

# Formation of morphological defences in response to YOY perch and invertebrate predation in two *Daphnia* species coexisting in a mesotrophic lake

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**Abstract** This study examined the formation of morphological defences by two coexisting *Daphnia* species, the large-sized *D. pulicaria* (2 mm) and the small-sized *D. mendotae* (1.4 mm), in response to the presence of young-of-the-year (YOY) yellow perch (*Perca flavescens*) and invertebrate predators (*Chaoborus*, *Leptodora*) during summer in a mesotrophic lake. We hypothesized that due to differential size-selective predation risk by YOY fish and invertebrates, the large-sized and the small-sized *Daphnia* species would show different morphological responses to predation threats. We followed changes in two morphological traits (relative length of the tail spine in *D. pulicaria* and of the helmet in *D. mendotae*) among different periods during summer accord-

ing to YOY fish and invertebrate predation. We defined four YOY fish predation periods based on the presence of YOY perch in the pelagic zone of the lake and the relative abundance of *Daphnia* preys in their gut contents, and two invertebrate predation periods based on exclusive or mutual occurrence of the invertebrate predators. The large-sized (*D. pulicaria*) and the small-sized (*D. mendotae*) species showed different morphological responses to YOY fish and invertebrate predators, respectively. The tail spine ratio of the juveniles and adults of *D. pulicaria* did not change in response to YOY fish predation or to invertebrate predation. A gradual increase in the helmet ratio was observed in the small-sized *D. mendotae* over the summer period. This change was related to the co-occurrence of the invertebrate predators (*Chaoborus* and *Leptodora*) and to YOY fish predation. The warmer temperature cannot be accounted for helmet elongation since it was constant across depths, and not related with the co-occurrence of *D. mendotae* and YOY perch.

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## Introduction

Evolution has forged an assortment of phenotypic adaptations in plankton to deal with different types of

predators through changes in prey morphology, behaviour and life history (Lass & Spaak, 2003; Riessen & Young, 2005). Planktonic crustaceans in freshwater habitats commonly face predation by multiple predators. Fish and invertebrate predators may occur simultaneously but usually their relative densities vary in space and time, allowing the coexistence of many planktonic species of different sizes (Weber & Declerck, 1997; González & Tessier, 1997).

Predation risk posed by fish and invertebrate predators depends on the occurrence of each predator, their size-selective feeding and competitive interactions. It is generally assumed that visual-hunting planktivorous fish tend to select large-sized zooplankton (Brooks & Dodson, 1965; Lazarro, 1987), while invertebrate predators feed on small and medium-sized zooplankton (Pastorok, 1981; Pourriot, 1995; Pinel-Alloul, 1995a). However, prey selection varies greatly along the summer season. Young-of-the-year (YOY) planktivorous fish change their prey selection with ontogenesis from negative size-selective feeding by gape-limited YOY fish larvae at spring to positive size-selective feeding by larger YOY fish later in summer (Hansen & Wahl, 1981; Mills & Forney, 1983; Mayer & Wahl, 1997; Wagner et al., 2004; Hülsmann et al. 2004). *Chaoborus* larvae generally select small- and medium-sized cladocerans (Dodson, 1974; Pastorok, 1981; Havel & Dodson, 1985; Krylov, 1992), and *Leptodora kindtii* is recognized as an efficient predator of small zooplankton (McNaught et al., 2004). As planktonic invertebrates are also preyed upon by fish, their predation pressure on smaller zooplankton can be alleviated when YOY fish are present, as shown experimentally (González & Tessier, 1997). According to the local adaptation hypothesis (Stibor & Lampert, 2000), *Daphnia* should show stronger antipredator responses to the predominant predator. However, multiple predators can induce phenotypic plasticity in antipredator responses of *Daphnia* populations coexisting in nature due to the seasonal changes in predator dominance, size-selective feeding and predator-prey interactions (Riessen, 1999; Tollrian & Dodson, 1999).

Among morphological defences, elongation of the tail spine or the helmet and the development of a neck tooth are common strategies developed by *Daphnia* in response to info-chemicals (kairomones) released by planktivorous fish and invertebrates (reviewed in Larsson & Dodson, 1993; Lass & Spaak, 2003).

