day (regardless of fish assemblage because it had no effect; see "Results" section) with sequential Bonferroni post hoc multiple comparison tests. The relative predation risk was normalized using arcsine square-root transformations.

Table 2 Total number of northern redbelly dace attached to chronographic tethers (i.e., the number of tethered fish considered in the analyses) and mean percent predation (±SD) in the study lakes in 2002 and 2003

Fish assemblage	Lake	Number of tethered fish		Mean percent predation ± SD	
		2002	2003	2002	2003
With competitors					
	Joe	134		25 ± 5	
	Lafleur	106		43 ± 18	
	Gauthier	109	50	46 ± 24	17 ± 18
	Grignon	112	63	23 ± 2	53 ± 17
	Grosse	94	70	55 ± 9	50 ± 28
	Tête	117		27 ± 7	
	Average	112	61	37 ± 13	40 ± 20
Without competitors					
	Bondi	110	78	38 ± 13	28 ± 6
	Cerné	124	68	40 ± 3	39 ± 15
	Diablos	120		46 ± 5	
	Lafond	126	81	23 ± 5	17 ± 4
	Osborn	120	82	22 ± 21	32 ± 10
	Average	120	77	34 ± 11	29 ± 9
Average all lakes		116	69	35 ± 12	34 ± 14

Percent predation was estimated as the mean percent of missing dace after one sampling day (mean is based on two sampling days in 2002 and three in 2003)

Results

Two percent of the tethers (n = 31 in 2002 and n = 16 in 2003) were not considered in the analyses because of entanglement of dace in the wires. Furthermore, 16 % of the chronographic tethers (n = 253 in 2002 and n = 96 in 2003) were not activated even though the dace was no longer attached to the wire. Because we were not sure that a predation event had occurred on these tethers, we did not consider them in the analyses (however, the results of the statistical analyses did not change much when we considered these cases as predation events). Considering all these exceptions, an average of 35 ± 12 % in 2002 and 34 ± 14 % in 2003 of the tethered dace were preyed upon during the experiments (number of predation events: 453 in 2002 and 170 in 2003; Table 2).

The tethering procedure caused the mortality of 41 and 38 % of the total dace tethered at the beginning of the experiments in 2002 and 2003, respectively (i.e., 64 % of the 822 uneaten dace in 2002 and of 58 % of the 322 uneaten dace in 2003). The validation experiment showed that 86 % of the mortality occurred during the first 3 h following the attachment of the tethers (from 19:00 to 22:00). Within the first 3 h, 26 predation events occurred, leaving 45 of the 71 dace (23 alive and 22 dead) still

Table 3 Results of model averaging based on the 95 % confidence set of models for the analyses comparing predation risk for northern redbelly dace at different isobaths for the surface layer only (surface layer analyses; see text for details)

Model	Variable	Estimate (±SE)	Risk ratio	
			Mean	95 % CI
2002 Surface layer				
	Isobath	**−0.13 (0.06)**	**0.88**	**0.78–0.99**
	Fish assemblage	0.32 (0.31)	1.38	0.75–2.50
	Sampling month	**−0.65 (0.23)**	**0.52**	**0.33–0.81**
	Isobath × fish assemblage	**−0.17 (0.09)**	**0.84**	**0.71–0.99**
2003 Surface layer				
	Isobath	0.02 (0.07)	1.02	0.89–1.16
	Fish assemblage	**1.86 (0.51)**	**6.42**	**2.36–17.51**
	Isobath × fish assemblage	−0.02 (0.34)	0.98	0.50–1.91

