

Effects of intra- and inter-annual variability in prey field on the feeding selectivity of larval Atlantic mackerel (*Scomber scombrus*)

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We identified to the lowest taxonomical level possible the preferred prey of Atlantic mackerel larvae from the southern Gulf of St Lawrence and assessed the extent to which prey selectivity varied within and among years. Mackerel larvae and their zooplankton prey were sampled in the summer of four consecutive years (1997–2000). The nauplii of the calanoid copepod Pseudocalanus sp. strongly dominated the diet of larvae <7 mm both in terms of numbers and carbon content, whereas larvae ≥7 mm mainly fed on fish larvae (including conspecifics) and cladocerans. Chesson's alpha index revealed strong selectivity in all years for Pseudocalanus sp. nauplii in first-feeding larvae. Selectivity shifted to cladocerans and fish larvae around a body length of 7 mm. Intra- and inter-annual prey selectivity changes were mainly observed for alternative prey, during the period surrounding the shift in diet from small to large prey. Our results underscore the importance of considering the availability of the main prey Pseudocalanus sp. nauplii (early larval stage) as well as cladocerans and fish larvae (late larval stage), rather than the entire prey field in the future assessment of the role played by prey availability on larval mackerel vital rates.

INTRODUCTION

The availability of adequate prey during the larval stage of marine fish has been considered a prerequisite for the emergence of a strong year class for about a century (Hjort, 1914; Lasker, 1975; Anderson, 1988; Cushing, 1990). In addition to increasing the probability of mortality by starvation (Platt *et al.*, 2003), low prey supply would hamper growth and intensify mortality due to predation, as slow-growing larvae remain exposed to their predators for a longer period (Chambers and Leggett, 1987) and show poor escape potential when attacked (Takasuka *et al.*, 2003). A more thorough understanding of the relationships linking fish larvae to their foraging environment could therefore provide

insight into the unresolved fraction of inter-annual variability in recruitment (Bartsch and Coombs, 2004).

Numerous field studies have described larval fish gut content to document the main prey and relate vital rates and subsequent recruitment to food availability (Last, 1980; Economou, 1991; Sampey *et al.*, 2007). Although a link between feeding performance and prey density was reported in several studies (Ellertsen *et al.*, 1989; Fortier *et al.*, 1996; Dower *et al.*, 2002), field evidence of a relationship between prey abundance and larval fish growth (Buckley and Durbin, 2006; Takasuka and Aoki, 2006) or survival (Zenitani *et al.*, 2007) has remained elusive. This apparent absence of causality

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may be attributable to the generally insufficient precision in the assessment of larval prey field and diet. For instance, several studies focused exclusively on gut content, independent of prey availability (Last, 1980; Cohen and Lough, 1983; Takatsu *et al.*, 2002). Such a description of diet may provide information on the common prey for a given larval fish population, but the respective importance attributed to these potential prey taxa is likely to be biased by their relative abundance during sampling. A rigorous identification of the most valuable prey in terms of energy gains and growth potential requires consideration of prey availability, essential for the assessment of prey selectivity.

An additional source of imprecision is the often low taxonomical resolution achieved in the identification of digested prey in prey selectivity studies. Based on many studies in which the genus or species of prey is not resolved (Kane, 1984; Young and Davis, 1992; Voss *et al.*, 2003), one could conclude that first-feeding larvae indiscriminately prey on copepod nauplii and that overall copepod nauplii abundance is a fair index of food availability. However, the few studies based on high taxonomical resolution systematically found that larvae selected for particular species of nauplii among the assemblage available (Peterson and Ausubel, 1984; Monteleone and Peterson, 1986; Hillgruber *et al.*, 1995; Dickmann *et al.*, 2007). This highlights the importance of assessing the diet and prey selectivity at the lowest taxonomical level possible to adequately identify key prey species. Finally, another concern is that most studies on feeding selectivity are restricted to short time periods. Seasonal or inter-annual variability in prey selectivity has received little attention, although this information is essential to insure an accurate description of diet (Economou, 1991; Anderson, 1994; Dickmann *et al.*, 2007).

In the present study, we describe the diet of Atlantic mackerel larvae captured during four consecutive years (1997–2000) on the Magdalen Shallows, Eastern Canada. In particular, we assess the extent to which prey selectivity varied within a given year and among years. Our objective was to provide the basis for future investigation of trophic regulation of growth and survival in larval mackerel from the southern Gulf of St Lawrence. Robert *et al.* (Robert *et al.*, 2007) showed that the strength of initial growth varied among years during the period 1997–2000 and concluded that fast larval growth is a prerequisite for the production of a strong year class. The present study constitutes a necessary first step in the examination of the role played by prey availability on the inter-annual variability in larval growth and recruitment found in Atlantic mackerel.

METHOD

Study area

The Gulf of St Lawrence is an enclosed sea connecting the St Lawrence River to the Atlantic Ocean by the Belle-Isle and Cabot straits (Fig. 1a). Within the southern part of the Gulf, the Magdalen Shallows represent a 50 000 km² bank characterized by relatively high zooplankton productivity (de Lafontaine *et al.*, 1991). The zooplankton assemblage is dominated by medium-sized copepods such as *Oithona similis*, *Pseudocalanus* spp. and *Temora longicornis*. Atlantic mackerel and several other commercially important fish species such as Atlantic cod (*Gadus morhua*), American plaice (*Hippoglossoides platessoides*), yellowtail flounder (*Limanda ferruginea*) and capelin (*Mallotus villosus*) spawn on the Magdalen Shallows.

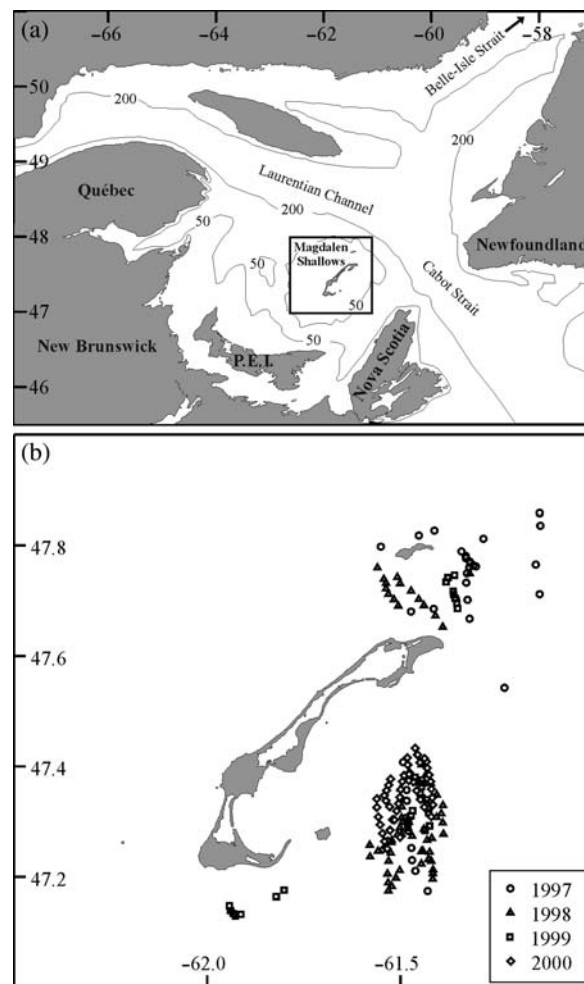


Fig. 1. (a) Gulf of St Lawrence with isobaths in metre; (b) stations where Atlantic mackerel larvae were sampled from 1997 to 2000.

