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CHAPITRE I
INTRODUCTION GÉNÉRALE

Depuis la fin du XIX^e siècle, les fluctuations interannuelles d'abondance des populations de poissons, principalement les espèces d'intérêt commercial, ont été le point central des recherches en sciences halieutiques (Hjort, 1914). Grâce à l'avancement des connaissances dans ce domaine, on sait aujourd'hui que ces fluctuations sont largement attribuables aux variations du recrutement des jeunes poissons dans la population (Cowan et Shaw, 2002). Le recrutement se définit comme étant la survie d'une cohorte annuelle à la fin de la première année de vie et constitue le principal intrant dans un stock de poissons et par conséquent, une des seules possibilités de renouvellement démographique d'une population (Cowan et Shaw, 2002; Robert, 2008). Ainsi, la variabilité du recrutement des stocks de poissons marins a été une question importante pendant plusieurs années (Anderson, 1988). Encore aujourd'hui, la prédiction des fluctuations du recrutement des poissons marins demeure le Saint Graal des sciences halieutiques (Castonguay *et al.*, 2008). Ces efforts de prédiction sont d'autant plus importants étant donné l'état lamentable de plusieurs pêcheries, attribuable entre autres à une gestion inadéquate des stocks de poissons (Cowan et Shaw, 2002; Robert, 2008). Afin d'assurer la viabilité à long terme de ces stocks et ainsi éviter de telles situations, il faut d'abord et avant tout comprendre les facteurs qui contrôlent la variabilité interannuelle du recrutement des populations de poissons (Bartsch *et al.*, 2004). Ces connaissances aideront ultimement à prédire la force des classes d'âge (c.-à-d. le nombre de recrues pour une année donnée) de même que la force du recrutement pour ainsi assurer une gestion durable de la ressource.

La variabilité naturelle de l'environnement est clairement impliquée en matière de recrutement des poissons, avec une influence plus prononcée sur les premiers stades de vie

(Bartsch et Coombs, 2004). La mortalité au cours de la période larvaire est donc très importante chez les poissons. D'ailleurs, depuis les travaux de Hjort (1914), on admet généralement que le recrutement d'une population de poissons est déterminé durant le stade larvaire, en fonction des variations du taux de mortalité élevé qui caractérise les quelques semaines suivant l'éclosion (Houde, 2002; Ringuelette *et al.*, 2002; Castonguay *et al.*, 2008; Robert, 2008). Lors de cette période, la nouvelle cohorte de poissons est réduite dramatiquement aux rares survivants qui contribueront au recrutement pour ainsi soutenir les populations dans le temps (Jones, 2002; Govoni, 2005). De ce fait, il est communément accepté que le nombre de poissons qui survivent pendant le stade larvaire est un indice fiable de la force de la classe d'âge (Leggett et Deblois, 1994; Platt *et al.*, 2003). Ainsi, les études sur la variabilité du recrutement mettent aujourd'hui l'emphasis sur les facteurs qui contrôlent la survie dans les premiers stades de vie. Des facteurs biotiques, tels que la disponibilité en proies (Cushing, 1990) et la prédation (Hunter, 1981; Anderson, 1988; Bailey et Houde, 1989; Pepin, 1991), de même que des facteurs abiotiques comme la température (Houde, 1987) et les courants, ont tous des impacts sur la survie larvaire et influencent donc le succès de recrutement.

Le taux de croissance lors des premiers stades de vie est d'ailleurs considéré comme un régulateur important de la dynamique du recrutement des poissons marins. Cette idée est particulièrement bien développée dans l'hypothèse croissance-mortalité d'Anderson (1988), qui postule que les plus gros individus et/ou les individus à croissance rapide survivent mieux que leurs congénères. Selon cette hypothèse, tout facteur modifiant le taux de croissance moyen d'une cohorte larvaire génèrera de la variabilité dans le recrutement des

poissons et les individus à croissance rapide ont généralement une meilleure survie larvaire. L'hypothèse croissance-mortalité est devenue aujourd'hui le principal schéma conceptuel en sciences halieutiques pour expliquer la variabilité dans le succès du recrutement. La compréhension des facteurs qui influencent la croissance larvaire est donc une étape cruciale pour arriver à comprendre la variabilité du recrutement des populations de poissons.

