

# Predation of larval benthic invertebrates in St George's Bay, Nova Scotia

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*Larval survival during planktonic dispersal is crucial to the connectivity among benthic populations. Although predation has been suggested as an important cause of larval mortality, this process has rarely been quantified in the field. We measured the abundance of various larval species in the water column in St George's Bay, Nova Scotia, Canada, on 3 different occasions in summer (August 2008, July and August 2009), the period of high larval abundance in our region. We sampled four numerically dominant predators (scyphozoans: *Cyanea capillata* and *Aurelia aurita*; fishes: *Gasterosteus aculeatus* and *Merluccius bilinearis*) and lobster larvae near the water surface with a neuston net and other larval species in the water column (3 m depth) with a ring net. Larvae found in the gut contents of the predators included various species of gastropods, crustaceans and bivalves, and these were more abundant in the scyphozoans than the fishes. We attribute these differences to variation in predation method. For certain larval taxa, we found significant differences between the proportional abundance in the guts of *C. capillata* and in the water column, indicating prey selectivity. This study evaluates the potential impact of predation on larval survival and indicates that the presence of predators can cause changes in abundance and consequent taxonomic shifts in species dominance of larvae, influencing their successful subsequent recruitment to the benthos.*

**Keywords:** larval abundance, predation, selectivity, meroplankton, benthic invertebrates, larval mortality

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## INTRODUCTION

The larval phase of benthic invertebrates with indirect development facilitates population connectivity and acts to maintain genetic diversity (Jones *et al.*, 2008). For most benthic invertebrates, high rates of mortality can occur during all stages of development between embryo release and juvenile recruitment (Eckman, 1996) and mortality in any stage can influence the structure (e.g. size, age and genetics) of benthic populations.

The highest mortality rates most likely occur during the planktonic dispersal stage (Rumrill, 1990; Morgan, 1995; but see Johnson & Shanks, 2003). Physiological stress due to extreme or variable temperatures and salinities, low dissolved oxygen, pollution, UV radiation, starvation, unavailability of substrate for settlement, advection to unsuitable habitats, sinking and predation have all been recognized as sources of larval mortality (Young & Chia, 1987; Rumrill, 1990; Morgan, 1995). Of these, predation is considered the most significant (Thorson, 1950; Morgan, 1995), with cnidarians, ctenophores (gelatinous zooplankton) and planktivorous fishes recognized as the most important predators (Young & Chia, 1987; Morgan, 1992).

Studies that have quantified predation rates on larval benthic invertebrates are limited. In the laboratory, experiments have mostly measured survival rates, using small containers and concentrations of prey much higher than those found in the field (Cowden *et al.*, 1984; Pennington *et al.*,

1986; Morgan, 1992; Johnson & Brink, 1998). Even fewer measurements of predation rates have been collected in the field, and they are much lower than those measured in the laboratory, most likely because both predators and prey are less abundant (Johnson & Shanks, 1997). Since larval abundance and supply to the benthos is directly linked to the regulation of adult populations, the identification of the sources and patterns in larval mortality due to predation is essential.

Prey selection by particular predators can amplify the effect of predation on species captured in greater proportion than their ambient concentration (Behrends & Schneider, 1995). 'Selectivity' is defined as the 'consumption of prey types in disproportion to their abundance in the environment' (Purcell & Sturdevant, 2001). It is a measurement of predation outcome, which can be influenced by both predator- and prey-related variables. For example, predation rates depend on encounter rates between predator and prey, which are, in turn, influenced by several factors such as size, swimming speed and swimming direction of both the predator and prey (Bailey & Batty, 1984; Hansson, 2006). The effect of these factors on encounter rates, and thus on selectivity, depends on the method used by the predator to capture its prey. On the part of the predator, two different types of selective predation by planktivorous species have been proposed (Vuorinen, 1986). Vertebrate predators, such as zooplanktivorous fish, select larger prey species, as they are more easily visually detected (Thiel, 1996). In contrast, invertebrate predators (such as scyphomedusae) consume smaller organisms, which they draw into their mouths through the creation of a current (via the contraction and relaxation of the medusan bell). Tactile behaviour in prey selection is then exhibited as they consume the particles drawn towards their mouths (Vuorinen, 1986). This method results in selectivity for

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smaller prey items as larger prey species are able to actively escape (Bailey, 1984) Larval growth rates can also play a role in predation pressure as slower growing (and thus smaller) larvae are more vulnerable to predation (Pechenik & Levine, 2007).

Predators have the potential to significantly influence the structure of benthic populations through their effect on larval populations in the plankton, or near the benthos, an effect that will be magnified under prey selection. Although it is established that the composition of holoplankton is influenced by predation (Fraser, 1969; Huntley & Hobson, 1978; Mills & Forney, 1983; Hrbacek, 1989; Vijverberg *et al.*, 1990), similar studies on meroplankton are lacking.

To quantify the impact of predators on the meroplankton, and thus on benthic populations, measures of predation rates, selectivity and population densities (predator and prey) are required (Morgan, 1995). The analysis of the gut contents of predators collected in the field is frequently used to measure feeding rates of gelatinous zooplankton (Larson, 1987; Fancett, 1988; Matsakis & Conover, 1991; Suchman & Sullivan, 2000; Sullivan, 2010), as they can provide a qualitative representation of prey consumed *in situ*. These can be combined with digestion rates to calculate feeding rates (Purcell, 1992). Prey selectivity (both positive and negative) by various predators has been demonstrated for holoplankton and depended on prey type (Fancett, 1988; Purcell & Sturdevant, 2001). To date, however, the potential impact of predation on meroplankton has been inferred mainly based on limited measures of feeding rates in the laboratory (Pennington *et al.*, 1986; Morgan, 1992; Pechenik *et al.*, 2004). Studies examining the potential effects of predation on the abundance of particular meroplanktonic species are limited.

In this study, we use three approaches in an effort to assess whether meroplanktonic species are selectively preyed upon by the numerically dominant predators at the time of high larval abundance, influencing the structure of larval (and consequently benthic) populations in St George's Bay, Nova Scotia, Canada. This study forms part of a larger project designed to measure larval dispersal and population connectivity in this system: (1) we determined the numerically dominant predators of larval benthic invertebrates in the bay at a time when larvae are at their highest abundance (summer); (2) we identified the larval species that had been consumed by these predators using gut content analysis; and (3) based on the relative composition of larvae in the gut contents of the predators and in the water column, we calculated a selectivity index for particular predator–prey combinations to

determine whether selection for particular prey taxa varied among predator types.