Sampling of mackerel larvae and their zooplanktonic prey

Mackerel larvae were captured in July and August of four consecutive years (1997–2000) within 1-day surveys conducted on a weekly basis in the south-eastern and north-eastern areas of the Magdalen Islands (Fig. 1b). Larval sampling details are given in Robert *et al.* (Robert *et al.*, 2007). Briefly, the sampling gear consisted of a rectangular frame carrying two 750 μm mesh nets of 1 m² mouth aperture to capture fish larvae, and two 64 μm mesh nets of 81 cm² mouth aperture to capture their zooplankton prey (Drolet *et al.*, 1991). The volume of water filtered was measured by two General Oceanic® flowmeters. During each survey, from 8 to 12 double-oblique tows of ~20 min duration were completed between 16:00 and 24:00 h to cover the peak feeding period (Grave, 1981). Mackerel larvae were immersed in a tricaine methane sulphonate

(MS-222) solution to avoid gut evacuation and preserved in 95% ethyl alcohol immediately after capture. Zooplankton samples from the 64 μm mesh nets were preserved in a 4% formaldehyde solution. Gut content analysis was performed on a stratified subsample of mackerel larvae randomly selected from predetermined length classes in each year.

The digestive tract of mackerel larvae was examined under a stereoscopic microscope at $\times 70$ magnification. Each prey found in the stomach was measured (prosome length and width for copepods and cladocerans) and identified to the lowest taxonomic level possible. Digested copepods that could not be identified (about 12% of all prey) were assigned to species in proportion to the relative abundance of identified copepods in the diet of a given larval length class. The carbon content of each prey was estimated from specific length–weight regressions and carbon–weight ratios (Table I).

Table I: Summary of references on relationships between carbon content (C , in μg), prosome or total length (L , in μm), volume (V , in μL), ash-free dry weight (ADW in μg) and dry weight (DW, in μg) for the main prey of larval mackerel

Taxon		Equation	Reference
Copepods			
Eggs	V	$4/3\pi (L/2)^3$	
	C	$140V$	Kjørboe <i>et al.</i> (1985)
Nauplii			
<i>Pseudocalanus</i> spp.	ADW	$10^{2.2692\log L - 5.57}$	Klein Breteler <i>et al.</i> (1982)
	DW	$\text{ADW} + 7\%$	Båmstedt (1986)
	C	$44.7\% \text{ DW}$	Mauchline (1998)
Cyclopoid	DW	$2.5968 \times L^{1.6349}$	Culver <i>et al.</i> (1985)
	C	$44.7\% \text{ DW}$	Mauchline (1998)
<i>T. longicornis</i>	ADW	$10^{2.1674 \log L - 5.5336}$	Klein Breteler <i>et al.</i> (1982)
	DW	$\text{ADW} + 7\%$	Båmstedt (1986)
	C	$44.7\% \text{ DW}$	Mauchline (1998)
<i>C. finmarchicus</i>	C	$4.29 \times 10^{-6} \times L^{2.05}$	Hygum <i>et al.</i> (2000)
Copepodites			
<i>Pseudocalanus</i>	C	$10^{3.64\log L - 10.155}$	McLaren (1969)
<i>O. similis</i>	C	$9.4676 \times 10^{-7} L^{2.16}$	Sabatini and Kjørboe (1994)
<i>T. longicornis</i>	DW	$10^{2.815\log L - 7.181}$	Hay <i>et al.</i> (1988)
	C	$44.7\% \text{ DW}$	Mauchline (1998)
<i>C. finmarchicus</i>	DW	$10^{3.46\log L - 9.553}$	Hay <i>et al.</i> (1991)
	C	$44.7\% \text{ DW}$	Mauchline (1998)
<i>Centropages</i> spp.	ADW	$10^{2.449\log L - 6.098}$	Klein Breteler <i>et al.</i> (1982)
	DW	$\text{ADW} + 7\%$	Båmstedt (1986)
	C	$44.7\% \text{ DW}$	Mauchline (1998)
<i>Microcalanus</i> spp.	C	$10^{3.07\log L - 8.37}$	Uye (1982)
<i>Microsetella</i> spp.	C	$e^{1.15\ln L - 7.79}$	Satapoomin (1999)
<i>Oncaea</i> spp.	C	$e^{2.90\ln L - 17.5}$	Satapoomin (1999)
Cladocerans	C	$10^{4.15\log L - 11.15}$	Uye (1982)
Gastropods	DW	$6.07 (L \times 10^{-6})^{2.59} \times 10^8$	Legendre and Michaud (1998)
	C	$22.1\% \text{ DW}$	Omori (1969)
Bivalve larvae	DW	$2.53 \times 10^{-9} L^{3.49}$	Jespersen and Olsen (1982)
	C	$22.1\% \text{ DW}$	Omori (1969)
Fish larvae	DW	$10^{4.09\log(L/1000) - 1.114}$	Laurence (1979)
	C	$40\% \text{ DW}$	Legendre and Michaud (1998)
Fish eggs	DW	$0.043 \times L^{2.941}$	Hislop and Bell (1987)
	C	$40\% \text{ DW}$	Legendre and Michaud (1998)

To assess prey selectivity, zooplankton was identified to species and developmental stage (whenever possible) in the 64 μm mesh net sample from each net tow where mackerel larvae were analysed. Successive known aliquots were taken with a Stempel pipette and all zooplankton organisms were identified at $\times 70$ until about 300 organisms were enumerated. Large copepods such as the late copepodite and adult stages of *Calanus finmarchicus*, as well as fish larvae, were enumerated from the 750 μm mesh net collections due to under-sampling by the 64 μm mesh nets (McLaren and Avendaño, 1995).

Data analysis

The selectivity of mackerel larvae for prey j was quantified using Chesson's (Chesson, 1978) α -electivity index (Anderson, 1994; Michaud *et al.*, 1996):

$$\alpha_j = \frac{d_j/p_j}{\sum (d_i/p_i)}, \text{ for } i = 1, \dots, N \quad (1)$$

where N is the number of prey taxa considered, (d_j/p_j) the relative frequency ratio of prey j in the diet and in the plankton and $\sum (d_i/p_i)$ the sum of this ratio for all prey taxa. Only prey taxa that contributed $>2\%$ of total carbon ingested were considered in the calculation of α (Govoni *et al.*, 1986). The index was computed independently for each individual larva and then averaged over length intervals. Inter-annual variability in prey selectivity was assessed by comparing the average α for each prey in a given predator length interval among the 4 years. We tested that positive values of α_j differed significantly from the neutral selectivity threshold $1/N$ through MANOVA analyses using procedure MIXED in SAS® and the REPEATED statement to account for the auto-correlation existing between α indices computed for the different prey. The indices were log-transformed to achieve normality and homoscedasticity of the residuals. Seasonal variability in the feeding behaviour of mackerel larvae was assessed by comparing the selectivity for the main prey of a given length category during the different surveys of the same year. Within-year investigations remained qualitative due to the low number of larvae from a given length class analysed in each sampling day.

RESULTS

Hatching season of Atlantic mackerel larvae

Newly hatched mackerel larvae (3 to <5 mm) were sampled over a period restricted to a maximum of 5 weeks ranging from the beginning of July to mid-August

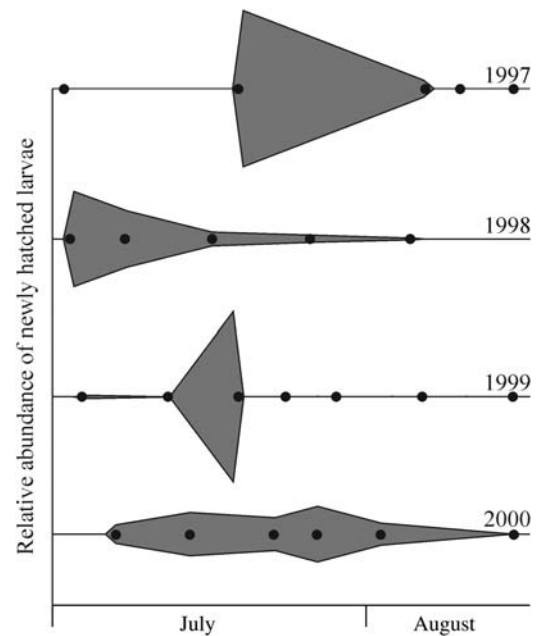


Fig. 2. Relative abundance (numbers per survey) of newly hatched (<5 mm) Atlantic mackerel larvae captured throughout the sampling season in each year. Black circles represent the days of sampling.