L'un des facteurs jugé comme étant le plus important pour la régulation de la croissance larvaire en milieu marin est la disponibilité en proies adéquates durant le stade larvaire. Ce facteur a d'ailleurs été longtemps considéré comme étant un préalable à l'émergence d'une forte classe d'âge (Hjort, 1914; Cushing, 1990). Une faible quantité de proies adéquates dans le milieu durant le stade larvaire peut avoir des conséquences désastreuses pour la survie des larves de poissons et le recrutement subséquent. En effet, en plus d'augmenter la probabilité de mort par famine, une faible disponibilité en proies entrave la croissance (diminution de l'énergie allouée à la croissance) et intensifie la mortalité due à la prédation. Ce dernier point est très bien expliqué par le concept de « *stage duration* » qui dicte que les larves à croissance lente demeurent exposées à leur prédateur sur une plus longue période de temps (Chambers et Leggett, 1987; Houde, 1987). Il est donc important de comprendre les facteurs qui pourraient influencer sur l'alimentation des larves, afin de comprendre les variations dans la croissance, la survie et le recrutement. Ces enjeux importants s'appliquent spécifiquement aux larves de maquereau bleu (*Scomber scombrus* L.) du sud du golfe du Saint-Laurent qui montrent d'importantes fluctuations interannuelles d'abondance.

Le maquereau bleu est un poisson pélagique présent des deux côtés de l'Atlantique Nord (Sette, 1943) et constitue, depuis quelques années, une des principales espèces visées par la pêche commerciale (Grégoire, 2009). Le maquereau bleu représente d'ailleurs l'un des poissons les plus importants dans les pêcheries du nord-est et du nord-ouest de l'Atlantique (Mendiola *et al.*, 2007). Pourtant, au départ, ce poisson n'était pas très apprécié des consommateurs, étant traditionnellement utilisé comme appât dans les cages à homards et à crabes. Mais, avec la diminution des poissons de fond, l'industrie de la pêche a dû réorienter ses pratiques vers de nouvelles espèces comme le maquereau bleu. Ces changements se sont opérés de manière assez drastique, puisque depuis les années 2000, les débarquements canadiens ont plus que doublé atteignant un maximum historique de 54 279 tonnes en 2005 (Grégoire, 2009). De plus, afin de contrer l'effondrement des stocks de gros poissons, de même que les problèmes environnementaux liés à l'aquaculture, beaucoup de chercheurs suggèrent qu'il faut se tourner vers la consommation de petits poissons, comme le maquereau bleu. Relativement abondants, ces poissons ont une meilleure valeur nutritive que les gros poissons et contiennent moins de polluants (Dewailly et Rouja, 2009). Ainsi, les pressions grandissantes pour l'exploitation du maquereau bleu de même que les importantes fluctuations interannuelles d'abondance font en sorte qu'il est primordial de continuer de surveiller l'abondance de cette espèce commerciale, mais surtout, de comprendre les variations de son recrutement.

Par chance, les connaissances actuelles sur la biologie du maquereau bleu sont relativement avancées comparativement à d'autres poissons du golfe du Saint-Laurent. Ainsi, on sait que le maquereau bleu du Canada entreprend chaque année une longue

migration qui l'amène de ses quartiers d'hiver situés au large des côtes américaines, entre Cape Cod et Cape Hatteras, vers ses aires de ponte et d'alimentation. Ces dernières se situent dans le golfe du Saint-Laurent de même que sur les côtes est et ouest de Terre-Neuve (Sette, 1950; Ware et Lambert, 1985; Armellin *et al.*, 1990; Grégoire *et al.*, 2004). Le sud du golfe du Saint-Laurent est généralement reconnu comme étant la principale aire de ponte du maquereau bleu. La période de frai la plus importante dans le golfe se déroule généralement dans la dernière partie du mois de juin (Ouellet, 1987).