## MATERIALS AND METHODS

### Study site and field sampling

St George's Bay ( $45^{\circ}45'N$   $61^{\circ}45'W$ ) is an  $\sim 900$  km<sup>2</sup> shallow embayment (Hargrave *et al.*, 1985) located on the north-western coast of Nova Scotia, Canada with the main opening facing northwards on the Northumberland Strait, and a smaller connection to Chedabucto Bay via the Canso causeway (Figure 1). There is a strong eastward flow across the mouth of the bay, which creates a clockwise gyre in the surface waters (up to 8 m depth) (Petrie & Drinkwater, 1977). The bottom depth ranges from  $\sim 20$  to 45 m, and salinity and temperature range from 25.7–29.0 and 15.4–16.9°C, respectively, in July–August. A thermocline exists in July and August at  $\sim 12$  m depth.

We sampled the prey species *Homarus americanus* (larval lobsters) (7–8 August 2008 only) and four major zooplanktivores (the scyphozoans: lion's mane jellyfish (*Cyanea capillata*) and moon jellyfish (*Aurelia aurita*); and the larval fishes: three-spined stickleback (*Gasterosteus aculeatus*) and silver hake (*Merluccius bilinearis*) (7–8 August 2008, and 11–12 July and 2–4 August 2009)) at 11 stations in St George's Bay, with a 500- $\mu$ m mesh neuston net ( $2 \times 1$  m). Sampling for lobster larvae and predators occurred during periods of reduced sunlight (before 10:00 and after 14:00), while prey other than lobster were sampled during all daylight hours (07:00–19:00) with similar light conditions between sampling dates, providing consistency for the temporal comparisons. While some larval groups exhibit vertical migration in this region, abundance at 3 m either did not vary temporally or was greater in the daytime (Lloyd, unpublished data). The neuston net was deployed at the surface and towed at average speeds of  $4.44 \pm 0.10$  km h<sup>-1</sup> ( $\pm$  SE) in a circular path for 30 minutes. Sampled water volume was estimated using two flowmeters (G.O. Environmental) attached to the starboard and port sides of the mouth of the net. In August 2008 and August 2009, on the same dates and at the same locations as the neuston sampling, zooplankton was also sampled with nets towed at 3 m depth, using a 200- $\mu$ m mesh plankton ring net (diameter = 75 cm). The ring net was opened at depth and towed at average speeds of  $4.54 \pm 0.09$  km h<sup>-1</sup> ( $\pm$  SE) in a linear path for 5 minutes and then closed at depth. We sampled predators and prey in the top

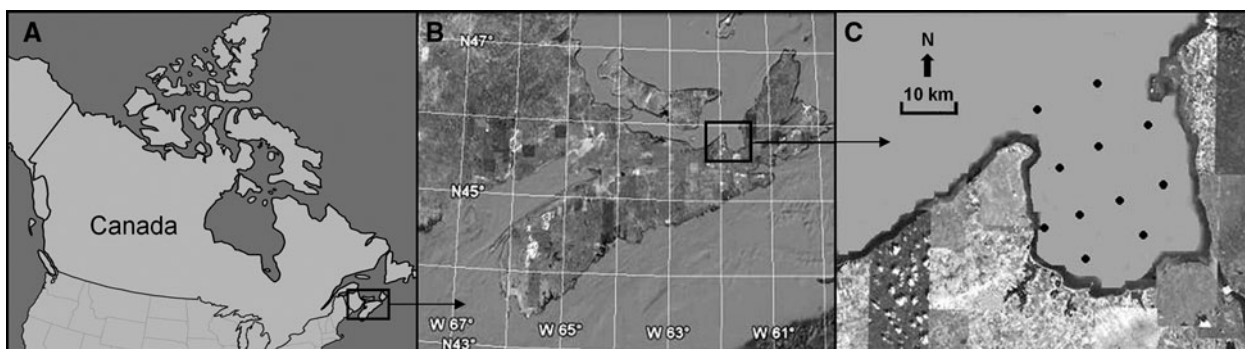


Fig. 1. Study site in St George's Bay, Nova Scotia, Canada in August 2008 and July and August 2009. Sampling stations are shown in C.

3 m of the water column as this was the depth with the highest abundance of the predators of interest (Lloyd, unpublished data). Sampled water volume was estimated using a flowmeter (G.O. Environmental) attached to the centre of the mouth of the net. On deck, the nets were rinsed with seawater and the contents of the cod-ends preserved. For the neuston net, scyphozoans and fishes were preserved separately in 4% buffered formaldehyde and the remainder of the sample in 95% ethanol; for the ring net, all cod-end contents were preserved in 95% ethanol.

## Sample processing

In the laboratory, scyphozoans and fishes were identified to species, counted and weighed to the nearest 0.001 g (wet weight), and total length of fishes measured to the nearest mm. Because many of the scyphozoans were damaged, we defined an 'individual' by the presence of a complete digestive system in an organism. All *Cyanea capillata* and the greatest of either all the fishes or a randomly selected subsample of 10 individuals of each species  $\times$  station  $\times$  sampling month combination were dissected. For all *C. capillata* sampled on all three sampling dates, as well as subset of 10 haphazardly selected fishes sampled in August 2008, all zooplankton (including holoplankton) in the guts were counted. For the scyphozoans, gut contents were directly extracted. The accuracy of this method was tested for a subset of 50% of the scyphozoans from each station sampled in August 2008 using a Nikon SMZ1500 stereomicroscope. After extraction, gut contents were preserved in 70% ethanol and later identified to the highest possible taxonomic resolution, as permitted by the extent of digestion. Only meroplankton inside the mouth or farther inside the digestive system were included; prey items caught in the tentacles or on the mucous-covered surfaces of the jellyfish were not included due to the potential for contamination in the neuston net.

For the larval fish, the stomach (digestive tract, excluding the mouth, the pharynx, and the intestine) was removed, opened, and the contents preserved in 95% ethanol. The organisms in the gut contents were later counted and identified to the highest possible taxonomic resolution using a Nikon SMZ1500 stereomicroscope.