(Fig. 2). Recently hatched individuals appeared at the same time period in the years 1998–2000. However, their occurrence was very punctual in 1999 (less than 3 weeks) compared with 1998 and 2000 (~ 5 weeks). Mackerel larvae emerged only from late July in 1997, but over a short time interval of 3 weeks.

Diet composition

Pseudocalanus sp. nauplii were the main prey of Atlantic mackerel larvae 3 to <7 mm in all years, contributing between 36 and 75% to the diet by numbers (Table II) and 27–81% in terms of carbon (Table III). The only exception to this pattern occurred for larvae 5 to <7 mm in 1999, where larval fish strongly dominated the carbon content (65%). Cyclopoid and *Temora* sp. nauplii completed the diet of young larvae by numbers, but only represented a small fraction of the total carbon ingested. Copepodites of *T. longicornis* contributed a significant fraction of the gut content of larvae 3 to <7 mm in 1997 and 1999.

Except in 2000 when *Pseudocalanus* sp. nauplii remained the dominant prey in terms of number and carbon, the diet shifted from copepod nauplii to larger prey such as copepodites, cladocerans and fish larvae, when mackerel larvae reached 7 mm (Tables II and III). Larvae >9 mm ingested large numbers of cladocerans, which represented more than 58% of the total number of prey in all years.

Table II: Diet composition by length classes and year of Atlantic mackerel larvae expressed as the percent contribution in numbers of the different prey taxa

Prey taxon	Length class (mm)															
	3 to <5				5 to <7				7 to <9				≥9			
	1997	1998	1999	2000	1997	1998	1999	2000	1997	1998	1999	2000	1997	1998	1999	2000
Copepods																
Eggs	6.1	1.5	0.4	—	0.5	0.2	—	0.5	1.6	0.7	0.6	0.5	9.6	2.2	0.8	1.6
Nauplii																
<i>Pseudocalanus</i> spp.	35.7	66.8	74.9	62.2	69.4	73.8	54.3	64.5	31.4	36.1	31.8	64.2	1.8	7.9	18.0	10.5
Cyclopoids	—	23.3	10.3	15.4	0.5	16.2	4.6	6.1	0.5	29.0	2.0	8.3	8.2	4.7	2.4	3.2
<i>T. longicornis</i>	12.2	4.0	7.2	16.7	17.6	4.2	6.1	12.7	3.1	2.9	22.6	5.8	0.1	2.0	6.9	—
<i>C. finmarchicus</i>	8.2	—	1.5	1.9	0.9	0.1	—	5.2	5.2	0.2	—	7.2	—	—	0.5	1.1
Copepodites																
<i>Pseudocalanus</i> spp.	6.1	2.0	1.1	0.6	1.4	0.8	1.0	0.9	17.0	3.5	4.9	—	7.8	14.3	2.4	3.0
<i>O. similis</i>	5.1	—	—	1.9	—	0.6	—	5.2	1.6	4.4	3.7	2.3	1.3	4.2	1.7	0.5
<i>T. longicornis</i>	10.2	0.5	3.0	—	6.9	0.8	21.8	1.7	8.3	1.0	7.7	0.5	0.9	0.1	1.9	0.2
<i>C. finmarchicus</i>	—	—	—	—	—	—	—	—	—	—	0.3	—	0.1	0.4	0.2	—
<i>Centropages</i> spp.	—	—	—	—	—	—	—	—	—	0.1	—	—	2.0	1.8	—	0.2
<i>Microcalanus</i> spp.	—	—	—	—	0.9	0.2	—	—	1.0	0.1	—	—	—	0.4	0.2	0.2
<i>Microsetella</i> spp.	9.2	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oncaea borealis</i>	—	—	—	—	—	—	0.5	—	—	—	—	—	—	—	0.3	—
Cladocerans	—	—	—	—	0.5	1.3	1.0	1.8	26.3	19.7	20.6	6.7	72.7	58.2	58.5	76.8
Gastropods	1.0	—	—	—	0.5	—	—	—	—	—	—	0.2	—	—	—	—
Bivalve larvae	6.1	—	—	—	0.9	—	—	0.2	—	—	0.2	0.5	0.4	—	0.2	—
Fish larvae	—	0.5	1.1	—	—	0.4	10.2	0.6	3.1	1.7	4.7	2.5	1.3	2.7	5.8	2.7
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—	1.5	1.0	0.2	—
Number of larvae analysed	25	22	42	22	29	30	41	68	20	40	47	33	25	52	40	20
Mean number of prey	4.0	9.2	6.3	7.1	7.5	28.4	4.8	9.6	9.7	23.3	13.9	13.1	40.2	19.0	14.9	22.0

Despite a low occurrence in number, fish larvae represented a large fraction (on average 42%) of the carbon content in larvae >7 mm. All fish larvae that could be identified to species (12%) were Atlantic mackerel, suggesting high rates of intra-cohort cannibalism.

The largest prey ingested by young mackerel larvae among the copepod nauplii assemblage were produced by *Calanus* sp. (Table IV). Among smaller nauplii, the main prey *Pseudocalanus* sp. accounted for about two and three times the carbon content of *Temora* sp. and cyclopoid nauplii, respectively. During the late larval stage, main cladoceran and larval fish prey both represented a much larger carbon content than copepod nauplii (more than 5 times and more than 20 times, respectively) (Table IV). The size of these large prey tended to increase with the larval mackerel body size. Fish larvae were by far the largest prey consumed by mackerel larvae as the carbon intake from a large individual (~6 mm) was equivalent to that of about 50 cladocerans or medium-sized copepodites.

Prey field of mackerel larvae

The naupliar and copepodite stages of the medium-sized copepods *O. similis*, *Pseudocalanus* spp. (mainly *P. elongatus*) and *T. longicornis* formed the largest part of the zooplankton assemblage on the Magdalen Shallows during the larval development season of Atlantic mackerel (Fig. 3). In all years, cyclopoid nauplii and copepodites (mainly *O. similis*) were the numerically dominant potential prey, reaching particularly high density in mid-July 1998 and in late August 1999. The most abundant calanoid copepod was *Pseudocalanus* sp., with peak abundance in July except in 2000. *Temora longicornis* availability was highly variable within and among years. For instance, *Temora* sp. nauplii were practically absent in 1997, but represented about 25% of the nauplii assemblage in early July 1998, before disappearing from the plankton in August. The abundance of the large calanoid copepod *C. finmarchicus* was low in all years. Non-copepod potential prey of mackerel larvae included bivalve larvae, cladocerans (*Evadne* sp. and

Table III: Diet composition by length classes and year of Atlantic mackerel larvae expressed as the percent contribution in carbon of the different prey taxa