Induction of morphological defences in *Daphnia* populations by either fish or invertebrate predators is well studied under experimental conditions (Spaak & Boersma, 1997; Kolar & Walh, 1998; Sell, 2000) but more rarely in field studies (Havel & Dodson 1985; Lindholm, 2002). Several experimental studies showed that *Daphnia* respond to fish kairomones by increasing tail spine length (Tollrian, 1994; Spaak & Boersma, 1997), whereas elongation of the helmet or formation of a neck tooth are common responses of *Daphnia* to invertebrate predators (mainly *Chaoborus*) (Tollrian, 1993; Brancelj et al., 1996; Sell, 2000). However, evidence of phenotypic plasticity in morphological defences in coexisting *Daphnia* populations facing multiple predators in natural environments is still missing.

In the present study, we examined the formation of morphological defences by two coexisting *Daphnia* species, the large-sized *D. pulicaria* (2 mm) and the small-sized *D. mendotae* (1.4 mm), in response to the presence of YOY yellow perch (*Perca flavescens*) and invertebrate predators (*Chaoborus punctipennis*, *Leptodora kindtii*) during summer in a mesotrophic lake. The main goal was to investigate temporal and spatial variation in two morphological traits (relative length of the tail spine in *D. pulicaria* and of the helmet in *D. mendotae*) according to changes in YOY fish and invertebrate predation pressure. We hypothesized that due to differential predation risk exerted by YOY perch and invertebrate predators, the small- and large-sized species would develop different morphological traits. Predation risks posed by YOY perch would trigger a stronger response in the large-sized *D. pulicaria*, whereas predation risks posed by invertebrate predators, mainly *Chaoborus*, would influence the small-sized *D. mendotae*.

## Methods

### Study site and field sampling

Lake Brome is a large (14 km<sup>2</sup>) mesotrophic lake of glacial origin situated in the Eastern Townships region, south-east of Montréal, Québec (45°14' N, 72°30' W). Mean and maximum depths are 5.9 and 12.2 m, respectively. The lake is normally ice-free from early April through late November, and thermal stratification developed from early June till late

August. Epilimnion extended to 7 m depth, the metalimnion ranged from 7 to 9 m depth, and the hypolimnion was below 9 m. Water temperature in the epilimnion increased from 10°C in spring to 24°C in late summer, while remaining at 15–17°C in the hypolimnion. Total phosphorus and chlorophyll *a* concentrations reached 19 µg l<sup>-1</sup> and 8 µg l<sup>-1</sup>, respectively. During summer, Secchi water transparency was consistently around 3 m and the euphotic depth (1% of surface light) remained around 9 m. Lake Brome was well oxygenated (>9 mg l<sup>-1</sup>) in the epilimnion while the hypolimnion became anoxic (<1 mg l<sup>-1</sup>) below 9 m depth after mid-July (Gélinas et al., 2007, in press).

Zooplankton was collected during the day (12 h–17 h) every week from May to August 2002 by vertical hauls (0–12 m) at the deepest site in the pelagic zone with a plankton net (14 cm diameter, 150 µm mesh size). The mesh size was small enough to collect all crustacean species, especially juvenile and adult daphnids, while filtering small rotifers and algae. In addition, zooplankton samples were also collected at six depths (1, 3, 5, 7, 9, 11 m) with a Schindler–Patalas trap (12 l) fitted with a net of 150 µm mesh size. A total volume of 24 l was filtered at every depth. Depth-discrete zooplankton sampling was carried out during summer at four dates corresponding to the different periods of YOY fish and invertebrate predation (for details see the *Analysis of YOY perch and invertebrate planktivory* section below). Zooplankton samples were fixed in the field in 4% sugar buffered-formalin solution for further analysis in the laboratory.

Sampling of YOY fish and invertebrate predators was carried out in the pelagic zone, at every week from 23 May until 29 July, 2002. Invertebrate predators were collected during night time (22 h–00 h) by vertical hauls (0–11 m) using a large plankton net (0.25 m<sup>2</sup>, 1 mm mesh size). YOY fish were caught with a large Bongo net (0.25 m<sup>2</sup> area, 7 m length, 2 mm mesh size) trawled in the centre of the lake along 200 m transects at 1, 3 and 5 m depths two hours after sunset (between 20 h and 22 h). Captured YOY fish, mainly yellow perch, were counted and measured before being fixed in methanol–formaldehyde solution. Density of YOY fish and invertebrates (ind.m<sup>-3</sup>) was evaluated at each sampling date. We analyzed the gut contents of 30 individuals of YOY perch collected on each sampling date, by identifying and counting all planktonic preys

(*Bosmina*, *Daphnia* species, cyclopoid and calanoid copepods and eggs).

