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

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Received February 13, 2008; accepted in principle February 13, 2008; accepted for publication February 15, 2008; published online February 19, 2008

Corresponding editor: Roger Harris

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, 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...
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 /C24 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 ×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                                                                 |
|---------------------|----------|---------------------------------------------------------------------------|
| Eggs                | V        | 4/3π(2L/2)³                                                               |
| Nauplii             | C        | 140V                                                                      |
| Pseudocalanus spp.  | ADW      | 10².2002log L – 5.57                                                     |
|                     | DW       | ADW + 7%                                                                  |
|                     | C        | 44.7% DW                                                                  |
| Cyclopid            | DW       | 2.5968 × L¹.6340                                                          |
|                     | C        | 44.7% DW                                                                  |
| T. longicornis      | ADW      | 10².1674 log L – 5.5336                                                    |
|                     | DW       | ADW + 7%                                                                  |
| C. finmarchicus     | C        | 4.29 × 10⁻⁸ × L².05                                                      |
| Copepodites         | Pseudocalanus |                                                         |
|                     | C        | 10².64log L – 10.155                                                      |
| O. similis          | C        | 9.4676 × 10⁻⁷ L².16                                                      |
| T. longicornis      | DW       | 10².815log L – 7.181                                                      |
| C. finmarchicus     | C        | 44.7% DW                                                                  |
|                     | DW       | 10².46log L – 9.553                                                       |
| Centropages spp.    | ADW      | 10².44log L – 6.098                                                        |
|                     | DW       | ADW + 7%                                                                  |
|                    | C        | 44.7% DW                                                                  |
| Microcalanus spp.   | C        | 10².57log L – 8.37                                                        |
| Microsetella spp.   | C        | 10⁻ⁱ.156log L – 7.79                                                      |
| Oncaea spp.         | C        | 10⁻².903log L – 17.5                                                     |
| Cladocerans         | C        | 10⁻².15log L – 11.5                                                      |
| Gastropods          | DW       | 6.07 × 10⁻⁶ × 0.579 × 10⁸                                                 |
|                     | C        | 22.1% DW                                                                  |
| Bivalve larvae      | DW       | 2.53 × 10⁻⁹ L².49                                                       |
|                     | C        | 22.1% DW                                                                  |
| Fish larvae         | DW       | 10².57log L – 1.114                                                        |
|                     | C        | 40% DW                                                                    |
| Fish eggs           | DW       | 0.043 × L².341                                                            |
|                     | C        | 40% DW                                                                    |
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 ×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 Avendano, 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):

\[
\alpha_j = \frac{d_j}{p_j} \sum \left( \frac{d_i}{p_i} \right) \quad \text{for } i = 1, \ldots, N
\]

where *N* is the number of prey taxa considered, \( \frac{d_j}{p_j} \) the relative frequency ratio of prey *j* in the diet and in the plankton and \( \sum \left( \frac{d_i}{p_i} \right) \) 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 differed significantly from the neutral selectivity threshold \( \frac{1}{N} \) 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). 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. Copepods 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 copepods, 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.
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 /C24 6 mm/ was equivalent to that of about 50 cladocerans or medium-sized copepods.

### 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 0.7 | 0.6 0.5 | 9.6 2.2 0.8 1.6 |
| *Pseudocalanus* 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 0.2 8.3 | 8.2 4.7 2.4 3.2 |
| *T. longicornis*    | 12.2 4.0 0.9 12.7  | 16.7 4.2 6.1            | 0.5 29.0 0.2 8.3 | 8.2 4.7 2.4 3.2 |
| *C. finmarchicus*   | 8.2                 | 1.5 1.9 0.9              | 0.1 5.2 2.0          | 7.2 2.0 0.5 1.1 |
| *Pseudocalanus* 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 |
| *O. similis*        | 5.1                 | — — 1.9                  | 0.6 5.2 1.6 4.4 | 3.7 2.3 1.3 4.2 1.7 0.5 |
| *T. longicornis*    | 10.2 0.5 3.0 1.7   | 6.9 0.8 21.8             | 8.3 1.0 7.7 0.5 | 0.9 0.1 1.9 0.2 |
| *C. finmarchicus*   | —                   | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| Centropages spp.    | —                   | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| Microcalanus spp.   | —                   | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| Microsetella spp.   | 9.2 1.0             | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| *Oncaea borealis*  | —                   | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| Cladocerans         | —                   | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| Gastropods          | 1.0                 | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 0.2 |
| Bivalve larvae      | 6.1                 | — — —                   | — — — — — 0.1 | — 2.0 1.8 — 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           | — — — —            | — — — — —              | — — — — — 0.1 | — 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 |