Prey taxon	Length class (mm)															
	3 to <5				5 to <7				7 to <9				≥9			
	1997	1998	1999	2000	1997	1998	1999	2000	1997	1998	1999	2000	1997	1998	1999	2000
Copepods																
Eggs	5.4	1.7	0.3	—	0.9	—	—	0.8	0.3	0.2	0.1	0.3	0.6	0.4	2.0	0.1
Nauplii																
<i>Pseudocalanus</i> spp.	26.8	70.5	63.5	80.6	63.2	68.6	15.0	56.7	5.9	10.5	12.2	34.1	0.1	0.5	1.7	1.9
Cyclopoids	—	8.0	2.8	5.6	0.1	5.0	0.4	1.5	—	3.0	0.2	1.5	—	0.1	0.1	0.1
<i>T. longicornis</i>	3.9	5.7	1.4	6.4	9.5	1.5	0.9	4.4	0.2	0.4	3.5	1.4	—	0.1	0.3	—
<i>C. finmarchicus</i>	14.8	—	1.5	5.0	1.3	0.4	—	11.8	1.5	0.2	—	8.1	—	—	0.1	0.3
Copepodites																
<i>Pseudocalanus</i> spp.	9.8	4.5	0.2	0.2	0.5	0.2	0.3	0.3	18.0	5.8	2.5	—	3.8	7.4	1.3	3.9
<i>O. similis</i>	7.1	—	—	2.3	—	0.5	—	6.9	0.3	3.0	2.2	2.5	0.1	0.6	0.3	0.2
<i>T. longicornis</i>	23.9	1.5	3.2	—	14.7	5.7	17.1	1.1	2.3	2.2	6.5	0.2	0.3	—	0.5	—
<i>C. finmarchicus</i>	—	—	—	—	—	—	—	—	—	—	4.4	—	0.3	1.3	0.3	—
<i>Centropages</i> spp.	—	—	—	—	—	—	—	—	—	0.7	—	—	2.6	1.4	—	0.4
<i>Microcalanus</i> spp.	—	—	—	—	0.3	0.7	—	—	0.2	—	—	—	—	0.1	0.1	0.2
<i>Microsetella</i> spp.	1.93	1.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Oncaea borealis</i>	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	0.1	—
Cladocerans	—	—	—	—	7.4	9.2	4.4	4.4	23.7	33.2	30.7	19.7	43.7	29.2	38.6	81.0
Gastropods	0.2	—	—	—	0.6	—	—	—	—	—	—	—	—	—	—	—
Bivalve larvae	6.2	—	—	—	1.6	—	—	—	—	—	—	0.1	—	—	—	—
Fish larvae	—	9.7	25.8	—	—	9.1	65.1	12.0	47.4	40.8	37.8	32.2	46.0	41.3	54.2	11.8
Fish eggs	—	—	—	—	—	—	—	—	—	—	—	—	2.6	17.6	0.5	—
Number of larvae analysed	25	22	42	22	29	30	41	68	20	40	47	33	25	52	40	20
Mean carbon ingested (μg)	1.2	1.4	1.4	1.3	1.9	5.7	4.0	2.5	14.2	15.3	10.0	5.6	172.4	62.6	36.8	31.3

Table IV: Average length (mm) and carbon content (μg) ± standard deviation of the main prey found in the stomachs of Atlantic mackerel larvae by length classes

Prey taxon	Length class (mm)							
	3 to <5		5 to <7		7 to <9		≥9	
	Length	Carbon	Length	Carbon	Length	Carbon	Length	Carbon
Cyclopoid N	0.16 ± 0.02	0.06 ± 0.01	0.17 ± 0.02	0.06 ± 0.01	0.17 ± 0.02	0.07 ± 0.01	0.17 ± 0.02	0.06 ± 0.01
<i>Pseudocalanus</i> sp. N	0.19 ± 0.04	0.21 ± 0.13	0.19 ± 0.03	0.21 ± 0.08	0.20 ± 0.03	0.23 ± 0.10	0.21 ± 0.03	0.26 ± 0.01
<i>Temora</i> sp. N	0.15 ± 0.04	0.08 ± 0.05	0.17 ± 0.05	0.11 ± 0.07	0.17 ± 0.04	0.10 ± 0.05	0.17 ± 0.04	0.11 ± 0.05
<i>Calanus</i> sp. N	0.31 ± 0.05	0.58 ± 0.18	0.33 ± 0.03	0.63 ± 0.11	0.29 ± 0.06	0.49 ± 0.18	0.32 ± 0.02	0.60 ± 0.08
<i>O. similis</i> C	0.38 ± 0.08	0.37 ± 0.14	0.38 ± 0.13	0.40 ± 0.25	0.44 ± 0.04	0.50 ± 0.08	0.44 ± 0.06	0.51 ± 0.12
<i>Pseudocalanus</i> sp. C	0.52 ± 0.04	0.54 ± 0.19	0.30 ± 0.02	0.03 ± 0.02	0.60 ± 0.23	1.46 ± 1.29	0.76 ± 0.10	2.35 ± 0.86
<i>Temora</i> sp. C	0.41 ± 0.06	0.68 ± 0.28	0.40 ± 0.12	0.74 ± 0.59	0.39 ± 0.14	0.81 ± 1.10	0.53 ± 0.14	1.63 ± 1.19
<i>Calanus</i> sp. C	—	—	—	—	1.38 ± 0.30	10.17 ± 7.11	1.53 ± 0.08	13.24 ± 2.47
Bivalve larvae	0.31 ± 0.04	0.30 ± 0.12	0.28 ± 0.13	0.29 ± 0.26	0.17 ± 0.09	0.06 ± 0.06	0.27 ± 0.11	0.25 ± 0.19
Cladocerans	—	—	0.42 ± 0.09	0.72 ± 0.58	0.46 ± 0.12	1.13 ± 1.35	0.50 ± 0.14	1.77 ± 2.16
Fish larvae	3.08	3.06	2.50 ± 0.90	5.17 ± 2.02	3.30 ± 1.60	9.44 ± 5.36	5.80 ± 2.84	54.38 ± 53.25

N and C represent the copepod nauplii and copepodites, respectively.