On sait aussi que l'alimentation du maquereau bleu varie beaucoup avec l'âge. Ainsi, les jeunes larves se nourrissent principalement d'œufs, de nauplii de copépodes et de cladocères (Grave, 1981; Fortier et Villeneuve, 1996; Hillgruber et Kloppmann, 2001). À mesure que les larves croissent, la taille de leurs proies augmente. Les larves se nourrissent alors de stades copépodites de plusieurs espèces de copépodes et de larves de poissons, optant même pour le cannibalisme (Last, 1980; Grave, 1981; Fortier et Villeneuve, 1996). Ainsi, un changement d'alimentation précoce de planctivore à piscivore s'effectue, ce qui permet aux larves de maquereau bleu d'augmenter leur taux de croissance et de réduire la durée de la période larvaire, phase la plus vulnérable à la mortalité (Houde, 1989). Par ailleurs, en matière d'alimentation, il est généralement accepté que les larves de poisson, comme celles du maquereau bleu, présentent une forte sélectivité pour leurs proies. Cette sélectivité pour les divers organismes zooplanctoniques est créée par les différences en matière de détection et de succès de capture des proies potentielles, qui à leur tour dépendent largement de la taille des proies, de la visibilité et de l'ouverture de la bouche du prédateur (Hunter, 1980; Buskey *et al.*, 1993). D'ailleurs, selon l'étude de Ware et Lambert

(1985), le régime alimentaire du maquereau bleu durant les premiers stades larvaires reflèterait les espèces les plus abondantes dans l'intervalle de taille préférentielle disponible, où le maximum serait déterminé par l'ouverture de la bouche.

De plus, à un certain moment de la vie larvaire, un compromis doit être effectué de façon à ce que la préférence quant à la taille des proies reflète le ratio optimal entre le gain d'énergie et l'énergie consacrée à les capturer. En-dessous ou au-dessus de cet intervalle de taille préférentielle, les proies potentielles ne sont pas aussi intéressantes en termes de bilan énergétique (Robert *et al.*, 2008). Cela est particulièrement important pour les larves de maquereau bleu, puisque les poissons de la famille des Scombridés sont considérés comme ayant adopté une stratégie de survie caractérisée par une croissance rapide et la capacité de consommer de larges proies à un stade de vie précoce (Hunter, 1981). Ainsi, pour que les larves de maquereau bleu puissent bénéficier de ce taux de croissance élevé, elles doivent satisfaire une demande grandissante de leur métabolisme. Cependant, au lieu d'ingérer un nombre croissant de petites proies, les larves de maquereau bleu cherchent à utiliser une source de nourriture plus efficace énergétiquement, comme les larves de poissons (Hillgruber et Kloppmann, 2001). Cela est donc conforme avec leur changement d'alimentation au cours de leur ontogenèse. Finalement, en terme de sélectivité, nombre d'études ont pu démontrer que les proies préférentielles des larves de maquereau bleu sont les copépodes *Pseudocalanus* spp., *Calanus finmarchicus* et *Temora longicornis*.