### 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 (*Euvadne* 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 | 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    | 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 |
| Pseudocalanus spp. |         |         |         |     |      |      |      |     |      |      |      |     |      |      |      |     |
| 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  | —   |
| T. longicornis | 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  | —   |
| Pseudocalanus copepodites |         |         |         |     |      |      |      |     |      |      |      |     |      |      |      |     |
| Pseudocalanus 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 |
| O. similis | 7.1     | —       | —       | 2.3 | —     | 0.5   | —    | 6.9 | 0.3  | 3.0  | 2.2  | 2.5 | 0.1  | 0.6  | 0.3  | 0.2 |
| C. finmarchicus | —      | —       | —       | —   | —     | —     | —    | —  | 2.3  | 2.2  | 6.5  | 0.2 | 0.3  | —    | 0.5  | —   |
| Centropages | —      | —       | —       | —   | —     | —     | —    | —  | 4.4  | —    | —    | —   | 0.3  | 1.3  | 0.3  | —   |
| Microcalanus spp. | —     | —       | —       | —   | 0.3   | 0.7   | —    | 0.2 | —    | —    | —    | —   | 0.1  | 0.1  | 0.2  | —   |
| Microsetella spp. | 1.93   | 1.6     | —       | —   | —     | —     | —    | —  | —    | —    | —    | —   | —    | —    | —    | —   |
| Onclea borealis | —     | —       | —       | —   | 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     | —       | —   | 0.2   | 1.6   | —    | —  | —    | —    | —    | —   | 0.1  | —    | —    | —   |
| Bivalve larvae | 6.2    | —       | —       | 1.8 | —     | —     | —    | —  | —    | —    | —    | —   | 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 | —       | —       | —       | —   | —     | —     | —    | —  | —    | —    | —    | —   | —    | —    | —    | —   |
| 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         | 3 to <5 | 5 to <7 | 7 to <9 | ≥9 |
|--------------------|---------|---------|---------|----|
|                   | Length  | Carbon  | Length  | Carbon  | Length  | Carbon  | Length  | Carbon  |
| Cyclopod 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 ± 01 |
| Pseudocalanus 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 |
| Temora sp. N      | 0.15 ± 0.04 | 0.08 ± 0.05 | 0.17 ± 0.06 | 0.11 ± 0.07 | 0.17 ± 0.04 | 0.10 ± 0.05 | 0.17 ± 0.04 | 0.11 ± 0.05 |
| Calanus sp. N     | 0.31 ± 0.05 | 0.59 ± 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 |
| O. similis 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 |
| Pseudocalanus 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 |
| Temora 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 |
| Calanus sp. C     | —        | —       | —        | —       | 0.13 ± 0.02 | 0.17 ± 0.09 | 0.06 ± 0.06 | 0.27 ± 0.11 |
| 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 |
| 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.