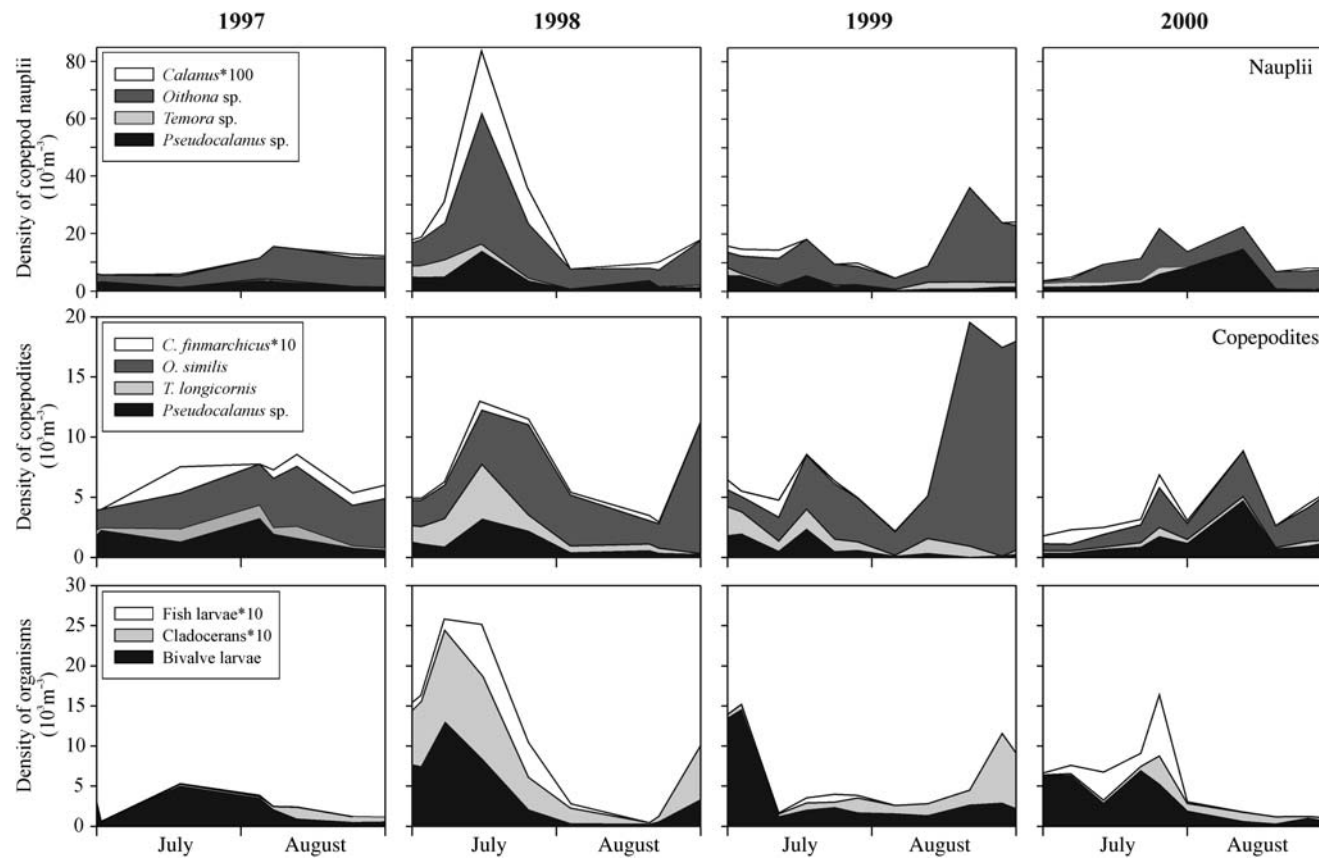


Fig. 3. Seasonal pattern in the availability of the main prey of Atlantic mackerel larvae on the Magdalen Shallows from 1997 to 2000. The abundance of scarce prey taxa was multiplied by 10 or 100 to allow visualization on the same scale.

Podon sp.) and fish larvae <7 mm (Fig. 3). Bivalve larvae represented a considerable part of the zooplankton in July only. The availability of fish larvae <7 mm varied widely from year to year and was generally higher in July than in August. Cladocerans were particularly abundant in 1998, with peak density in July. In other years, the abundance of this group varied little from mid-July to the end of August.

Prey selectivity: among-year variability

Atlantic mackerel larvae strongly selected for the naupliar stages of *Pseudocalanus* sp. from first feeding up to a body length of 7 mm in all years (Fig. 4). Larvae of length 3 to <7 mm also selected for *Temora* sp. nauplii in 1997 and 1999, but average negative or neutral selectivity was observed for this prey in other years. Small larvae usually avoided the most abundant prey taxon in the environment, cyclopoid nauplii, with the exception of neutral selectivity by individuals of length 3 to <5 mm in 2000. Larger prey such as *Calanus* sp. nauplii (except 1997), copepodites of all species, cladocerans and fish larvae were also generally avoided by small larvae. The length class 5 to <7 mm contradicted this general pattern by selecting fish larvae in 1999 and *Calanus* sp. nauplii in 2000.

Changes in selectivity patterns were observed in the 7 to <9 mm larval length class. *Pseudocalanus* sp. nauplii were still selected in some years (1998, 2000), but feeding preference generally shifted towards the larger *Calanus* sp. nauplii (2000), cladocerans (1998) and fish larvae (all years) (Fig. 4). This shift was completed in larvae >9 mm which selected exclusively for cladocerans and fish larvae.

Prey selectivity: within-year variability

Selectivity of mackerel larvae for their main prey remained generally positive in the 3 to <5 mm and 5 to <7 mm length classes (*Pseudocalanus* sp. nauplii), as well as in the >9 mm length class (cladocerans and fish larvae) (Fig. 5). Low α values indicating negative selectivity for the main prey occurred in only two surveys out of the 4 years of sampling in both the 5 to <7 mm and >9 mm length classes. Intra-annual selectivity patterns were more diffuse in larvae 7 to <9 mm for their main cladoceran and larval fish prey as negative or neutral selectivity was frequently recorded albeit a trend for positive selectivity. The α index reached for the alternative *Temora* sp. nauplii prey during the early larval stage (3 to <7 mm) varied widely between surveys in a given year, fluctuating between negative and positive selectivity values.

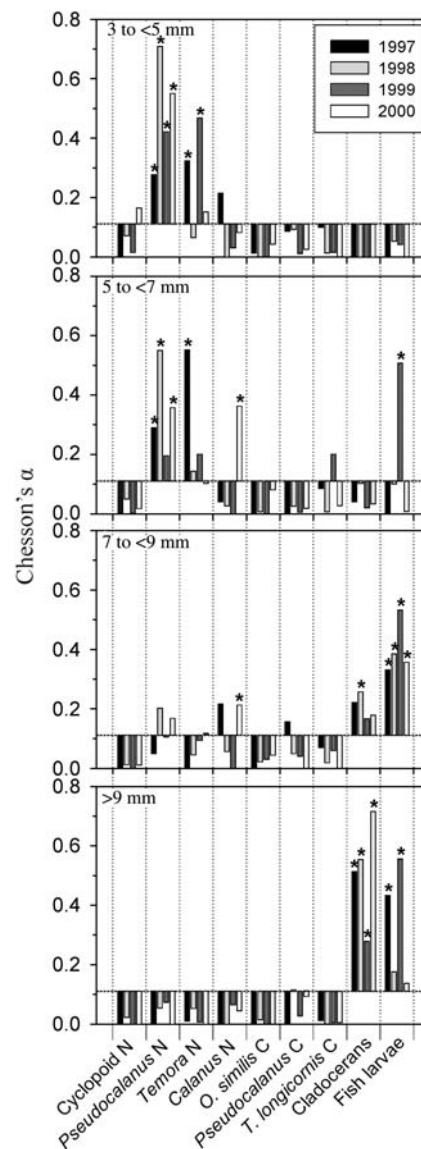


Fig. 4. Inter-annual comparison of prey selectivity (α index; Chesson, 1978) of Atlantic mackerel larvae for their prey for different larval length classes. The dotted line represents the $1/N$ threshold where selectivity is neutral. Selectivity for a given prey taxon is positive when the α value is higher than the threshold and negative when it is lower. N and C indicate nauplii and copepodites, respectively. In contrast, selection for a given prey ($\alpha > 1/N$) is plotted above the $1/N$ axis, whereas avoidance ($\alpha < 1/N$) is plotted below the axis. Asterisk indicates that α is significantly higher ($P = 0.05$) than the $1/N$ threshold.

DISCUSSION

Studies on larval fish trophodynamics have identified selective foraging from the initiation of exogenous feeding in a large number of species (Anderson, 1994; Conway *et al.*, 1998; Voss *et al.*, 2003), including scombrids (Peterson and Ausubel, 1984; Young and Davis,

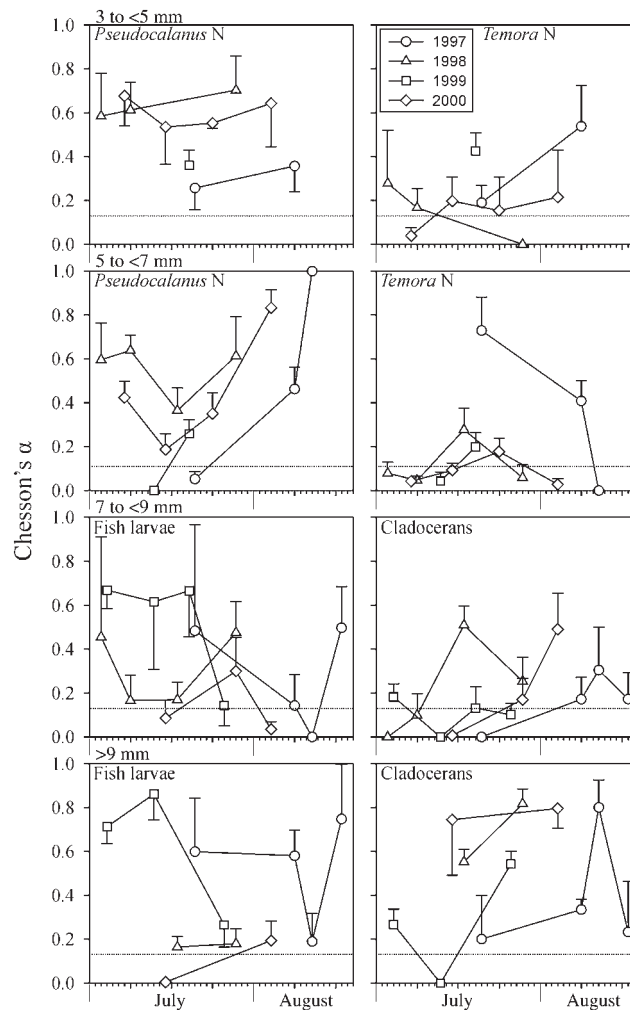


Fig. 5. Intra-annual temporal evolution of prey selectivity (α index; Chesson, 1978) of Atlantic mackerel larvae for their main prey by length classes and year. Mean values \pm SE are shown. The dotted line represents the $1/N$ threshold where selectivity is neutral. Selectivity for a given prey taxon is positive when the α value is higher than the threshold and negative when it is lower. N indicates the nauplius stage for copepods.