All larval species in the plankton samples collected using the ring net at 3 m depth were counted and identified to the highest possible taxonomic resolution under a Nikon SMZ1500 stereomicroscope.

## Data analysis

Average numerical abundance (individuals  $1000\text{ m}^{-3}$ ) and biomass (g  $1000\text{ m}^{-3}$ ) of each predator were compared among the three sampling dates using one-way analysis of variance. The assumption of equal variances was tested using Levene's tests, and Tukey's *post-hoc* tests were used for pairwise comparisons. No further analyses were carried out on *Aurelia aurita* as it was nearing the end of its lifecycle during the sampling period and was often dead or dying. For this reason very few larval prey species were extracted from the guts of this predator. For the numerically dominant meroplanktonic prey taxa in August 2008 and August 2009, percentage composition of predator gut contents (averaged across all predators from all sampling stations for each sampling period) was compared, when possible, between

July and August 2009 and between August 2008 and August 2009 to detect variability among sampling times, using a Student's *t*-test.

Selective feeding on specific meroplankton taxa was assessed as:

$$\alpha_i = r_i/p_i\{(r_i/p_i)/[(r_i/p_i) + (r_j/p_j)]\}$$

where  $r_i$  is the frequency of prey  $i$  in the diet,  $p_i$  is the frequency of prey  $i$  in the environment,  $r_j$  is the frequency of other prey in the diet and  $p_j$  is the frequency of other prey in the environment (Chesson, 1978). If  $\alpha_i < 0.5$ , predators are consuming prey  $i$  in a lower proportion than they are available in the environment. If  $\alpha = 0.5$ , non-selective feeding on prey  $i$  is occurring. Lastly, if  $\alpha > 0.5$ , predators are exhibiting selection for prey  $i$ .

The  $\alpha$  index was calculated for each of *Cyanea capillata*, *Merluccius bilinearis* and *Gasterosteus aculeatus*, using the proportion of each prey taxon in the guts [ $r_i/(r_i + r_j)$ ] and the proportion in the plankton samples [ $p_i/(p_i + p_j)$ ] collected at 3 m depth (or at the surface for *Homarus americanus*) in the water column. For each prey taxon and species of predator, Chi-square ( $\chi^2$ ) tests were used to compare the observed frequency in the guts with an expected frequency, calculated to reflect the proportional prey abundance in the water column. These tests were only done when a prey taxon was consumed by more than a single individual of a particular predator species.

All statistical analyses were done with SPSS 17.0. For all tests,  $\alpha = 0.05$  was used.

## RESULTS

### Predator abundance and biomass

The abundance and biomass of *Cyanea capillata* differed significantly among sampling events (abundance:  $F_{2,30} = 4.54$ ,  $P = 0.019$ ; biomass:  $F_{2,30} = 4.15$ ,  $P = 0.026$ ) (Figure 2), being greater in August than July 2009, but not differing between August 2008 and August 2009 (Tukey's Honestly Significant Difference tests). Since the abundance of *C. capillata* was low in July 2009, we did not include this month in the analyses of gut contents. In contrast, there were no significant differences detected for *Aurelia aurita* (abundance:  $F_{2,30} = 1.41$ ,  $P = 0.26$ ; biomass:  $F_{2,30} = 1.74$ ,  $P = 0.192$ ), *Gasterosteus aculeatus* (abundance:  $F_{2,30} = 0.14$ ,  $P = 0.872$ ; biomass:  $F_{2,28} = 1.51$ ,  $P = 0.237$ ) or *Merluccius bilinearis* (abundance:  $F_{2,30} = 1.87$ ,  $P = 0.171$ ; biomass:  $F_{2,28} = 0.13$ ,  $P = 0.876$ ) (Figure 2).

### Scyphozoan gut contents

In August 2008 and August 2009, *Cyanea capillata* from almost all stations had consumed larvae of *Cancer irroratus*. Other larval species, such as the gastropods *Margarites* sp. and *Bittium alternatum*, and the decapods *Homarus americanus* and *Carcinus maenas* had been consumed less frequently (Figure 3). Unlike August 2008, in August 2009 the scyphozoan consumed larvae of the gastropod *Littorina littorea* and had not consumed larvae of *Margarites* sp., *C. maenas*, or bivalve species. Calanoid copepods and