Estimates, unconditional standard error, and risk ratio (mean and 95 % confidence interval) are shown. Bold indicates variables that were important in explaining the relative predation risk of dace based on the 95 % CI for the risk ratio

attached to the chronographic tethers. Our results show that the proportion of predation on these 45 dace (two predations on live fish and 5 on dead fish) did not differ according to their condition (live or dead tethered dace; $\chi^2 = 1.77$, df = 1, p > 0.05, n = 45). At the end of this experiment, 46 % of the tethered dace were preyed upon by brook trout (33 predation events) and 32 % were dead due to the tethering procedure (i.e., 60 % of the uneaten tethered dace). Furthermore, there was no significant correlation between the mortality rates of uneaten dace at the end of trials and the mean percent of predation in the study lakes (n = 22, r = −0.19, p > 0.05 in 2002; n = 20, r = −0.28, p > 0.05 in 2003). These results suggest that dace do not need to be moving to elicit attack from brook trout.

Effects of asymmetrical competition on predation risk

When analyzing the tethering data without taking into account their spatial distribution, the fish assemblage did not significantly affect the overall relative predation risk of dace in lakes (2002: risk ratio = 1.04, 95 % CI = 0.66–1.63; 2003: risk ratio = 1.58, 95 % CI = 0.84–2.94). However, when taking into account the spatial structure, surface layer and pelagic zone analyses showed that fish assemblage had a significant effect on the spatial pattern of relative predation risk in six out of seven comparisons (Tables 3, 4).

Table 4 Results of model averaging based on the 95 % confidence set of models for the analyses comparing predation risk of northern redbelly dace at different depths for the 3, 4, 5, and 8 m isobaths (pelagic zone analyses; see text for details)

Model	Variable	Estimate (±SE)	Risk ratio	
			Mean	95 % CI
2002 Pelagic zone				
Isobath 4 m	Depth	**1.05 (0.11)**	**2.85**	**2.24–3.56**
	Fish assemblage	−0.21 (0.31)	0.81	0.44–1.46
	Sampling month	**−0.81 (0.24)**	**0.44**	**0.27–0.71**
	Depth × fish assemblage	**−0.61 (0.21)**	**0.54**	**0.36–0.82**
Isobath 8 m	Depth	**0.96 (0.10)**	**2.61**	**2.16–3.19**
	Fish assemblage	0.03 (0.09)	1.03	0.87–1.23
	Sampling month	−0.16 (0.30)	0.85	0.47–1.53
	Depth × fish assemblage	−0.12 (0.18)	0.88	0.62–1.26
2003 Pelagic zone				
Isobath 3 m	Depth	**0.98 (0.43)**	**2.66**	**1.15–6.20**
	Fish assemblage	**1.36 (0.64)**	**3.89**	**1.12–13.60**
	Depth × fish assemblage	**−0.96 (0.36)**	**0.38**	**0.19–0.77**
Isobath 4 m	Depth	**1.09 (0.23)**	**2.97**	**1.90–4.64**
	Fish assemblage	0.61 (0.34)	1.84	0.94–3.59
	Depth × fish assemblage	**−0.72 (0.28)**	**0.48**	**0.28–0.86**
Isobath 5 m	Depth	**1.55 (0.14)**	**4.71**	**3.59–6.11**
	Fish assemblage	0.13 (0.56)	1.13	0.38–3.35
	Depth × fish assemblage	**−1.48 (0.29)**	**0.22**	**0.12–0.40**

Estimates, unconditional standard error, and risk ratio (mean and 95 % confidence interval) are shown. Bold indicates variables that were important in explaining the relative predation risk of dace based on the 95 % CI for the risk ratio

The surface layer analysis in 2003 showed that the presence of competitors significantly increased the overall predation risk by 6.4-fold in this zone (the fish assemblage term was significant), whereas there was only a non-significant 1.4-fold increase in 2002 (Table 3). In contrast, there was a significant inshore–offshore increase in 2002 in the relative predation risk (the isobath term was significant) in the presence of competitors (the isobath × fish assemblage interaction term was significant) (Table 3; Fig. 1).