1990, 1992). However, although diet and selective feeding behaviour of late larval stages were described with a high taxonomical resolution, few studies have investigated prey selectivity at the species or genus prey level during the first-feeding stage (Table V; Peterson and Ausubel, 1984; Monteleone and Peterson, 1986; Hillgruber *et al.*, 1995; Dickmann *et al.*, 2007). Prior to this study, the prey species composition of first-feeding mackerel from the Northwest Atlantic was examined for larvae captured on a grid covering the whole southern Gulf of St Lawrence (Ringuette *et al.*, 2002) and in Long Island Sound (Peterson and Ausubel, 1984). Ringuette *et al.* (Ringuette *et al.*, 2002) observed that *Pseudocalanus* spp. and *C. finmarchicus* nauplii accounted for the major part of the gut content. However, no conclusion could be drawn regarding prey selectivity as copepod nauplii were not sampled along with mackerel larvae. Larvae

captured in Long Island Sound fed selectively on *T. longicornis* and *Pseudocalanus* sp. nauplii and exhibited negative selectivity against *Acartia hudsonica* (Peterson and Ausubel, 1984). Consistent with these results, *Pseudocalanus* sp. nauplii were strongly selected for by larvae <7 mm on the Magdalen Shallows (Figs 4 and 5) and were the main prey by numbers and carbon content in all years (Tables II and III). The most important alternative prey was *Temora* sp. nauplii, which was selected for on average in most years (Fig. 4). The nauplii of large calanoids (mainly *C. finmarchicus*) or small cyclopoids (mainly *O. similis*) were generally selected against, as they were consumed in disproportionately small numbers compared with their abundance in the environment (Fig. 4). The low incidence in the gut of *Calanus* sp. nauplii observed in this study compared with the average in the entire southern Gulf of

Table V: Summary of the references for larval fish prey selectivity during the first-feeding and late larval stages

Family	Species	Region	Preferred prey		Reference
			First-feeding stage	Late larval stage	
Ammodytidae	<i>Ammodytes americanus</i>	Long Island Sound	<i>T. longicornis</i> N	<i>T. longicornis</i> C	Monteleone and Peterson (1986)
	<i>A. marinus</i>	Northern North Sea	Calanoid N	Calanoid N	Economou (1991)
Callionymidae	<i>Callionymus lyra</i>	Western English Channel	Copepod N	<i>Calanus Helgolandicus</i> C	Fortier and Harris (1989)
	Not defined	Offshore western Australia	—	Cyclopoid C, <i>Euterpina acutifrons</i> C	Sampey <i>et al.</i> (2007)
Carangidae	<i>Trachurus declivis</i>	Tasman Sea	copepod N	<i>Microsatella rosea</i> C	Young and Davis (1992)
Clupeidae	<i>Clupea harengus</i>	Blackwater Estuary	<i>Acartia</i> C	<i>Acartia</i> C	Fox <i>et al.</i> (1999)
		Newfoundland	Calanoid N, cyclopoid N, bivalve larvae		Pepin and Penney (1997)
	<i>Ethmidium maculatum</i>	Central Chile	Copepod E	Copepod E and C	Llanos-Rivera <i>et al.</i> (2004)
	<i>Sardinops sagax</i>	Central Chile	Mollusk larvae	Copepod C	Llanos-Rivera <i>et al.</i> (2004)
	<i>Sprattus sprattus</i>	Baltic Sea	Copepod N	<i>Acartia</i> C	Voss <i>et al.</i> (2003)
		Baltic Sea	<i>Acartia</i> N, <i>Centropages hamatus</i> N, <i>T. longicornis</i> N	<i>Acartia</i> C, <i>Centropages hamatus</i> C	Dickmann <i>et al.</i> (2007)
		Western English Channel	Copepod N	<i>Paracalanus parvus</i> C	Fortier and Harris (1989)
	<i>Strangomera bentincki</i>	Central Chile	Copepod E and N	Copepod E and C	Llanos-Rivera <i>et al.</i> (2004)
Cynoglossidae	<i>Cynoglossus</i> spp.	Offshore western Australia	—	Cyclopoid C	Sampey <i>et al.</i> (2007)
Engraulidae	<i>Engraulis anchoita</i>	Argentine Sea	Small copepod N	—	Viñas and Ramírez (1996)
	<i>E. encrasicolus</i>	Northwest Adriatic Sea	Calanoid and cyclopoid N	—	Conway <i>et al.</i> (1998)
	<i>Engraulis ringens</i>	Central Chile	Copepod E and N	Copepod E and C	Llanos-Rivera <i>et al.</i> (2004)
Gadidae	<i>Boreogadus saida</i>	Northeast Water Polynya	Copepod N	—	Michaud <i>et al.</i> (1996)
	<i>G. morhua</i>	Southerly populations	<i>Pseudocalanus</i> N	<i>Pseudocalanus</i> C, <i>Paracalanus</i> C	Heath and Lough (2007) and references therein
		Northerly populations	<i>Calanus</i> N	<i>C. finmarchicus</i> C	Heath and Lough (2007) and references therein
	<i>Melanogrammus aeglefinus</i>	Northern North Sea	Calanoid N, <i>Calanus</i> eggs	<i>P. elongatus</i> C, <i>T. longicornis</i> C, <i>Evadne</i> sp., Euphausiids	Economou (1991)
		Irish Sea	Copepod N	—	Rowlands <i>et al.</i> (in press)
		Georges Bank	Copepod E, medium-sized calanoid N	<i>P. minutus</i> C	Kane (1984)
	<i>Merlangius merlangus</i>	Northern North Sea	Calanoid N	<i>P. elongatus</i> C, <i>Acartia clausii</i> C, <i>Calanus finmarchicus</i> C	Economou (1991)
		Irish Sea	Copepod N	—	Rowlands <i>et al.</i> (in press)
		Western English Channel	Copepod N	Copepod N, <i>P. elongatus</i> C	Fortier and Harris (1989)
	<i>Pollachius virens</i>	Northern North Sea	Calanoid N	<i>C. finmarchicus</i> C, <i>Acartia clausii</i> C, <i>Oithona</i> C	Economou (1991)