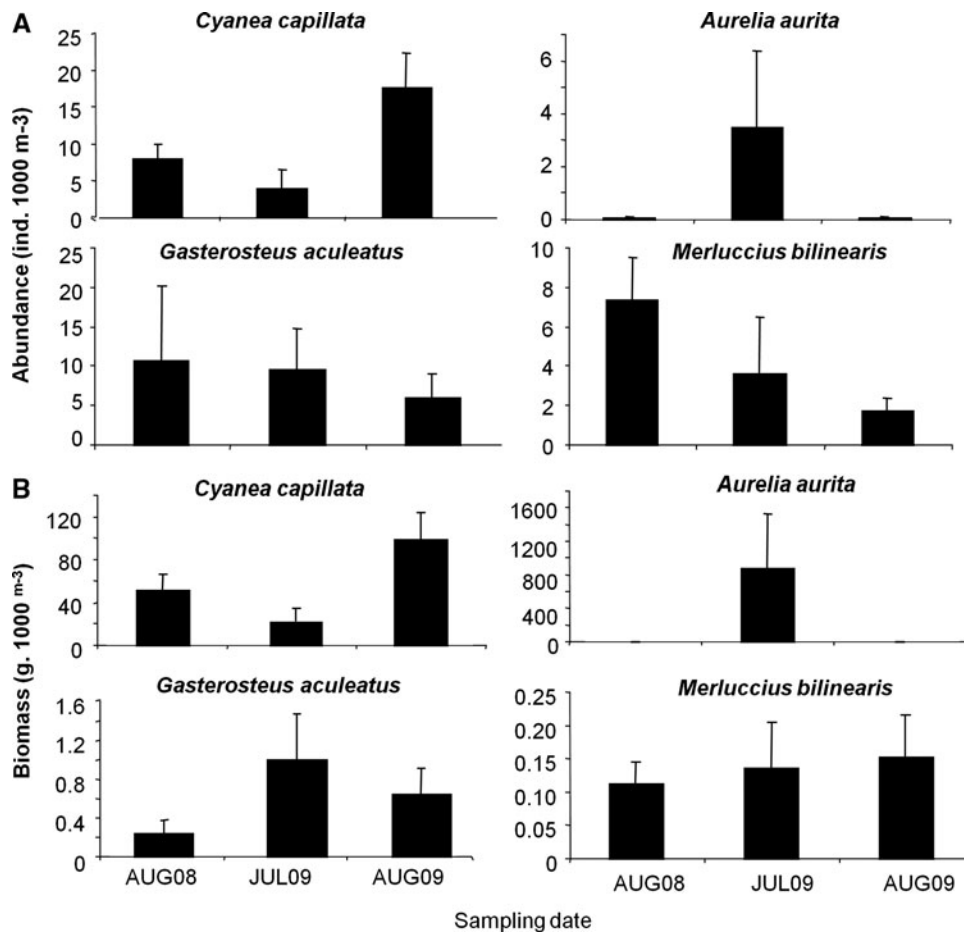


Fig. 2. Abundance (A) and biomass (B) (mean ± SE, N = 11) of 4 larval predators (scyphozoans: *Cyanea capillata* and *Aurelia aurita*; fishes: *Gasterosteus aculeatus* and *Merluccius bilinearis*), sampled in August 2008 and July and August 2009 averaged across all stations in St George’s Bay, Nova Scotia.

cladocerans were found in the guts of almost all dissected *C. capillata* (Table 1).

For *C. capillata*, the relative abundance of brachyurans ( $t_{83} = -2.46, P = 0.016$ ) and bivalves in the guts was

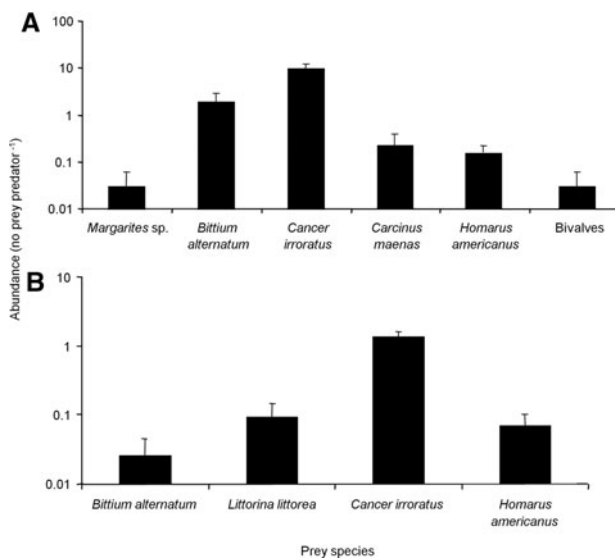


Fig. 3. Abundance of meroplankton in the gut contents of *Cyanea capillata* (mean ± SE, August 2008: N = 33; August 2009: N = 59) averaged over all individuals collected in August 2008 (A) and August 2009 (B).

greater in August 2008 than August 2009, while no differences were found for total gastropods ( $t_{57} = 1.58, P = 0.120$ ) (Figure 4A). Specifically, the gastropods *B. alternatum* ( $t_{33} = -2.39, P = 0.022$ ) and *Margarites* sp. and the brachyurans *C. maenas* and *C. irroratus* ( $t_{82} = -2.07, P = 0.042$ ) were relatively more abundant in the gut contents in August 2008 than August 2009, whereas the opposite was observed for *L. littorea*. No differences between August 2008 and August 2009 were found in the relative abundance of *H. americanus* ( $t_{58} = 1.84, P = 0.071$ ) (Figure 4B).

For *C. capillata*, we recorded prey selectivity based both on calculated  $\alpha$  values and on significant differences between the

Table 1. Average abundance of prey items (excluding meroplanktonic invertebrate larvae) in the gut contents of all *Cyanea capillata* sampled in August 2008 and August 2009. N is the number of predators used to calculate prey abundance, pooled across all sampling stations.

Date	Prey species	Abundance (prey predator <sup>-1</sup> ± SE)	N
August 2008	Copepods	1.94 ± 0.65	54
	Cladocerans	1.30 ± 0.35	
	Amphipods	4.30 ± 1.11	
August 2009	Copepods	4.81 ± 1.08	60
	Cladocerans	0.53 ± 0.13	
	Amphipods	1.19 ± 0.48	
	Fish eggs	1.93 ± 0.45	



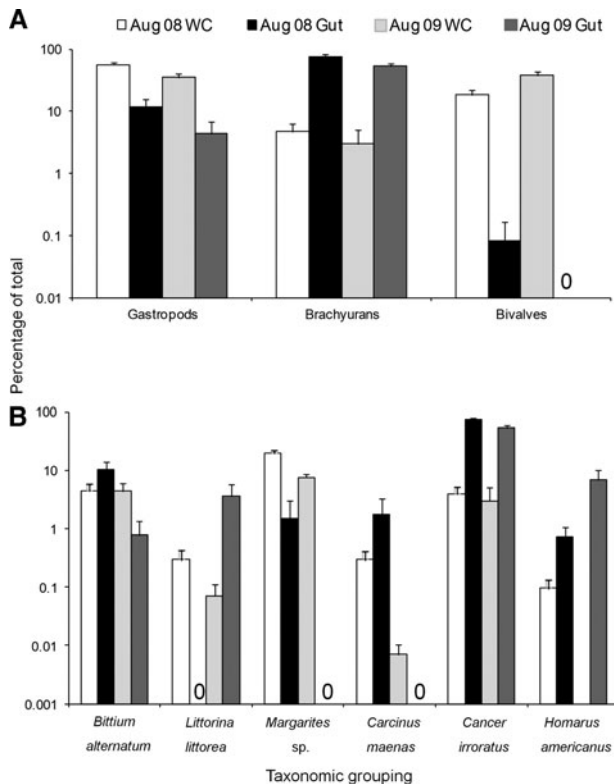


Fig. 4. Relative abundance (mean  $\pm$  SE,  $N = 11$ ) of the most abundant taxonomic group (A) and larval species (B) in the gut contents of *Cyanea capillata* (August 2008 gut and August 2009 gut) and at 3 m depth in the water column (surface for *Homarus americanus*) (August 2008 water column (WC) and August 2009 WC) averaged across all stations in August 2008 and August 2009.

larval composition in the gut contents and in the water column in August 2008 and August 2009. At both sampling times, gastropods were selected against, while brachyurans were selected for by this predator (Table 2). At the species level, *C. capillata* showed selectivity for *C. irroratus*. For the less abundant prey species, results were not as consistent among sampling times and patterns in the selectivity index did not coincide with consistent statistically significant effects. For example, in August 2008, *B. alternatum*, *C. maenas* and *H. americanus* were selected for by this predator (Figure 4B). In contrast, in August 2009, *B. alternatum* was selected against, whereas the opposite was observed for *L. littorea* (Figure 4B; Table 2).