The pelagic zone analysis showed that the presence of competitors increased the overall predation risk in the upper pelagic relative to the lower pelagic zone (the fish assemblage term was significant in 2003 and the depth × fish assemblage interaction term was significant in four out of five cases; Table 4; Fig. 1). We found no effect of competitors on the relative predation risk in only in one case (2002, isobath 8 m; Table 4; Fig. 1).

Table 5 Results of the mixed models fitted to the 2002 and 2003 data to determine the effects of period of the day (afternoon, sunset, night, sunrise, and morning) and fish assemblage (1 = with competitors; 0 = without competitors) on the mean relative predation risk of northern redbelly dace

Model	Variable	df	*F* value	*p* value
2002				
	Day period	4, 36	15.61	<0.001
	Fish assemblage	1, 9	0.04	0.847
	Day period × fish assemblage	4, 36	0.72	0.583
2003				
	Day period	4, 20	5.65	0.003
	Fish assemblage	1, 5	0.37	0.568
	Day period × fish assemblage	4, 20	0.62	0.651

General spatial and temporal patterns

The surface-layer analysis for 2002 revealed that the relative predation risk decreased by 12 % for each 1-m increase in the isobath (Table 3; isobath risk ratio = 0.88). Similarly, the pelagic zone analysis revealed a significant surface–bottom gradient of predation risk at all isobaths and for both sampling years: for each 1-m increase in the prey depth, the relative predation risk increased by 2.61–4.71 times (Table 4). A comparison of all data (i.e., littoral, lower and upper pelagic) showed that the riskiest zone in all cases (i.e., with or without competitors) was the lower pelagic (isobath >2 m; 2.5–6 m depth).

Contrary to the spatial pattern, the presence of competitors did not significantly affect the temporal pattern of relative predation risk for dace (Table 5). Regardless of the fish assemblage (i.e., with or without competitors), the mean relative predation risk was lowest at night (Fig. 2).

Discussion

Our study shows how asymmetrical competition among top predators can affect the fine-scale spatial pattern of predation risk for their prey in natural conditions. Even though both the overall predation risk for dace and their diel pattern were similar in lakes with or without competitors, we observed a spatial difference, suggesting a change in the predation risk of dace in the presence of competitors.

Overall, an average of 35 % of the tethered dace was preyed upon during the 2 years of the experiments. Mortality due to the tethering procedure, estimated on the basis of uneaten dace at the end of the experiments, was in accordance with the results of our validation experiment. On average, 39 % of the tethered dace were dead (corresponding to 60 % of the uneaten dace) at the end of the experiments. The results of the validation experiment
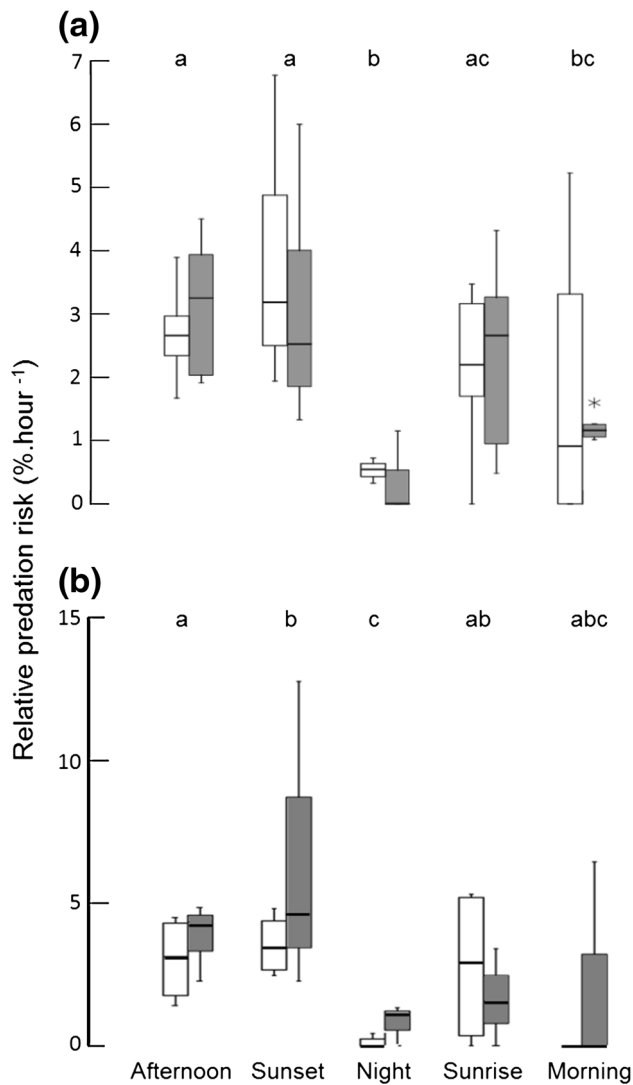
(a)