Gobiidae	<i>Theragra chalcogramma</i> <i>Trisopterus esmarkii</i> Not defined	Bering Sea Northern North Sea offshore western Australia	<i>Metridia</i> N, <i>Microcalanus</i> N Calanoid N, <i>Calanus</i> eggs —	— <i>P. elongatus</i> C, <i>C. finmarchicus</i> C <i>Bestiolina similis</i> C, <i>Oithona</i> C	Hillgruber <i>et al.</i> (1995) Economou, 1991 Sampey <i>et al.</i> (2007)
Labridae	<i>Tautoglabrus adspersus</i>	Newfoundland	Calanoid N, cladocerans		Pepin and Penney (1997)
Leiognathidae	Not defined	Offshore western Australia	—	<i>Oithona attenuata</i> C, calanoid N and C	Sampey <i>et al.</i> (2007)
Liparidae	<i>Liparis</i> sp.	Newfoundland	Calanoid N, euphausids		Pepin and Penney (1997)
Monacanthidae	Not defined	Offshore western Australia	—	Polychaetes	Sampey <i>et al.</i> (2007)
Osmeridae	<i>M. villosus</i>	Newfoundland	Cyclopoid N, calanoid C		Pepin and Penney (1997)
Pinguipedidae	Not defined	Offshore western Australia	—	<i>Temora</i> C, <i>B. similis</i> C, cyclopoid C, decapod larvae	Sampey <i>et al.</i> (2007)
Pleuronectidae	<i>Glyptocephalus cynoglossus</i> <i>H. platessoides</i>	Newfoundland Northern North Sea	Calanoid N and C, bivalve larvae, cladocerans Calanoid N	<i>C. finmarchicus</i> C	Pepin and Penney, 1997 Economou (1991)
	<i>Pleuronectes americanus</i>	Newfoundland	Calanoid N and C		Pepin and Penney (1997)
	<i>P. ferrugineus</i>	Newfoundland	Bivalve larvae, cladocerans		Pepin and Penney (1997)
Sciaenidae	<i>Leiostomus xanthurus</i>	Newfoundland	Calanoid N, cladocerans		Pepin and Penney (1997)
		Northern Gulf of Mexico	<i>Oncaea</i> C	<i>Paracalanus</i> C, <i>Oncaea</i> C	Govoni <i>et al.</i> (1986)
	<i>Micropogonias undulates</i>	Northern Gulf of Mexico	<i>Oncaea</i> C, <i>Oithona</i> C, <i>Acartia tonsa</i> C	<i>Paracalanus</i> C	Govoni <i>et al.</i> (1986)
Scophthalmidae	<i>Phrynorhombus norvegicus</i>	Western English Channel	Copepod N	<i>Acartia</i> C, <i>Oithona</i> C	Fortier and Harris (1989)
Scombridae	<i>Katsuwonus pelamis</i> <i>S. scombrus</i>	Eastern Indian Ocean Long Island Sound Magdalen Shallows	Appendicularians <i>T. longicornis</i> N, <i>Pseudocalanus</i> N <i>Pseudocalanus</i> N, <i>Temora</i> N	Appendicularians — Cladocerans, fish larvae	Young and Davis (1990) Peterson and Ausubel (1984) This study
	<i>Scomberomorus</i> spp.	Scotian Shelf Coral Sea	Copepod N Fish larvae	Fish larvae fish larvae	Fortier and Villeneuve, 1996 Jenkins <i>et al.</i> , 1984
	<i>Thunnus alalunga</i>	Eastern Indian Ocean	Copepod N, corycaeid C	Copepod N, corycaeid C	Young and Davis, 1990
	<i>T. maccoyi</i>	Eastern Indian Ocean	Copepod N, corycaeid C	Corycaeid C	Young and Davis, 1990
Sebastidae	<i>Sebastes</i> spp.	Flemish Cap Northern Gulf of St Lawrence	<i>Calanus</i> E and N <i>Calanus</i> E	<i>Calanus</i> E and N, cyclopoid C <i>Calanus</i> E	Anderson, 1994 Runge and de Lafontaine (1996)
Soleidae	<i>Microchirus variegates</i>	Western English Channel	Copepod N	<i>T. longicornis</i> C, <i>Evadne</i> , Polychaete larvae	Fortier and Harris (1989)
Stichaeidae	<i>Stichaeus punctatus</i> <i>Ulvaria subbifurcata</i>	Newfoundland Newfoundland	Calanoid N and C, cyclopoid C, euphausids Calanoid N, cladocerans		Pepin and Penney (1997) Pepin and Penney (1997)

No stage differentiation was made for species described by Pepin and Penney (Pepin and Penney, 1997) as prey selectivity was integrated over entire larval life. E, N and C represent the copepod eggs, nauplii and copepodites, respectively.

St Lawrence (Ringuette *et al.*, 2002) may reflect the lower abundance of this copepod on the Magdalen Shallows than in other areas of the southern Gulf of St. Lawrence (Castonguay *et al.*, 1998). The combined results of these three feeding studies nevertheless indicate that *Pseudocalanus* sp. nauplii stages stand as key prey for sustaining the metabolic demand during and shortly after the initiation of exogenous feeding in larval Atlantic mackerel.

The diet and prey selectivity of marine fish generally exhibit a shift from copepod nauplii during the early larval stage towards copepodites during the mid- and late-larval stage (Anderson, 1994; Pepin and Penney, 1997; Voss *et al.*, 2003). Copepodites of medium-sized calanoid species are the preferred prey in the late larval stage of numerous species (Table V). Scombrid larvae represent a rare exception to this pattern as they display a piscivorous behaviour (including cannibalism) shortly after the first-feeding stage (Jenkins *et al.*, 1984; Young and Davis, 1990; Shoji and Tanaka, 2006). The shift in selection from *Pseudocalanus* spp. and *Temora* sp. nauplii to large cladocerans and fish larvae (including Atlantic mackerel larvae) from ~7 mm in body length is consistent with these and other studies of the late larval mackerel stages (Last, 1980; Grave, 1981; Fortier and Villeneuve, 1996; Hillgruber and Kloppmann, 2001).

Variability in selectivity of fish larvae for the diverse zooplankton organisms is driven by differences in detection and average capture success for potential prey species, which in turn largely depend on prey size, prey visibility and gape aperture of the predator (Hunter, 1980; Buskey *et al.*, 1993). At a given moment during larval life, the preferendum in prey size reflects the optimum of the ratio between energy gain and energy spent for the capture of prey. Below or over this preferred size interval, potential prey are not as valuable in terms of energy balance due to an insufficient gain relative to the basic foraging energy demand (small prey) or to an excessive average attack cost compared with the potential energy benefits (large prey). During the first-feeding stage, larval mackerel selected for the medium-sized *Pseudocalanus* sp. and *Temora* sp. nauplii, and generally against large *Calanus* sp. and small cyclopoid nauplii (Fig. 4). One of the main causes of this selection pattern may be that *Pseudocalanus* sp. and *Temora* sp. nauplii fall in the optimal size interval. Within that size interval, *Pseudocalanus* sp. nauplii could be strongly preferred due to their higher carbon content (Table IV). The coexisting negative selectivity for cyclopoid and *Calanus* sp. nauplii would be attributable to prey size falling under or over the optimal size range. This hypothesis is partly supported in the case of *Calanus* sp. nauplii as the frequency of positive selectivity

increased with larval size (Fig. 4). Characteristics enhancing visual detection of a prey, such as high pigmentation (e.g. red colour in cladocerans) level or active swimming behaviour, are also expected to increase selectivity among organisms of comparable size (Arthur, 1976; Peterson and Ausubel, 1984; Buskey *et al.*, 1993). In addition to their small size, cyclopoid copepods often exhibit a lower level of activity compared with calanoids (Buskey *et al.*, 1993). This factor may also explain in part the selectivity against cyclopoid nauplii observed for first-feeding mackerel larvae in this study and in walleye pollock from the Bering Sea (Hillgruber *et al.*, 1995). The depth-integrated sampling conducted in this study did not allow determining if mackerel larvae were associated to the same degree with all potential prey. Inter-specific differences in vertical distribution, especially at the first-feeding stage when larvae and their prey exhibit low motility, may also account for the differences found in selectivity. Young mackerel larvae, as well as *Temora* sp. and *Calanus* sp. nauplii, are known to be distributed in the surface layer (top 20 m) (Peterson and Ausubel, 1984; Fortier and Villeneuve, 1996; Titelman and Fiksen, 2004). Cyclopoid (*Oithona* sp.) and *Pseudocalanus* sp. nauplii are distributed more evenly within the first 30–40 m of the water column (Peterson and Ausubel, 1984; Titelman and Fiksen, 2004), which may result in a partial spatial mismatch with mackerel larvae. While negative selectivity for cyclopoid nauplii could be overestimated, we conclude that the strong positive selectivity values obtained for *Pseudocalanus* sp. nauplii are conservative.