En ce qui concerne le recrutement du maquereau bleu du nord-ouest de l'Atlantique, la variabilité dans la force du recrutement a été détectée dans les prises commerciales depuis le XIX^e siècle (Hjort, 1926; Anderson et Paciorkowski, 1980). Dans le golfe du Saint-

Laurent, l'indice du recrutement du maquereau bleu (MACREC), mesuré à partir des pêches commerciales, montre d'importantes fluctuations interannuelles, caractérisées par la présence sporadique de classes d'âge exceptionnelles (Runge *et al.*, 1999). L'apparition de ces fortes classes d'âge chez le maquereau bleu est sporadique, et les cohortes dominantes sont généralement espacées par plusieurs années de faible recrutement (de Lafontaine *et al.*, 1991). Au cours des trois dernières décennies, les classes d'âge de 1982 et 1999 ont fortement dominé les prises commerciales. Toutefois, malgré plusieurs années de recherches, les processus exacts qui influencent le recrutement du maquereau bleu ne sont pas encore bien établis.

Pour résoudre les variations dans le recrutement du maquereau bleu, des travaux de recherches ont été menés sur l'écologie des larves de maquereau bleu dans le sud du golfe du Saint-Laurent. D'ailleurs, le maquereau bleu est une des rares espèces dans le monde pour laquelle un lien a été établi entre recrutement, croissance larvaire et climat. Par contre, le lien entre recrutement et disponibilité en proie est moins bien défini puisqu'il existe dans la littérature certaines contradictions sur le rôle des différentes proies zooplanctoniques dans le recrutement du maquereau bleu. En effet, les travaux de Ringuette *et al.* (2002) menés sur l'ensemble du sud du golfe du Saint-Laurent, ont mis en évidence le rôle du copépode *C. finmarchicus* dans la détermination du recrutement du maquereau bleu. Selon leur résultat, pour une année donnée, un nombre important de larves de maquereau bleu survivent lorsqu'il y a beaucoup de proies *C. finmarchicus* disponibles. Runge *et al.* (1999) ont eux aussi montré l'existence de liens entre l'abondance des proies zooplanctoniques, particulièrement *C. finmarchicus*, et la force du recrutement du maquereau bleu. À

l'opposé, les travaux de Robert *et al.* (2008), basés sur un échantillonnage restreint à l'est des Îles-de-la-Madeleine, ont mis en lumière l'importance des copépodes *Pseudocalanus* spp. dans le déterminisme du recrutement du maquereau bleu. Ils ont même découvert que les larves de maquereau bleu ne sélectionnaient pas *C. finmarchicus*. Il existe donc un désaccord certain sur le rôle du copépode *C. finmarchicus* dans le recrutement du maquereau bleu.

De plus, à partir des différentes connaissances sur les proies préférentielles de maquereau bleu, Castonguay *et al.* (2008) ont présenté un modèle prédictif permettant d'anticiper le recrutement du maquereau bleu trois ans à l'avance. Ce modèle est basé sur la production des œufs des trois espèces de copépodes mentionnées plus haut durant les premières semaines de vie planctonique dans le sud du golfe du Saint-Laurent. Le modèle prédictif de Castonguay *et al.* (2008) montre qu'il y a une relation linéaire entre la force des classes d'âge et la production totale d'œufs des trois espèces de copépodes mentionnés plus haut. D'ailleurs, les deux fortes classes d'âge (1982 et 1999) ont été caractérisées par une disponibilité exceptionnelle de ces proies. Toutefois, cet outil prédictif utilise la production d'œufs de copépodes pour lesquelles il existe encore de l'ambiguïté quant à leur rôle dans l'alimentation des larves de maquereau bleu. Cela rend donc les prédictions incertaines pour l'avenir. Il est donc fondamental d'approfondir le rôle des différentes espèces de copépodes dans le recrutement du maquereau bleu en accordant une plus grande importance à la variabilité spatiale.

L'objectif principal de cette étude était d'examiner l'influence de divers assemblages de proies zooplanctoniques sur l'alimentation des larves de maquereau bleu. Cette étude

visait également à clarifier les contradictions dans la littérature sur l'importance des différentes proies zooplanctoniques pour le recrutement du maquereau bleu du sud du golfe du Saint-Laurent.