### Fish gut contents

In contrast to the scyphozoans, *Gasterosteus aculeatus* consumed the larval gastropods *Margarites sp.* and *Aporrhais occidentalis*, as well as some bivalve species, bryozoans, brachyurans and fish eggs, but not in high abundance (Table 3). As was the case for the scyphozoans, the gut contents of all *G. aculeatus* dissected consistently included holoplanktonic copepods and cladocerans (Table 4). Gastropods, bivalves and bryozoans were consumed in August 2008 and July 2009, but not in August 2009 (Figure 5A). Brachyurans were the only meroplanktonic group consumed in August 2009. Both identified species of gastropods (*Margarites sp.* and *A. occidentalis*) were consumed in August 2008, while

*Margarites sp.* was the only gastropod consumed in July 2009 (Figure 5B). No statistically significant difference was found between the relative abundance of brachyurans in the guts in July and August 2009 ( $t_{54} = 1.83$ ,  $P = 0.072$ ) (Figure 5A).

Patterns in prey selection by *G. aculeatus* were not consistent between sampling events. In August 2008, this predator selected for bivalves, and selected against gastropods and bryozoans (Figure 5A) and *Margarites sp.* (Figure 5B). In contrast, in August 2009, the brachyurans were selected, while few gastropod and bivalve species were consumed by *G. aculeatus* (Figure 5B; Table 2).

The gut contents of *Merluccius bilinearis* were very similar to those of *G. aculeatus* (Table 3). The only larval taxa consumed by this predator in August 2008 were bivalves and gastropods, while no meroplanktonic species were extracted from the guts of predators sampled in July and August 2009. Like *G. aculeatus*, *M. bilinearis* also consumed mostly copepods and cladocerans (Table 4). In August 2008, *M. bilinearis* selected against larval bivalves (Figure 6; Table 2).

### DISCUSSION

In our study, larval benthic invertebrate species formed a large proportion of the gut contents of *Cyanea capillata*. In contrast, Morgan (1992) concluded that scyphomedusae do not have a large impact on invertebrate larvae because their diet consists primarily of fish larvae and copepods. Large differences were observed between the gut contents of the scyphozoan and the fish predators, and *C. capillata* and *Gasterosteus aculeatus* appeared to be consuming different prey species. Variations in the method of capture can result in differences in prey consumed due to different drivers of prey selection. Scyphomedusae, like *Aurelia aurita* and *C. capillata*, are tactile predators (Elliot & Leggett, 1996), and the contraction and relaxation of the scyphomedusan bell creates a current which draws passive particles towards the predator, allowing scyphomedusae to capture their prey with the nematocysts lining their tentacles. In contrast, fish species such as *G. aculeatus* and *Merluccius bilinearis* are active, visual predators (Elliot & Leggett, 1996) using vision and buccal suction to locate, pursue and capture their prey (Morgan, 1995). Because the methods used by these predator groups are so different, variation in prey composition is expected.

In our study, prey selection varied between predator types (tactile versus visual) and prey characteristics. In addition to mode of predation, high capture success of a particular prey species could also be a consequence of prey size or shape. While prey size does not affect medusan predation (Elliot & Leggett, 1996), prey swimming speed does (Bailey & Batty, 1984). A larval form with extensions such as arms (e.g. echinoderms), legs or spines (e.g. brachyurans) may become trapped in scyphomedusan tentacles and mucous more easily than a larval form lacking such projections (e.g. gastropods and bivalves). Prey behavioural changes in the presence of predators may also influence capture success (Forward & Rittschof, 2000; Cohen & Forward, 2003; Carr & Pitt, 2008). We observed a clear and consistent pattern of prey selection by *Cyanea capillata* across sampling times, when higher taxonomic groupings were considered. The abundance of bivalves was extremely low in the guts on all sampling dates, likely due to a combination of low abundance, small size and lack of

**Table 2.** Selectivity index ( $\alpha$ ) values and results of  $\chi^2$ -tests comparing observed prey frequency in the guts of three predators with an expected frequency calculated based on prey proportional abundance in the water column, in St George's Bay, Nova Scotia, in August 2008 and August 2009. NA,  $\chi^2$ -tests were not done because prey abundance in the predator gut contents was low.

Sampling date	Predator	Prey*	Selectivity index ( $\alpha$ )	$\chi^2_{df}$ -value	P		
August 2008	<i>C. capillata</i>	Brachyurans	16	$\chi^2_{28} = 44470$	<0.001		
		Gastropods	0.019	$\chi^2_8 = 104$	<0.001		
		Bivalves	1.6E-5	NA	NA		
		<i>C. irroratus</i>	18	$\chi^2_{28} = 51200$	<0.001		
		<i>C. maenas</i>	5.3	$\chi^2_2 = 8596$	<0.001		
		<i>H. americanus</i>	6.7	$\chi^2_4 = 1316$	<0.001		
		<i>B. alternatum</i>	1.6	$\chi^2_7 = 3436$	<0.001		
		<i>L. littorea</i>	1.1E-5	NA	NA		
		<i>Margarites</i> sp.	0.0044	NA	NA		
		August 2009		Brachyurans	17	$\chi^2_{31} = 97260$	<0.001
Gastropods	0.0099			$\chi^2_3 = 245.9$	<0.001		
Bivalves	0.0			NA	NA		
<i>C. irroratus</i>	17			$\chi^2_{31} = 97390$	<0.001		
<i>C. maenas</i>	0.018			NA	NA		
<i>B. alternatum</i>	0.026			$\chi^2_1 = 206.5$	<0.001		
<i>L. littorea</i>	50			$\chi^2_2 = 80100$	<0.001		
<i>Margarites</i> sp.	1.6E-8			NA	NA		
August 2008	<i>G. aculeatus</i>			Brachyurans	0.0	NA	NA
				Gastropods	0.0018	$\chi^2_1 = 5235$	<0.001
		Bivalves	0.68	$\chi^2_5 = 26290$	<0.001		
		Bryozoans	0.44	$\chi^2_9 = 5290$	<0.001		
		<i>Margarites</i> sp.	0.020	$\chi^2_1 = 390.4$	<0.001		
		<i>A. occidentalis</i>	0.090	NA	NA		
		August 2009		Brachyurans	1.4	$\chi^2_3 = 12560$	<0.001
Gastropods	0.0			NA	NA		
Bivalves	0.0			NA	NA		
Bryozoans	0.0			NA	NA		
August 2008	<i>M. bilinearis</i>	Bivalves	0.18	$\chi^2_1 = 5993$	<0.001		
		<i>Margarites</i> sp.	0.016	NA	NA		