(b)

Fig. 2 *Box plots* representing the variation in mean relative predation risk on northern redbelly dace at different periods of the day (from 14:00 to 07:30) for lakes with brook trout and competitors (lakes with competitors; *white boxes*) and with brook trout only (lakes without competitors; *grey boxes*) during the summer of 2002 (**a**) and 2003 (**b**). *Each box plot* shows the middle quartiles, and the *horizontal line* in the middle of the box marks the median. The *edges of each box* (hinges) mark the 25th and 75th percentiles. The length of the box corresponds to the interquartile range (IQR). The whiskers show the range of values that fall within 1.5 IQR of the hinges. Outliers (values between 1.5 and 3 IQR outside of the hinges) are marked by an *asterisk*. The sunset and sunrise periods were defined as 1 h before to 1 h after sunset and sunrise (average times for July–August), respectively. Sunset and sunrise times were found in the sunrise/sunset tables produced by the National Research Council of Canada for Trois-Rivières (Québec, Canada). Mean relative predation risks (regardless of fish assemblage) with *different letters* were significantly different (p < 0.010)

suggest that dace do not need to be moving to elicit attack, and thus that prey mortality due to the tethering procedure was unlikely to have biased our estimation of relative predation risk. Furthermore, the objective of our study was

to test the effects of asymmetrical competition among top predators on predation risk of dace by comparing predation risk among two types of fish communities. The estimation of predation risk through tethered prey should not have prevented us from testing our hypothesis since it is reasonable to assume that any bias due to the methodology was the same in the two types of lakes.

As predicted, we observed a higher number of predation events in the upper pelagic zone and a smaller number in the lower pelagic zone in lakes with competitors compared to those without competitors. This may be due to brook trout shifting from benthic invertebrates to more open-water prey when living in sympatry with chub and sucker (Magnan and FitzGerald 1982; Tremblay and Magnan 1991), presumably increasing the consumption rate on dace when brook trout are restricted to feeding in the upper pelagic zone (East and Magnan 1991). This interpretation is also in agreement with the higher occurrence of dace in the stomach content of brook trout in lakes with competitors than without (East and Magnan 1991; Lacasse and Magnan 1992; Magnan et al. 1994).

The lower use of the littoral zone by brook trout observed in lakes with creek chub and/or white sucker (Magnan and FitzGerald 1982; Tremblay and Magnan 1991) is at odds with our results, showing that the relative predation risk of dace in the littoral zone tends to be higher in lakes with competitors than without competitors for both years. Creek chub occur mainly in the littoral zone (Magnan and FitzGerald 1982, 1984b), and gillnet sampling showed that this species is not found beyond the 3 m isobath in our study lakes (Magnan and FitzGerald 1984b). Since large creek chub specimens could prey upon dace (A. Dupuch, personal observation), it is possible that—contrary to our assumption—predation by creek chub also contributed to the higher relative predation risk of dace in the littoral zone of our lakes. In Lake de la Grosse, where some large creek chub were captured, the relative predation risk of dace was indeed higher (an average of 72 % for 2002–2003) than in the other 10 lakes. Also, among the lakes with competitors, the relative predation risk of dace was the lowest in Lake Joe (an average of 8 % for 2002), a lake containing white sucker but no creek chub. Because tethering impedes avoidance behaviour, it is possible that dace were vulnerable prey even for a generalist predator such as chub. Furthermore, a previous study showed that the abundance of dace in structured vegetated habitats (i.e., refuge) relative to open (risky) habitats in the littoral zone was higher in lakes with than without competitors (Dupuch et al. 2009a), suggesting a higher predation risk in the littoral zone of lakes with competitors.