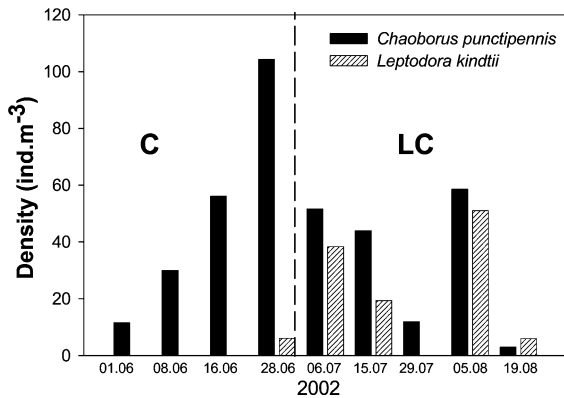
#### Analysis of *Daphnia* morphological traits

Analysis of morphological traits was done on both juvenile and adult instars of *D. pulicaria* and *D. mendotae* collected from vertical hauls and at discrete depths in the pelagic zone of the lake. We analysed *Daphnia* morphological traits only on a biweekly interval on zooplankton samples collected with the plankton net. Adult and juvenile status for *Daphnia* individuals was established based on the estimation of the size at maturity of each species (SAM) (Stibor & Lampert, 1993). Individuals smaller than the SAM were categorized as juveniles while the ones larger as adults. Around 100 specimens of each species from vertical haul samples and 50 specimens of each species from the discrete-depth samples were randomly selected and measured. The animals were examined at 100× magnification with a dissecting microscope (Leica MZ12) and measured with an image analyser (Image-Pro Plus). The body length from the top of the eye to the base of the tail spine was measured on each species. For *D. pulicaria*, we measured the tail spine length from the base to the tip, and we estimated the tail spine elongation based on the ratio of the tail spine length to the body length (so-called tail spine ratio). For *D. mendotae*, the helmet length was measured from the tip of the helmet to the top of the eye, and we estimated the helmet elongation based on the ratio of the helmet length to the body length (so-called helmet ratio).

#### Analysis of YOY perch and invertebrate planktivory

According to the single or conjoint occurrence of invertebrate predators in the pelagic zone, the summer survey was divided into two periods. The C period corresponded to the month of June when *Chaoborus punctipennis* was the single invertebrate predator in high-abundance. The LC period corresponded to the months of July and August when both *Chaoborus punctipennis* and *Leptodora kindtii* were co-dominant but less abundant (Fig. 1).

According to the presence/absence of YOY perch in the pelagic zone of the lake and the importance of



**Fig. 1** Variations in *Chaoborus* larvae and *Leptodora kindtii* densities (ind m<sup>-3</sup>) over the summer 2002 in Lake Brome with the distinction between the *Chaoborus* predation period (C) and the combined *Chaoborus* and *Leptodora* predation period (LC)

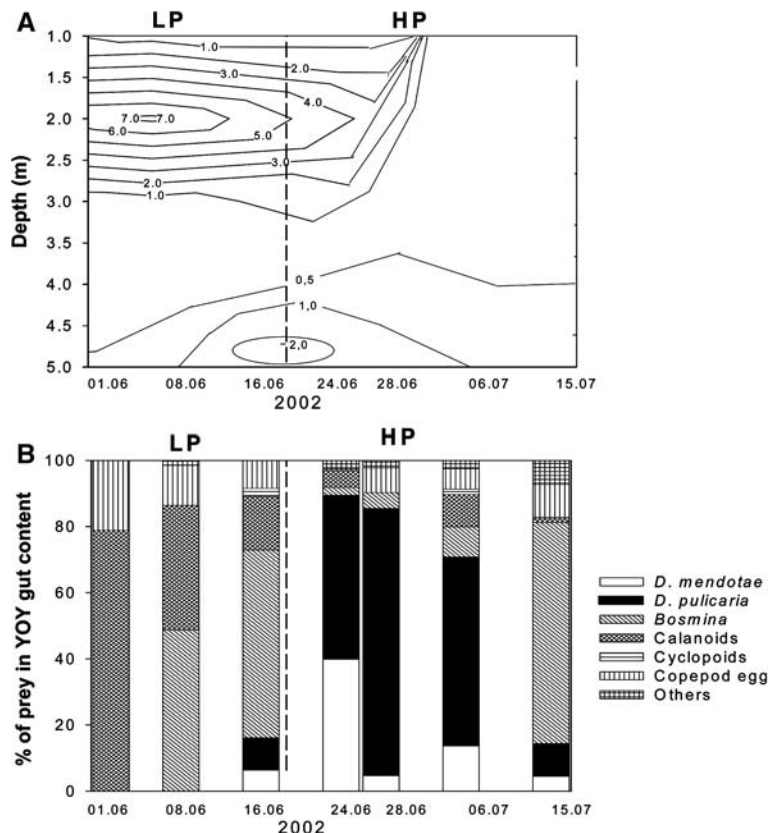
*Daphnia* preys in their gut contents, the summer was divided into four YOY fish periods: the before-predation period (B), the low-predation period (LP), the high-predation period (HP), and the after-predation period (A) (Fig. 2). The B period (27 April–31 May)