CHAPITRE II

SPATIAL VARIABILITY IN ZOOPLANKTON AND FEEDING OF LARVAL ATLANTIC MACKEREL (*Scomber scombrus* L.) IN THE SOUTHERN GULF OF ST. LAWRENCE

2.1 INTRODUCTION

Interannual fluctuations in the abundance of commercial marine fish stocks have been an important issue in fisheries science since the late 19th century (Hjort, 1914). It has now become widely accepted that these fluctuations are largely due to changes in recruitment of young fish to the population (Cowan and Shaw, 2002). Therefore, most of the studies on recruitment variability focused on factors controlling survival during early life stages. Growth rate during early life stages of marine fishes is considered as an important regulator of recruitment dynamics. According to the “growth–mortality” hypothesis (Anderson, 1988), larger and/or fast-growing individuals have a higher probability of survival. As a result, factors influencing growth rate during early life are likely to significantly influence survival and recruitment. The growth–mortality hypothesis has become the main conceptual framework in fisheries science to explain the variability in recruitment success. Understanding factors that influence larval growth would therefore be a crucial step to improve our understanding of recruitment variability in fish populations.

The availability of adequate prey during the larval stage is one of the most important factors for the regulation of larval growth in the marine environment. It has also long been considered a prerequisite for the emergence of a strong year-class (Hjort, 1914; Cushing, 1990). Larvae that experience favourable feeding conditions will grow faster and therefore experience lower predation mortality during the larval stage, thus contributing to recruitment to the population (Cushing, 1975; Robert *et al.*, 2007). It is therefore important to understand factors that could affect larval feeding in order to understand variations in growth, survival, and recruitment. This concept applies to Atlantic mackerel (*Scomber*

scombrus L.) larvae in the southern Gulf of St. Lawrence (GSL) (Canada), which exhibit high interannual variability in year-class strength (Castonguay *et al.*, 2008).

Atlantic mackerel is a schooling pelagic species present on both sides of the North Atlantic Ocean that sustains major commercial fisheries. Mackerel from Canada perform long migrations each year from overwintering areas on Georges Bank and the mid-Atlantic Bight to the southern GSL, which constitutes the main spawning area for the species in Canada (Sette, 1950). The spawning peak in the southern GSL typically occurs in the latter part of June (Ouellet, 1987). Since 1982, mackerel spawning stock biomass has been assessed in the GSL in late June by estimating egg abundance during the spawning period using a grid of 65 stations covering the entire southern GSL. In this area, the mackerel recruitment index (MACREC), measured from the proportion of age 3 fish in the commercial fishery, shows significant interannual fluctuations characterized by the presence of sporadically strong year-classes (Runge *et al.*, 1999). Dominant cohorts (boomer years) are generally separated by several years of low or average recruitment (de Lafontaine *et al.*, 1991). The recent increase in mackerel landings in the northwest Atlantic (Grégoire *et al.*, 2009) as well as the large interannual fluctuations in abundance emphasize the importance of monitoring its abundance and improving our understanding of its recruitment fluctuations.

A model based on the egg production of populations of the three copepod species that contribute the most to the diet of mackerel larvae (*Calanus finmarchicus*, *Pseudocalanus* spp., and *Temora longicornis*) was proposed to predict mackerel recruitment three years later. The predictive model of Castonguay *et al.* (2008) shows a linear relationship between

year-class strength and egg production of the three copepod species. However, there is a weakness in this model since inconsistencies exist in the literature on the importance of two main copepod species in the diet of mackerel larvae in the southern GSL. Ringuette *et al.* (2002) identified *C. finmarchicus* as the most important prey influencing mackerel recruitment. According to their results, a large number of mackerel larvae survive when *C. finmarchicus* nauplius prey are abundant. More recently, Robert *et al.* (2008) highlighted the importance of *Pseudocalanus* spp. and showed that mackerel larvae tended to avoid *C. finmarchicus*. Hence, these two studies based on different datasets reached different conclusions on the influence of *C. finmarchicus* on mackerel recruitment. Results from Robert *et al.* (2008) were based on a limited sampling near the Îles-de-la-Madeleine while the work of Ringuette *et al.* (2002) was conducted throughout the southern GSL (see Fig. 1). It is therefore essential to further examine the role of different copepod species in influencing mackerel recruitment by taking into account the spatial variability in prey availability throughout the southern GSL spawning area.