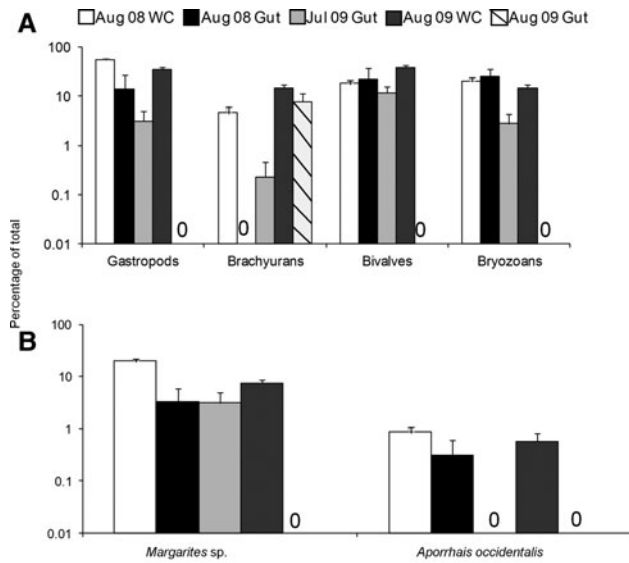
\*, for species names in full see text.

projections. Brachyurans and gastropods, however, were frequently consumed by this predator and were selected for and against, respectively. At the species level, while we detected selection for *Cancer irroratus*, selectivity was not

consistent for the decapod *Carcinus maenas*. This was likely because the low abundance of *C. maenas* in the water column relative to *C. irroratus* skewed the observed proportion in the predator guts. *Homarus americanus* was

**Table 3.** Average abundance of meroplankton in the gut contents of *Gasterosteus aculeatus* and *Merluccius bilinearis* sampled in August 2008, and July and August 2009. For each species, the smallest of the total number or a subsample of 10 individuals were dissected and their gut contents analysed. N is the number of predators used to calculate prey abundance, pooled across all sampling stations.

Predator	Date	Prey	Abundance (prey predator <sup>-1</sup> $\pm$ SE)	N
<i>Gasterosteus aculeatus</i>	August 2008	<i>Margarites</i> sp.	0.09 $\pm$ 0.09	47
		<i>Aporrhais occidentalis</i>	0.02 $\pm$ 0.02	
		Bivalves	0.15 $\pm$ 0.07	
		Bryozoans	0.21 $\pm$ 0.07	
		Brachyurans	0 $\pm$ 0	
<i>Gasterosteus aculeatus</i>	July 2009	<i>Margarites</i> sp.	0.11 $\pm$ 0.07	72
		<i>Aporrhais occidentalis</i>	0 $\pm$ 0	
		Bivalves	0.5 $\pm$ 0.21	
		Bryozoans	0.07 $\pm$ 0.03	
		Brachyurans	0.015 $\pm$ 0.015	
<i>Gasterosteus aculeatus</i>	August 2009	<i>Margarites</i> sp.	0 $\pm$ 0	51
		<i>Aporrhais occidentalis</i>	0 $\pm$ 0	
		Bivalves	0 $\pm$ 0	
		Bryozoans	0 $\pm$ 0	
		Brachyurans	0.08 $\pm$ 0.04	
<i>Merluccius bilinearis</i>	August 2008	<i>Margarites</i> sp.	0.06 $\pm$ 0.06	34
		<i>Aporrhais occidentalis</i>	0 $\pm$ 0	
		Bivalves	0.06 $\pm$ 0.04	
		Bryozoans	0 $\pm$ 0	
		Brachyurans	0 $\pm$ 0	



**Fig. 5.** Relative abundance (mean  $\pm$  SE, N = 11) of the most abundant taxonomic group (A) and larval gastropod species (B) in the gut contents of *Gasterosteus aculeatus* (August 2008 gut and August 2009 gut) and at 3 m depth in the water column (August 2008 water column (WC) and August 2009 WC) averaged across all stations in August 2008 and August 2009.

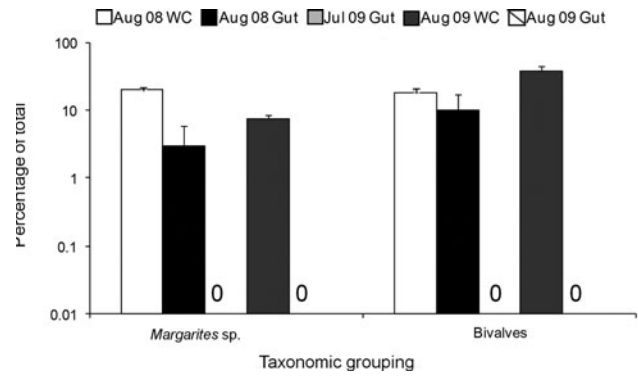
selected for in August 2008. The larval form of *H. americanus* is large, even in its youngest stages, and may be easily captured by scyphozoan tentacles despite its fast swimming speed.

In contrast, we did not observe consistent selectivity for any larval invertebrates by fishes, but rather they appeared to have consumed prey based on availability. Fish are active and visual predators and the swimming ability of the prey does not play as important a role in prey selection as it does for scyphozoans (Elliot & Leggett, 1996). In fact, larger larvae can usually swim faster than small larvae, and are, therefore, potentially more easily detected by visual predators and more likely to be consumed selectively. The lack of evidence for selectivity by fish predators in our study may have been the result of negligible differences in the size and swimming speed among prey species.