corresponded to the absence of YOY fish in the pelagic zone of the lake as no fish were caught in the Bongo net until the end of May. The LP period (1–16 June) corresponded to the presence of YOY fish in high-density (up to 7 ind m<sup>-3</sup>) in the pelagic zone, however, not yet feeding on *Daphnia* but mainly on *Bosmina* sp. and small calanoid copepods (Fig. 2). The HP period (17 June–15 July) represented the period of low abundance but of high-predation by YOY fish on both *Daphnia* species (Fig. 2). The period A (15 July–19 August) was the after-predation period when YOY fish were not longer captured in the pelagic zone.

Statistical analysis

Repeated-measured ANOVAs (RM-ANOVAs) were used to test the difference in the mean values of morphological defences in adults and juveniles of each *Daphnia* species (tail spine ratio of *D. pulicaria*; helmet ratio of *D. mendotae*) between the two invertebrate predation periods, and between the four

**Fig. 2** Contour plot of the YOY yellow perch density according to depth (A) and seasonal changes in the percentage of different zooplankton prey in YOY gut content (B) in Lake Brome during two YOY fish predation periods (LP, HP) in summer 2002. The periods B (before-predation) and A (after predation) are not shown because no YOY perch were captured in the pelagic zone



YOY fish periods. RM-ANOVA was also used to test the effects of depths on the body length and morphological defences of each *Daphnia* species. For *D. mendotae*, the 11-m depth was removed from the analysis since no *D. mendotae* were found at that depth during the last two YOY fish periods. Data were checked for normality in distribution with a Kolmogorov–Smirnov test (Lilliefors) (Sokal & Roff, 1995). All computations were run using Systat 8.

## Results

### Invertebrate and YOY perch planktivory

The dominant invertebrate predator was *Chaoborus punctipennis*, whose larvae were present at night in the water column throughout summer (Fig. 1). Its abundance increased during the C period until a maximum density above 100 ind m<sup>-3</sup> at the end of June. During the LC period, *Chaoborus* density decreased and ranged from 10 to 60 ind m<sup>-3</sup>, and the carnivorous Cladocera *Leptodora kindtii* appeared in the water column at densities under 50 ind m<sup>-3</sup> (Fig. 1).

Before 1 June (period B) no YOY fish were caught with the Bongo net in the pelagic zone of the lake. During the LP period, new-hatched yellow perch of small size (8–15 mm) appeared in the pelagic zone at the beginning of June and aggregated at 2-m depth with a maximum density of 7 ind m<sup>-3</sup> (Fig. 2A). During the HP period, YOY perch having size

>15 mm stayed in surface waters but their density decreased from 4 to 1 ind m<sup>-3</sup> during the last 2 weeks of June. YOY perch measuring around 27 mm avoided surface waters and were only caught at 5 m depth from the end of June until mid-July (Fig. 2A). After 15 July (period A), no more YOY perch were caught in the pelagic zone of the lake. Gut content analysis showed that during the LP period, new-hatched yellow perch fed on small calanoids, eggs of copepods, and on the small cladoceran *Bosmina* (Fig. 2B). *Daphnia* species became the preferred food item of YOY perch >15 mm during the HP period (Fig. 2B). Both *D. mendotae* and *D. pulicaria* were found in the YOY gut content. *D. pulicaria* was the predominant item in the diet of larger YOY perch (20–27 mm) (Fig. 2B).