The aim of this project was to evaluate the spatial variability of the larval mackerel diet throughout the southern GSL in relation to zooplankton species composition. To reach this objective, the diet of mackerel larvae was described qualitatively and quantitatively and compared with the zooplankton prey field available in different areas of the southern GSL. Following Robert *et al.* (2008), an energetic index expressed as mean carbon biomass per prey was used.

2.2 MATERIALS AND METHODS

2.2.1 Study site

The study area was sampled by a grid of 65 stations spaced 20 nautical miles apart, except for northernmost stations (Fig. 1). This sampling grid, which represents the main mackerel spawning area in Canada, covers the entire southern GSL. It has been sampled each year in late June since 1982 (except in 1995 and 1997) to assess the spawning stock biomass of mackerel in Canada.

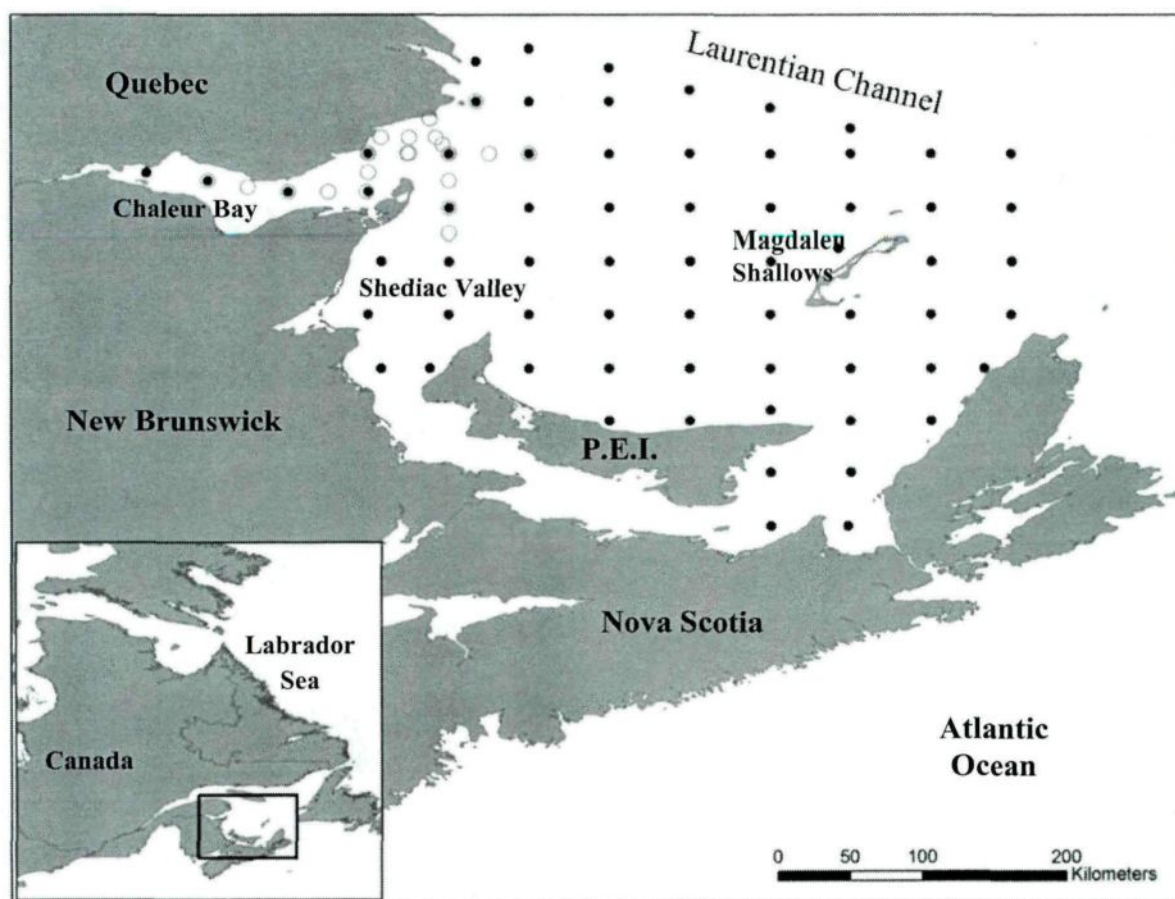


Figure 1. Sampling grid used for the mackerel egg and larval survey in the southern Gulf of St. Lawrence. Dots represent stations sampled in June 2008 and open circles represent stations sampled during an additional survey in July 2010.

2.2.2 Sampling of mackerel larvae and their zooplankton prey

Atlantic mackerel larvae and their zooplankton prey were collected at the 65 stations in late June 2008 during a three-week survey. This survey targets the sampling of mackerel eggs, so larvae from these samples are generally young. An additional four-day survey limited to Chaleur Bay and the northern part of Shediac Valley was conducted in early July 2010 to collect larger mackerel larvae. Fish larvae were collected using 333 μm bongo nets with a 61 cm diameter opening. A General Oceanics flowmeter was attached near the opening of each net to measure the volume of water filtered. The tows, which lasted a minimum of 10 minutes, were made following a double-oblique pattern (Hempel, 1973) between the surface and a maximum depth of 50 m, or to 5 m from the bottom for shallower stations. A CTD probe (SBE19, Sea-Bird Electronics, Inc.) attached to the sampler's frame provided temperature and salinity data for the sampled portion of the water column. Ichthyoplankton samples from