The larval length class 7 to <9 mm was characterized by a diet and selective behaviour shift from copepod nauplii to cladocerans and fish larvae, indicating a rapid increase in the preferential prey size range. In scombrids, this feeding transition from small to large prey including conspecifics corresponds to the initiation of an accelerated growth phase (Hunter and Kimbrell, 1981; Shoji and Tanaka, 2001; Shoji and Tanaka, 2006). Piscivory would be the main mechanism fuelling these high growth rates as the ingestion of larval fish provides the highest carbon uptake per prey capture among planktonic organisms (Table IV). Foraging on these large organisms is promoted by the early development of specific morphological characteristics such as sharp teeth (Conway *et al.*, 1999) and a functional digestive system (Tanaka *et al.*, 1996; Kaji *et al.*, 2002), and to behavioural foraging traits such as high manoeuvrability and persistence in attack (Hunter, 1980; Peterson and Ausubel, 1984; Shoji and Tanaka, 2001).

The patterns observed in the prey selectivity of Atlantic mackerel larvae remained relatively constant on an inter-annual basis. Main prey *Pseudocalanus* sp. nauplii

for larvae <7 mm, as well as cladocerans and fish larvae for larvae >7 mm, were systematically and highly selected for in all years (Fig. 4). The most remarkable inter-annual differences observed concerned alternative prey such as *Temora* sp. and *Calanus* sp. nauplii during the early larval stage or *Calanus* sp. nauplii in the 7 to <9 mm length class. *Temora* sp. nauplii were selected against by first-feeding larvae in 1998, even though they were more abundant compared with the 3 other years. This could be attributable to the simultaneous peak abundance of the main prey *Pseudocalanus* spp. nauplii recorded during that year (Fig. 3), making it unnecessary for young larvae to forage on alternative prey. Positive selection of *Calanus* sp. nauplii occurred only in 1997 (albeit non-significant) and 2000, the 2 years of lowest *Temora* sp. nauplii and cladoceran abundance. This is a possible indication that larvae need to utilize the relatively large *Calanus* sp. nauplii shortly before or during the shift from a medium-sized nauplii diet towards larger prey if the abundance of usual preferred prey is scarce. Another notable inter-annual difference in prey selectivity was the early selection for fish larvae in 1999 relative to the 3 other years (Fig. 4). Larval fish preyed by 5 to <7 mm mackerel larvae in 1999 were on average smaller (mean length of 2.5 mm) than those captured by 7 to <9 mm larvae in all years (mean length of 3.3 mm) and were not likely to be conspecifics as the hatching size in mackerel is 3 mm. This suggests that, in some years, the spawning of other fish species producing small larvae (e.g. yellowtail flounder) may coincide with the emergence of mackerel larvae and strongly benefit feeding performance during the early larval stage. The co-occurrence of 5 to <7 mm mackerel larvae and suitable larval fish prey in 1999 could explain in part the exceptionally fast growth recorded by Robert *et al.* (Robert *et al.*, 2007) from the early larval stage during that year.

The sign of selectivity displayed by mackerel larvae for their main *Pseudocalanus* sp. nauplii, cladoceran and larval fish prey remained relatively constant within a given year, despite important variations in α values (Fig. 5). An exception to this pattern was found for the length class 7 to <9 mm where, despite an average positive selectivity for the main prey in all annual cohorts (Fig. 4), selectivity varied from negative, neutral and positive throughout the season in all years (Fig. 5). This reflects the feeding behaviour transition period when larvae rapidly switch from a diet based on copepod nauplii to a diet composed of the larger cladocerans and fish larvae. At 9 mm, the transition is completed and mackerel larvae systematically selected for cladocerans and larval fish throughout all years, with

the exception of two surveys (Fig. 5). Within-year sign inversions in selectivity were also detected in young larvae (3 to <7 mm) for their alternative prey *Temora* sp. nauplii. These variations may depend in part on the availability of the main prey *Pseudocalanus* sp. nauplii, inducing (or not) the necessity of exploiting an alternative prey. The high intra-annual variability in the selectivity of certain prey taxa observed in this study could be in part attributable to the small size of samples used for the comparisons. Our results, as well as those of Dickmann *et al.* (Dickmann *et al.*, 2007), however, suggest that studies on food preferences relying on temporally restricted sampling periods could lead to spurious conclusions regarding the relative importance of the different potential prey. This highlights the necessity of examining prey selectivity under the widest temporal interval possible.

The availability of adequate prey is of prime importance during the transition from endogenous to exogenous feeding, when young larvae show low capacity to capture dispersed prey (Hjort, 1914; May, 1974; Platt *et al.*, 2003). In the North Atlantic, among-year variability in the abundance and spawning time of the copepod *C. finmarchicus* has been considered the principal trophic factor of inter-annual variability in larval growth, survival and subsequent recruitment (Runge, 1988; Sundby, 2000). A large part of the physical–biological modelling studies aiming to predict fish recruitment has thus considered this large calanoid copepod as a key prey for young fish larvae (Runge *et al.*, 2004). However, direct evidence that first-feeding larvae select or rely on *C. finmarchicus*, as their main prey is scarce (Table V) and limited to particular species/systems such as redfish *Sebastes* spp. (Anderson, 1994; Runge and de Lafontaine, 1996) or Atlantic cod at the northern edge of its distribution (Heath and Lough, 2007). *Calanus* spp. copepods often dominate zooplankton assemblages in terms of biomass, and constitute ideal prey for juvenile (Sameoto *et al.*, 1994; Islam and Tanaka, 2006) or adult pelagic fish (Darbyson *et al.*, 2003; Prokopchuk and Sentyabov, 2006; Wilson *et al.*, 2006). In larval fish, because maximal preference prey size corresponds to 3–5% of body length (Munk, 1992, 1997; Fiksen and MacKenzie, 2002), the large *Calanus* spp. nauplii could become a profitable prey item starting only in mid-larval life for most species (Kane, 1984; Fortier *et al.*, 1995). This is supported by our results as selectivity for *C. finmarchicus* nauplii was observed primarily during the mid-larval stage (length class 7 to <9 mm), when nauplii measured $\sim 4\%$ of larval mackerel standard length in average (Table IV). Considering that the early larval stage constitutes the most vulnerable period to starvation, life cycle and modelling studies should put

more emphasis on medium-sized calanoid copepods, which often constitute critically important prey for first-feeding larvae.

CONCLUSION

Because fish larvae exhibit selectivity for their prey at the species level right from the critically important first-feeding stage, it is necessary to define the effective prey field with the highest taxonomical resolution possible through all larval life prior to attempting correlations between food availability and vital rates. The rare field observations of prey density effects on larval life dynamics usually concern suboptimal feeding performance of first-feeding larvae under low prey availability (Ellertsen *et al.*, 1989; Young and Davis, 1990; Fortier *et al.*, 1996). A more precise identification of the key prey during the early larval stage would provide a means to detect relationships between prey availability, growth and survival, which remain concealed when data are examined at an insufficient taxonomic level. In Atlantic mackerel from the Magdalen Islands area, the strong prey selection displayed from the first-feeding stage, which remained relatively constant in time and among years, stresses the importance of considering the abundance of the main prey *Pseudocalanus* sp. nauplii (early larval stage), cladocerans and fish larvae (late larval stage), rather than the entire zooplankton or copepod assemblage in the assessment and modelling of the role played by prey availability on vital rates.

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