### Variation in morphological defences among YOY fish and invertebrate predation periods

The mean values of body length of the juveniles and adults of *D. pulicaria* were always greater than those of the juveniles and the adults of *D. mendotae* in each of the YOY fish periods (Table 1). The morphological defences were more pronounced in the juvenile instars than in the adults for both *Daphnia* species. The tail spine ratio of *D. pulicaria* and the helmet ratio of *D. mendotae* were always greater in the juveniles than in the adults (Table 1). RM-ANOVAs testing for differences among the YOY fish periods did not demonstrate any significant change in the tail spine ratio of both the juveniles and adults of

**Table 1** Mean values for the body length (mm) and the morphological defences of *Daphnia pulicaria* and *Daphnia mendotae* in juveniles and adults during the 4 YOY periods (B, LP, HP, A)

Traits		B	LP	HP	A
<i>D. pulicaria</i>					
Juveniles	Body length	0.973 (0.317)	1.206 (0.257)	0.842 (0.166)	1.26 (0.45)
	Tail spine ratio	0.471 (0.101)	0.431 (0.075)	0.492 (0.068)	0.413 (0.096)
Adults	Body length	1.992 (0.211)	1.881 (0.177)	1.732 (0.383)	1.722 (0.337)
	Tail spine ratio	0.317 (0.059)	0.308 (0.055)	0.350 (0.076)	0.356 (0.100)
<i>D. mendotae</i>					
Juveniles	Body length	0.776 (0.179)	0.869 (0.12)	0.635 (0.138)	0.835 (0.205)
	Helmet ratio	0.138 (0.035)	0.163 (0.036)	0.217 (0.039)	0.246 (0.038)
Adults	Body length	1.292 (0.157)	1.249 (0.176)	1.228 (0.221)	1.319 (0.283)
	Helmet ratio	0.098 (0.025)	0.145 (0.046)	0.178 (0.038)	0.215 (0.031)

Standard deviations are in brackets

*D. pulicaria* ( $F_{3,3} = 1.749$ ,  $P = 0.329$ ;  $F_{3,3} = 0.228$ ,  $P = 0.872$ ). In average, the tail spine ratios of the juveniles and adults of *D. pulicaria* were relatively similar along the YOY fish periods (Table 1). In contrast, the helmet ratios of the juveniles and adults of *D. mendotae* were significantly different between the YOY fish periods ( $F_{3,3} = 112.3$ ,  $P < 0.001$ ;  $F_{3,3} = 15.0$ ,  $P = 0.026$ ). In average, the helmet ratios steadily increased along the YOY fish periods (Table 1).

The mean body lengths of the juveniles and adults of *D. pulicaria* were similar during the two invertebrate periods (Table 2). As seen before, morphological defences of both *Daphnia* species were relatively more pronounced in the juvenile instars than in the adults (Table 2). RM-ANOVAs did not indicate significant difference in the tail spine ratio of the juveniles and adults of *D. pulicaria* between the invertebrate periods (C vs. LC) ( $F_{1,3} = 0.216$ ,  $P = 0.674$ ;  $F_{1,3} = 0.406$ ,  $P = 0.569$ ). In contrast, the helmet ratios of the juveniles and adults of *D. mendotae* were significantly different between the C and LC invertebrate periods ( $F_{1,3} = 309.6$ ,  $P < 0.001$ ;  $F_{1,3} = 36.0$ ,  $P = 0.009$ ). The helmet ratios in the juveniles and adults of *D. mendotae* were 1.7- and 1.5-fold higher during the LC period when both invertebrate predators co-occurred (Table 2).

**Table 2** Mean values for the body length (mm) and the morphological defences of *Daphnia pulicaria* and *Daphnia mendotae* in juveniles and adults during the 2 invertebrate predation periods (C, LC)

Traits		C	LC
<i>D. pulicaria</i>			
Juveniles	Body length	1.086 (0.311)	1.030 (0.386)
	Tail spine ratio	0.452 (0.091)	0.457 (0.091)
Adults	Body length	1.910 (0.193)	1.732 (0.380)
	Tail spine ratio	0.310 (0.056)	0.350 (0.077)
<i>D. mendotae</i>			
Juveniles	Body length	0.818 (0.161)	0.722 (0.203)
	Helmet ratio	0.149 (0.037)	0.230 (0.041)
Adults	Body length	1.275 (0.166)	1.276 (0.209)
	Helmet ratio	0.116 (0.042)	0.198 (0.039)