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, 1998; Voss et al., 2003), including scombrids (Peterson and Ausubel, 1984; Young and Davis,
(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                                      |
|-------------|----------------------|-------------------------------|--------------------------------------------------------------------------------|------------------------------------------------|
| Ammodytidae | Ammodytes americanus | Long Island Sound             | *T. longicornis* N                                                             | Monteleone and Peterson (1988)                 |
|             | *A. marinus*         | Northern North Sea            | Calanoid N                                                                     | Economou (1991)                                |
| Callionymidae| Callionymus lyra     | Western English Channel       | Copepod N                                                                      | Fortier and Harris (1989)                      |
|             |                      | Offshore western Australia    | —                                                                              | Sampey et al. (2007)                           |
| Carangidae  | Trachurus declivis   | Tasman Sea                    | copepod N                                                                      | Young and Davis (1992)                         |
| Clupeidae   | Clupea harengus      | Blackwater Estuary            | *Acartia* C                                                                    | Fox et al. (1999)                               |
|             |                      | Newfoundland                  | Calanoid N, cyclopoid N, bivalve larvae                                        | Pepin and Penney (1997)                        |
|             |                      | Central Chile                 | Copepod E                                                                      | Llanos-Rivera et al. (2004)                    |
|             |                      | Baltic Sea                    | Copepod N                                                                      | Llanos-Rivera et al. (2004)                    |
|             |                      | Western English Channel       | *Acartia*, *Centropages hamatus* N, *T. longicornis* N                        | Dickmann et al. (2007)                         |
|             | Strangomera bentincki| Central Chile                 | Copepod N                                                                      | Paracalanus parvus C                           | Fortier and Harris (1989)                      |
|             |                      | Offshore western Australia    | —                                                                              | Sampey et al. (2007)                           |
| Cynoglossida| Cynoglossus spp.     | Argentine Sea                 | Small copepod N                                                               | Viñas and Ramírez (1996)                       |
|             |                      | Northwest Adriatic Sea        | —                                                                              | Conway et al. (1998)                           |
|             |                      | Central Chile                 | Copepod E and N                                                               | Llanos-Rivera et al. (2004)                    |
|             |                      | Northeast Water Polynya       | —                                                                              | Michaud et al. (1996)                          |
|             | *G. mohua*           | Southerly populations         | *Pseudocalanus* N                                                             | Heath and Lough (2007) and references therein  |
|             |                      | Northern populations          | *Calanus* N                                                                    | Heath and Lough (2007) and references therein  |
|             |                      | Calanoid N, Calanus eggs      | *P. elongatus* C, *T. longicornis* C, *E. evadne* sp., *Euphausiidae*         | Economou (1991)                                |
|             |                      | Irish Sea                     | Copepod N                                                                      | Rowlands et al. (in press)                     |
|             |                      | Georges Bank                  | Copepod E, medium-sized Calanoid N                                            | Kane (1984)                                    |
|             | Melanogrammus aeglefinus | Northern North Sea            | *P. elongatus* C, *Acartia clausii* C, *Calanus finmarchicus* C               | Economou (1991)                                |
|             |                      | Calanoid N                    | —                                                                              | Rowlands et al. (in press)                     |
|             |                      | Irish Sea                     | —                                                                              | Fortier and Harris (1989)                      |
|             |                      | Western English Channel       | —                                                                              |                                                 |
|             | Pollachius virens    | Northern North Sea            | Calanoid N                                                                    | Economou (1991)                                |
| Family               | Species                          | Location                           | Stage | Prey Details                                                                 | References |
|---------------------|----------------------------------|------------------------------------|-------|-----------------------------------------------------------------------------|------------|
| Theragra chalcogramma | Bering Sea                        | Metridia N, Microcalanus N         |       | —                                                                           | Hillgruber et al. (1995) |
| Trisopterus esmarkii | Northern North Sea                | Calanoid N, Calanus eggs           |       | —                                                                           | Economou, 1991 |
| Gobidae             | Not defined                       | —                                  |       | —                                                                           | Sampey et al. (2007)    |