Predation rates, and consequently selectivity, can be confounded by differences in digestion rates among prey taxa

**Table 4.** Average abundance of prey items (excluding meroplanktonic invertebrate larvae) in the gut contents of *Gasterosteus aculeatus* and *Merluccius bilinearis* sampled in August 2008. The greatest of the total number or a subsample of 10 fish were dissected and their gut contents analysed. Data from July and August 2009 are not included as holoplankton and fish eggs were not counted in the guts of the planktivorous fishes sampled during these dates. N is the number of predators used to calculate prey abundance, pooled across all sampling stations.

Predator	Date	Prey	Abundance (prey predator <sup>-1</sup> $\pm$ SE)	N
<i>Gasterosteus aculeatus</i>	August 2008	Copepods	83.11 $\pm$ 11.26	35
		Cladocerans	71.80 $\pm$ 18.50	
		Fish eggs	5.63 $\pm$ 3.10	
<i>Merluccius bilinearis</i>		Copepods	44.60 $\pm$ 9.48	20
		Cladocerans	8.55 $\pm$ 2.74	
		Fish eggs	1.00 $\pm$ 0.40	



**Fig. 6.** Relative abundance (mean  $\pm$  SE, N = 11) of the most abundant taxonomic groups found in the gut contents of *Merluccius bilinearis* (August 2008 gut and August 2009 gut) and at 3 m depth in the water column (August 2008 water column (WC) and August 2009 WC) averaged across all stations in August 2008 and August 2009.

(Sullivan, 2010). In the extreme case, all preys are eaten exactly in proportion to their availability in the water column and their relative abundance in the guts of the predators is an artefact of their digestion rates alone. If this was the case and a particular prey item was digested much more slowly than another, it might be concluded incorrectly that the predator was selectively consuming this particular prey species. Additionally, not all prey taxa are similarly recognizable in consumer guts after the same amount of digestion, and differential recognition can bias the evaluation of prey selection toward larger, more easily identifiable prey (Sullivan, 2010). We believe it is unlikely that digestion rates confounded our results. Gastropod larvae have a thick and, presumably difficult to digest, shell. Conversely, brachyuran larvae have a thin shell and are therefore potentially digested faster. Martinussen & Bamstedt (1999) found the digestion of a single *Mytilus* sp. larva by scyphozoan predators took  $\sim$ 12 hours, while that of up to 30 individuals of the copepod *Calanus finmarchicus* took  $<$ 2 hours. Since copepods have a similar chitin exoskeleton to brachyurans, the above digestion rates are a good proxy for those of the brachyuran species consumed by scyphozoan predators in our study. If the proportions of prey in the gut contents of the predators were determined by digestion rate then more gastropod larvae relative to brachyurans would be present in the gut contents of *C. capillata*. In fact, the opposite was observed.

To compare the average ambient prey composition with the average gut contents of each predator species, we assumed that prey were consumed inside the sampling grid and in the top 3 m of the water column. Ambient prey composition is difficult to estimate given that an individual predator could have travelled beyond the boundaries of a station or even beyond the sampling grid while consuming spatially variable prey (Hansson, 2006). Given that larvae are present in the guts of scyphozoan species for 3–5 hours (Bailey & Batty, 1984), and that these predator species swim relatively slowly, it is unlikely that prey found in the guts of these predators were consumed outside the sampling grid. Fish predators were  $<$ 10 cm in length, and it is unlikely that these predators were able to swim beyond the boundaries of our sampling grid before digesting the prey species consumed. While medusae are found, and presumably feed, at all depths (Riisgard, 2007), most scyphozoans and fish predators in our study site remained near the surface during the

sampling periods. Concurrent plankton net sampling carried out at 8, 12, 18 and 24 m depth (total of 18 tows) captured only 2 scyphozoans (*C. capillata* at 18 m depth) and a single planktivorous fish (*G. aculeatus* at 12 m depth) (Lloyd, unpublished data).

In summary, we have shown that at least two meroplanktonic larval taxa are selectively consumed by the scyphozoan *C. capillata*, which selected against gastropods and for brachyurans. This is likely a result of prey-specific characteristics that influence encounter rates with this predator, such as prey behavioural responses, morphology and swimming speeds. Gastropods are the most abundant group of meroplankton in St George's Bay in summer (Lloyd *et al.*, unpublished data), and the avoidance of this group by the most abundant predator in the water column at that time can affect its survival and recruitment potential. In contrast, meroplanktonic preys were rare in the gut contents of the most abundant planktivorous fishes (*Gasterosteus aculeatus* and *Merluccius bilinearis*). The identification of specific predators of larval species and the demonstration of selection for particular prey taxa increases our understanding of the effect of predation on larval benthic invertebrate populations. Additional data on consumption and digestion rates, as well as a spatially (horizontal and vertical) comprehensive sampling coverage can allow the assessment of the overall impact of predation on these populations at the system scale. Predation during the larval dispersal phase can retard larval settlement and recruitment, limit connectivity of benthic metapopulations, and alter species composition during the supply of competent larvae to the benthos.