Standard deviations are in brackets

## Variation in morphological defences between depths

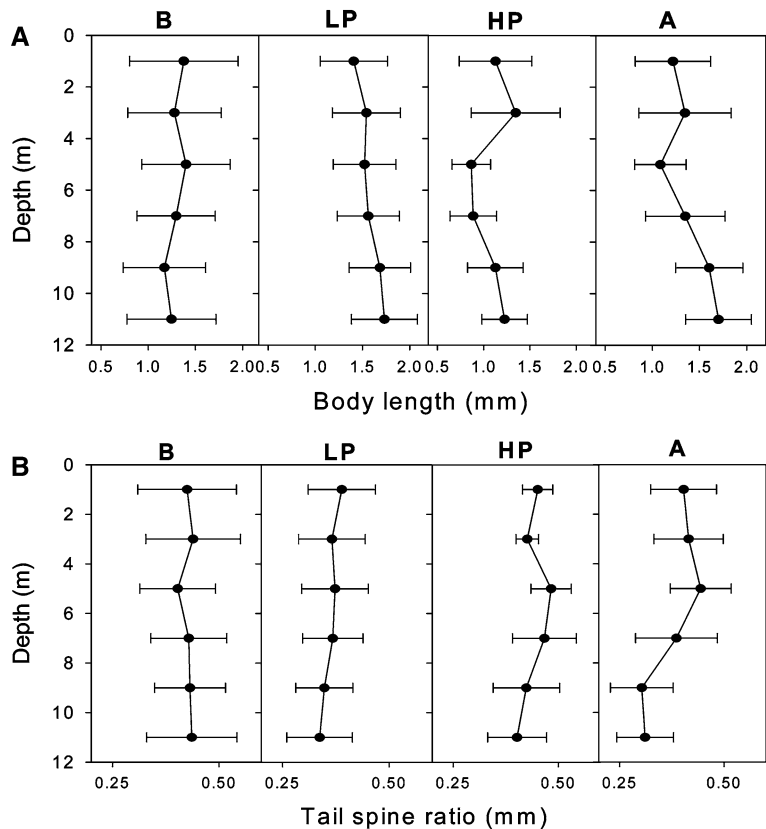
We examined the changes in body length and in morphological defences of each *Daphnia* species (juveniles and adults pooled) at different depths using mean values during the four YOY fish periods. Depth variation in the mean body length and tail spine ratio of *D. pulicaria* (Fig. 3) tended to indicate that during the HP period the smallest individuals with the longest tail spine were situated at 5-m depth, whereas the largest individuals with the shortest tail spine were located at 11-m depth (Fig. 3). However, RM-ANOVAs did not indicate significant differences among depths neither for the mean body length nor the mean tail spine ratio of *D. pulicaria* ( $F_{5,15} = 1.489$ ,  $P = 0.251$ ;  $F_{5,15} = 2.279$ ,  $P = 0.099$ ). The body length of *D. mendotae* seemed slightly smaller during the HP, especially closer to the surface, while the helmet ratio increased drastically along the YOY fish periods (Fig. 4). However, no significant difference among depths was found neither for the mean body length nor the mean helmet ratio of *D. mendotae* ( $F_{4,12} = 1.471$ ,  $P = 0.272$ ;  $F_{4,12} = 0.914$ ,  $P = 0.487$ ).

## Discussion

### Relative importance of YOY perch and invertebrate predation

In Lake Brome, *Daphnia* populations faced important seasonal changes in predation pressure by the three predators (YOY perch, *Chaoborus*, *Leptodora*) inhabiting the pelagic zone during summer. In spring (first 2 weeks of June), predation pressure was weak because the new-hatched YOY perch were gape-limited and did not feed on *Daphnia*, and the density of *Chaoborus* was also low. It is only during a short period of 1 month (16 June–15 July) that the three predators were exerting predation pressure on both coexisting *Daphnia*. Following 15 July, YOY perch disappeared from the water column, whereas invertebrate predators remained relatively abundant. One interesting point in our study is that both YOY fish and invertebrate predators exerted negative-size selection on *Daphnia* during the spring and early summer. Recent laboratory experiment (Hülsmann

**Fig. 3** Variation in the body length (mm) ( $\pm$ SD) (A) and the tail spine ratio (B) of *D. pulicaria* across depths during the four YOY fish periods (B, LP, HP, A)