| Labridae            | Tautogolabrus adspersus           | Calanoid N, cladocerans            |       | Oithona attenuata C, calanoid N and C                                     | Pepin and Penney (1997) |
| Leiognathidae       | Not defined                       | —                                  |       | Polychaetes                                                                 | Sampey et al. (2007)    |
| Liparidae           | Liparis sp.                       | Calanoid N, euphausids             |       | —                                                                           | Pepin and Penney (1997) |
| Monacanthidae       | Not defined                       | —                                  |       | —                                                                           | Sampey et al. (2007)    |
| Osmeridae           | M. villosus                       | Cyclopid N, calanoid C             |       | Temora C, B. similis C, cyclopoid C, decapod larvae                      | Sampey et al. (2007)    |
| Pinguipedidae       | Not defined                       | —                                  |       | —                                                                           | Pepin and Penney (1997) |
| Pleuronectidae      | Glyptocephalus cynoglossus        | Calanoid N and C, bivalve larvae, cladocerans |       | —                                                                           | Pepin and Penney, 1997 |
| H. platessoides     | Northern North Sea                | Calanoid N                         |       | C. finmarchicus C                                                          | Economou (1991)         |
| Pleuronectes americanus | Newfoundland                      | Calanoid N and C                  |       | —                                                                           | Pepin and Penney (1997) |
| P. ferrugineus      | Newfoundland                      | Bivalve larvae, cladocerans        |       | —                                                                           | Pepin and Penney (1997) |
| Sciaenidae          | Leiostomus xanthurus              | Oncaea C                           |       | —                                                                           | Govoni et al. (1986)    |
| Micropogonias undulates | Northern Gulf of Mexico            | Oncaea C, Oithona C, Acartia tonsa C |       | Paracalanus C                                                               | Govoni et al. (1986)    |
| Pseudocolus          | Western English Channel           | Copepod N                          |       | Acartia C, Oithona C                                                       | Fortier and Harris (1989) |
| Scophthalmidae      | Phrynornhombus norvegicus         | —                                  |       | —                                                                           | Fortier and Harris (1989) |
| Scombridae          | Katsuwonus pelamis                | Appendicularians                   |       | Appendicularians                                                           | Young and Davis (1990)  |
| S. scombrus         | Eastern Indian Ocean              | T. longicornis N, Pseudocolus N    |       | —                                                                           | Peterson and Ausubel (1984) |
| Magdalen Shallows   | Long Island Sound                 | Pseudocolus N, T. longicornis N    |       | Cladocerans, fish larvae                                                   | This study              |
| Scotian Self        | Coral Sea                         | Copepod N                          |       | Fish larvae                                                                | Jenkins et al., 1984    |
| Scomberomorus spp   | Eastern Indian Ocean              | Copepod N, corycaeid C             |       | fish larvae                                                                | Young and Davis, 1990   |
| Thunnus alalunga    | Eastern Indian Ocean              | Copepod N                          |       | fish larvae                                                                | Anderson, 1994          |
| T. maccocy         | Eastern Indian Ocean              | Copepod N, corycaeid C             |       | fish larvae                                                                | Runge and de Lafontaine (1996) |
| Sebastidae          | Sebastes spp.                     | Calanus E and N                    |       | Calanus E                                                                  | Fortier and Harris (1989) |
|                    | Flemish Cap                       | Calanus E                          |       | Calanus E                                                                 | Fortier and Harris (1989) |
|                    | Northern Gulf of St Lawrence      | Calanus N                          |       | Calanus E                                                                  | Fortier and Harris (1989) |
| Soleidae            | Microchirus variegates            | Copepod N                          |       | T. longicornis C, Evadne, Polychaete larvae                               | Fortier and Harris (1989) |
| Stichaeidae         | Stichaeus punctatus               | Calanoid N and C, cyclopoid C, euphausids |       | —                                                                           | Pepin and Penney (1997) |
|                    | Newfoundland                      | Calanoid N, cladocerans            |       | —                                                                           | Pepin and Penney (1997) |
|                    | Ulvaria subbifurcata              | Calanoid N, cladocerans            |       | —                                                                           | 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 ~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.

ACKNOWLEDGEMENTS

This study is a contribution to the programs of Québec-Océan (Université Laval) and the Institut Maurice-Lamontagne (Department of Fisheries and Oceans Canada). Support from the Natural Science and Engineering Research Council of Canada (NSERC) and the NSERC Research Network GLOBEC-Canada to LF is acknowledged. K. Levesque, A.-M. Leckman, P. Lafrance, L. Michaud, K. Levesque, A.-M. Leckman, P. Lafrance, L. Michaud, GLOBEC-Canada to LF is acknowledged. K. Levesque, A.-M. Leckman, P. Lafrance, L. Michaud, L. Létourneau, V. Perron and M. Pilote contributed to the field work and/or laboratory analyses. Statistical advice by V. Jomphe was of great help. The manuscript benefited from the constructive comments of two anonymous reviewers.

FUNDING

D.R. was funded by NSERC, the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) and Québec-Océan.

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