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## REFERENCES

- Bailey K.M. (1984) Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. *Marine Biology* 79, 303–309.
- Bailey K.M. and Batty R.S. (1984) Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. *Marine Biology* 83, 287–291.
- Behrends G. and Schneider G. (1995) Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Marine Ecology Progress Series* 127, 39–45.
- Carr E.F. and Pitt K.A. (2008) Behavioural responses of zooplankton to the presence of predatory jellyfish. *Journal of Experimental Marine Biology and Ecology* 354, 101–110.
- Chesson J. (1978) Measuring preference in selective predation. *Ecology* 59, 211–215.
- Cohen J.H. and Forward R.B. (2003) Ctenophore kairomones and modified aminosugar disaccharides alter the shadow response in a larval crab. *Journal of Plankton Research* 25, 203–213.
- Cowden C., Young C.M. and Chia F.S. (1984) Differential predation on marine invertebrate larvae by two benthic predators. *Marine Ecology Progress Series* 14, 145–149.
- Eckman J.E. (1996) Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *Journal of Experimental Marine Biology and Ecology* 200, 207–237.
- Elliot J.K. and Leggett W.C. (1996) The effect of temperature on predation rates of a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 53, 1393–1402.
- Fancett M.S. (1988) Diet and prey selectivity of scyphomedusae from Port Phillip Bay, Australia. *Marine Biology* 98, 503–509.
- Forward R.B. and Rittschof D. (2000) Alteration of photoresponses involved in diel vertical migration of a crab larva by fish mucus and degradation products of mucopolysaccharides. *Journal of Experimental Marine Biology and Ecology* 238, 271–281.
- Fraser J.H. (1969) Experimental feeding of some medusae and Chaetognatha. *Journal of the Fisheries Research Board of Canada* 26, 1743–1762.
- Hansson L.J. (2006) A method for *in situ* estimation of prey selectivity and predation rate in large plankton, exemplified with the jellyfish *Aurelia aurita* (L.). *Journal of Experimental Marine Biology and Ecology* 328, 113–126.
- Hargrave B.T., Harding G.C., Drinkwater K.F., Lambert T.C. and Harrison W.G. (1985) Dynamics of the pelagic food web in St George's Bay, southern Gulf of St Lawrence. *Marine Ecology Progress Series* 20, 221–240.
- Hrbacek J. (1989) The monitoring of the influence of fish management on the plankton association of reservoirs. In Talling J.F., Brandl Z. and Straskrabova V. (eds) *Proceedings of the International conference on reservoir limnology and water quality. 2. Chemical limnology, primary production, plankton, benthos and fish interactions*. Stuttgart, Germany.
- Huntley M.E. and Hobson L.A. (1978) Medusa predation and plankton dynamics in a temperate fjord, British Columbia. *Journal of the Fisheries Research Board of Canada* 35, 257–261.
- Johnson K.B. and Brink L.A. (1998) Predation on bivalve veligers by polychaete larvae. *Ecology and Evolution* 194, 297–303.
- Johnson K.B. and Shanks A.L. (1997) The importance of prey densities and background plankton in studies of predation on invertebrate larvae. *Marine Ecology Progress Series* 158, 293–296.
- Johnson K.B. and Shanks A.L. (2003) Low rates of predation on planktonic marine invertebrate larvae. *Marine Ecology Progress Series* 248, 125–139.
- Jones G.P., Russ G.R., Sale P.F. and Steneck R.S. (2008) Theme section on 'Larval connectivity, resilience and the future of coral reefs'. *Coral Reefs* 28, 303–305.
- Larson R.J. (1987) Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. *Journal of Sea Research* 21, 35–44.
- Martinussen M.B. and Bamstedt U. (1999) Nutritional ecology of gelatinous planktonic predators. Digestion rate in relation to type and amount of prey. *Journal of Experimental Marine Biology and Ecology* 232, 61–84.
- Matsakis S. and Conover R.J. (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in



- Bedford Basin (Nova Scotia, Canada) during spring. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 1419–1430.
- Mills E.L. and Forney J.L.** (1983) *Impact on Daphnia pulex of predation by young yellow perch on Oneida Lake, New York*. PhD thesis. University of Rostock, Rostock, Germany.
- Morgan S.G.** (1992) Predation by planktonic and benthic invertebrates on larvae of estuarine crabs. *Journal of Experimental Marine Biology and Ecology* 163, 91–110.
- Morgan S.G.** (1995) Life and death in the plankton: larval mortality and adaptation. In McEdward L.R. (ed.) *Ecology of marine invertebrate larvae*. Boca Raton, FL: CRC Press, pp. 279–321.
- Pechenik J.A., Blanchard M. and Rotjan R.** (2004) Susceptibility of larval *Crepidula fornicata* to predation by suspension feeding adults. *Journal of Experimental Marine Biology and Ecology* 306, 75–94.
- Pechenik J.A. and Levine S.H.** (2007) Estimates of planktonic larval mortality using the marine gastropods *Crepidula fornicata* and *C. plana*. *Marine Ecology Progress Series* 344, 107–118.
- Petrie B. and Drinkwater K.** (1977) *Physical oceanographic measurements in St George's Bay, Nova Scotia, 1974*. Report Series of the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada.
- Pennington J.T., Rumrill S.S. and Chia F.S.** (1986) Stage-specific predation upon embryos and larvae of the Pacific sand dollar, *Dendraster excentricus*, by 11 species of common zooplankton predators. *Bulletin of Marine Science* 39, 234–240.
- Purcell J.E.** (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. *Marine Ecology Progress Series* 87, 65–76.
- Purcell J.E. and Sturdevant M.V.** (2001) Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Marine Ecology Progress Series* 210, 67–83.
- Riisgard H.U.** (2007) Feeding behaviour of the hydromedusa *Aequorea vitrina*. *Scientia Marina* 71, 395–404.
- Rumrill S.S.** (1990) Natural mortality of invertebrate larvae. *Ophelia* 32, 163–198.
- Suchman C.L. and Sullivan B.K.** (2000) Effects of prey size on vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. *Journal of Plankton Research* 22, 2289–2306.
- Sullivan L.J.** (2010) Gut evacuation of larval *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *Journal of Plankton Research* 32, 69–74.
- Thiel R.** (1996) The impact of fish predation on the zooplankton community in a southern Baltic bay. *Limnologica* 26, 123–137.
- Thorson G.** (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25, 1–45.
- Vijverberg J., Boersma M., Densen W.L.T., Van Hoogenboezem W., Lammens E.H.R.R. and Mooij W.M.** (1990) Seasonal variation in the interactions between piscivorous fish, planktivorous fish and zooplankton in a shallow eutrophic lake. *Hydrobiologia* 200/201, 279–286.
- Vuorinen I.** (1986) Selective planktivory—effect on vertical migration and life-cycle parameters of zooplankton. *Finnish Marine Research* 253, 3–33.
- and
- Young C.M. and Chia F.S.** (1987) Abundance and distribution of pelagic larvae as influenced by predation, behavior and hydrographic factors. In Giese A.C., Pearse J.S. and Pearse V.B. (eds) *Reproduction of marine invertebrates. Volume 9. Seeking unity in diversity*. Palo Alto, CA: Blackwell/Boxwood Press, pp. 385–463.

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