The lower relative predation risk of dace in the upper pelagic than in the lower pelagic zone in both fish assemblages is likely related to the lower abundance of brook

trout in this zone (Tremblay and Magnan 1991). Similarly, previous studies performed in lakes of the same area found that brook trout remain preferentially in water of about 12–14 °C during the daylight period (Bourke et al. 1996; Bertolo et al. 2011), which corresponds to depths between 4 and 6 m based on our temperature profiles.

Regardless of fish assemblage, the relative predation risk of dace was very low during the night compared to daylight hours, which is in agreement with the notion that the brook trout is a visual predator (Power 1980). The mean relative predation risk was underestimated for the sunset, night, sunrise, and morning periods because we did not replace the tethered dace after each of these periods. However, the fact that the mean relative predation risk significantly decreased after sunset and significantly increased at sunrise clearly indicates that predation risk of dace was lowest during the night. This low relative predation risk during the night suggests that if dace are in the pelagic zone during this period, the light intensity is too low to allow brook trout to detect and capture them. This supports the hypothesis that light intensity is an important determinant of predation risk for visually oriented predators such as brook trout, as assumed in the "antipredator window" concept (Clark and Levy 1988). This is also in agreement with the hypothesis that diel onshore–offshore migrations of northern redbelly dace in Canadian Shield lakes have an adaptive value by reducing predation risk by pelagic piscivores while increasing feeding efficiency on zooplankton (Naud and Magnan 1988; Gaudreau and Boisclair 1998; Dupuch et al. 2009a). Dace form shoals and preferentially use submerged vegetation in the littoral zone during the day, disperse in the pelagic zone during night to feed on zooplankton, and then return to littoral zone at sunrise (Naud and Magnan 1988; Gauthier et al. 1997). The use of structured habitats during the day, when predation risk is relatively high, and the pelagic zone during the night, when predation risk is low, would thus allow dace to significantly reduce predation risk by brook trout (Naud and Magnan 1988; East and Magnan 1991; Dupuch et al. 2009a, b).

The similar temporal patterns of predation risk observed in both fish assemblages suggest that the temporal pattern of brook trout piscivory was not affected by asymmetric competition. Whereas visual predators such as brook trout appear able to adapt both their diet and habitat use in response to interspecific competition, their pattern of feeding activity seems less plastic. This suggests that a reduction in their ability to visually detect prey at low light intensities cannot be compensated by switching to other feeding strategies that rely on sensory organs such as the lateral line. The general observation that temporal shifts in activity patterns are less frequent responses to competition than habitat and diet shifts (Kronfeld-Schor and Dayan 2003) suggests that such a constraint may be common.

In conclusion, the among-lake variation in asymmetric interspecific competition is a good predictor of the spatial pattern of predation risk of dace at the within-lake level. In contrast, neither the diel pattern nor the overall level of predation risk in lakes was adequately predicted by this variable. By showing the importance of considering fine-scale patterns of predation risk rather than only coarse-scale ones, this study identifies indirect in situ effects of asymmetrical competition. Given that most estimates of interaction strength in nature are derived from relatively small-scale experiments (Wootton and Emmerson 2005), extrapolation to a whole ecosystem may be misleading. Similarly, whole-lake estimates of predation risk might be misleading when assessing the effects of asymmetrical interactions. Therefore, studies on biological interactions should consider spatial resolution in order to avoid missing key responses.

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