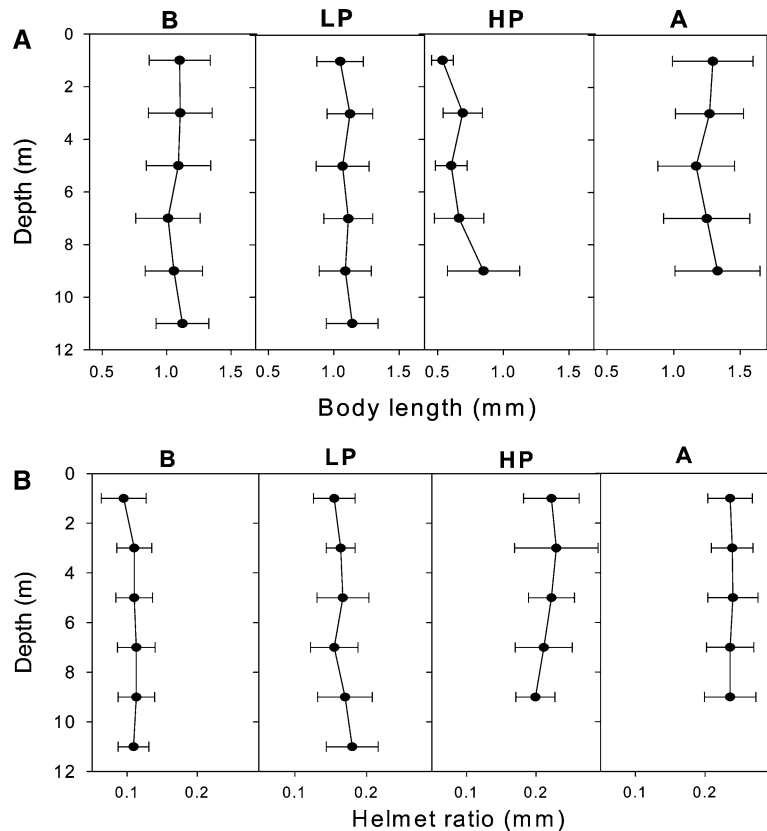


et al., 2004) and field studies (Mehner et al., 1998; Graeb et al., 2004) showed that small YOY perch (< 25–30 mm) were gape-limited predators. We also found in a companion study conducted in Lake Brome that gape-limited YOY perch from 8 to 27 mm selected *Daphnia* smaller than 1.75 mm (Gélinas et al., 2007, in press). Invertebrate predators are known to exert negative size-selection on daphnids (Pinel-Alloul, 1995a, b). *Chaoborus* larvae generally select *Daphnia* smaller than 1.3 mm (Dodson, 1974; Pastorok, 1981; Havel & Dodson, 1985; Krylov, 1992; Brett, 1992), and *Leptodora kindtii* is recognized as an efficient predator of small zooplankton due to its transparency (McNaught et al., 2004).

In this study, to some extent, YOY perch might be considered the dominant predator in Lake Brome in early summer (mid-June to mid-July) since *Daphnia* were their preferred food. Indeed, the density of both *Daphnia* drastically declined at the end of the high-predation period (HP) of YOY perch (Gélinas et al., 2007, in press). However, the co-occurrence of the

three common predators might have resulted in complex interactions due to YOY fish predation on the two invertebrate predators. In general, large planktivorous fish with positive size-selective feeding exhibit a strong preference for *Chaoborus* larvae (Pinel-Alloul, 1995a, b). Although *Chaoborus* were present in high numbers in the water column at the end of June no *Chaoborus* larvae were found in the gut contents of the small YOY perch. However, some individuals of *Leptodora kindtii* were ingested by the YOY perch. Thus, the presence of invertebrate predators did not mediate or reduce the risk that gape-limited YOY perch (8–27 mm) posed to the *Daphnia* population, at least until mid-July. In another study, Makino et al. (2001) also found that the sudden emergence of chironomids did not alleviate fish predation pressure on daphnids. Later in summer, when gape-limitation was offset, large YOY perch >30 mm might have preyed on invertebrate predators. However, the possible interaction among fish and invertebrate predators during late summer remains unknown because we did not capture larger

**Fig. 4** Variation in the body length (mm) ( $\pm$ SD) (A) and helmet ratio (B) of *D. mendotae* across depths during the four YOY fish periods (B, LP, HP, A)



YOY perch after mid-July in Lake Brome. Based on previous studies, we suggest that two main factors could have limited YOY fish predation on the two invertebrate predators occurring in Lake Brome in late summer: the inversed diel vertical migration of Chaoborids (Soranno et al., 1993), and the transparency of the cladoceran predator (McNaught et al., 2004). Therefore, in Lake Brome, the presence of simultaneous predators with similar prey-size selectivity might force coexisting *Daphnia* species to develop morphological defences against their greatest predators, namely YOY perch for the large *D. pulicaria*, and the invertebrate predators for the small *D. mendotae*.

#### Tail spine elongation in *D. pulicaria*

Neither gape-limited predation exerted by YOY perch nor the presence of invertebrate predators in high-abundance induced morphological defences in *D. pulicaria*. The large-sized *D. pulicaria* did not respond to predation threats by increasing its tail

spine ratio during the high-predation (HP) period of gape-limited YOY perch or during the C period when *Chaoborus* were present in high-abundance during night in the pelagic zone. No response to invertebrate predator was expected because of the large size of *D. pulicaria*; however, the lack of response to YOY fish predation was unexpected. Dodson (1989) found that *D. pulicaria* tail spine ratio increased in adults subjected to positive size-selective predation, but not in juveniles. In our study, in accordance with the negative size-selective predation exerted by YOY perch in early summer, we were expecting to observe a relatively longer tail spine during the high YOY fish predation period in the juveniles of *D. pulicaria*. Our results demonstrated only that the tail spine ratio was always relatively larger in juveniles than in adults. In Lake Brome, as YOY perch were gape-limited, they selected preferentially the juveniles of *D. pulicaria* <1 mm (Gélinas et al., 2007, in press). We can only assume that YOY fish selection of smaller-sized daphnids may have greatly increased predation pressure on juveniles, in turn forcing them to develop



relatively longer tail spine than the adults. However, we were not able to demonstrate higher tail spine ratio during the high-predation (HP) period, although the maximum mean value of tail spine ratio was observed during the HP period.

Our study did not indicate that the induction of morphological defences by *D. pulicaria* varied among depths. However, as both *D. pulicaria* and large YOY perch colonized the oxygenated 5-m metalimnetic water layer during the HP period, *D. pulicaria* had higher tail spine ratio and smaller body size. In contrast, *D. pulicaria* inhabiting deep water layers (9–11 m) not colonized by YOY fish, probably due to the low oxygen concentration ( $<1 \text{ mg l}^{-1}$ ), had larger body size and smaller tail spine ratio. Similar decrease in tail spine ratio with depth was reported by Spaak & Boersma (1997) for *Daphnia galeata* facing predation by roach, perch and *Chaoborus flavicans*.

#### Helmet elongation in *D. mendotae*

In Lake Brome, helmet elongation in adults and juveniles of *D. mendotae* during summer was related to seasonal changes in both YOY perch and invertebrate predation. This result is similar to the field study of Lindholm (2002) that showed induction of cyclomorphosis (increase in relative helmet and tail spine length) in *Daphnia leavis* facing predation by Cichlid fish of large size (40–53 mm length) in a tropical floodplain. In Lake Brome, the formation of a longer helmet was probably triggered in early summer during the low-predation YOY fish period when *D. mendotae* faced predation by the gape-limited YOY perch of small size (8–27 mm). This antipredator defence was fully developed later in summer, when YOY perch vanished from the pelagic zone while invertebrate predators were still abundant. Relatively high-abundance of both *Chaoborus* and *Leptodora* at the beginning of August may have enhanced the occurrence of longer helmet in the small *D. mendotae*. Under experimental conditions, Brett (1992) showed that the *Chaoborus* predation led to an increased incidence of helmets in small-sized *Daphnia* relatively to both the fish treatment and the predator-free control. Brancelj et al. (1996) also reported higher frequency of cornered head in small-bodied *D. hyalina* (0.9–1.3 mm) in the presence of a high-density of *Chaoborus* larvae under

field and experimental conditions. In addition, it has been suggested that increasing water temperature during summer, above a threshold value of 25–28°C, may induce helmet elongation in *D. cucullata* and *D. lumholtzi*, (Lampert & Wolf, 1986; Yurista, 2000). However, the constant elongation in the helmet of *D. mendotae* over summer seems unlikely to be attributed to the increasing water temperature in the epilimnion, because the elongation of the helmet was consistent throughout the water column without any effect of depth. In Lake Brome, *D. mendotae* experienced a wide range of temperature seasonally and vertically within the water column. As the lake was thermally stratified, the difference of 7°C in temperature between water surface (20–24°C) and deeper layers (15–17°C) did not induce a decrease in the helmet ratio of *D. mendotae* with depth.

Our study showed that a full understanding of the development of predator-specific morphological defences in coexisting different-sized *Daphnia* require several environmental cues from fish and invertebrate predators. *Daphnia* species coexisting in Lake Brome showed phenotypic plasticity in morphological anti-predator strategy when facing predation by both YOY perch and invertebrate predators. Only the small-sized *D. mendotae* developed morphological defences to cope with negative size-selective predation by both YOY fish and invertebrate predators. The large-sized *D. pulicaria* did not respond to YOY fish predation by increasing its tail spine probably because of its lower vulnerability to predation by gape-limited YOY fish and invertebrate predators, and of its ability to do diel migration and stay deeper in the water column (Gélinas et al., 2007, in press), and produce resting eggs (Ślusarczyk et al., 2005).

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