one of the two bongo nets were kept in concentrated ethanol (95%) in 2008 and frozen on dry ice in 2010. Samples were taken during both day and night, while the peak feeding period of mackerel larvae is between 16:00 and 24:00 (Grave, 1981). For the two surveys, 67 larvae were sampled in the peak feeding period with a feeding incidence of 60%, while 89 larvae were sampled outside this period with a feeding incidence of 73%. However, there was no significant difference between feeding incidence ($p = 0.079$) as revealed by a Pearson's Chi square test. Consequently, we considered all larvae for analysis.

Zooplankton was collected using a 73 μm mesh net with a 50 cm diameter opening to quantitatively sample the early stages of mesozooplankton, the main prey for mackerel

larvae, because these are not efficiently captured by the 333 μm bongo nets (Runge *et al.*, 1999). The 73 μm mesh net was towed vertically, between the surface and a maximum depth of 100 m or to 5 m off the bottom for shallower stations. Zooplankton samples were preserved in a 4% formaldehyde–seawater solution.

2.2.3 Laboratory analyses

In the laboratory, mackerel larvae were sorted and identified from the bongo samples under a binocular microscope. The standard length of each larva was measured to the nearest 0.1 mm with an ocular micrometer. The stomach content of each larva was examined under a microscope. Each prey found was identified to the lowest taxonomic level possible and development stages were determined whenever possible to have a complete description of the larval diet. Zooplankton prey were identified according to specific morphological characteristics and size (prosome or total length). The size criterion was especially useful for the identification of copepod eggs and nauplius stages. For example, the discrimination between *Pseudocalanus* spp. and *C. finmarchicus* nauplii was mainly made by comparison of the total length ranges from Demontigny *et al.*, 2012. Copepod eggs were identified to species using diameter range values: < 135 μm for more than one species but mainly *Oithona similis* and *T. longicornis*; 135–165 μm for *C. finmarchicus*; 165–195 μm for *C. glacialis*, and 195–250 μm for *C. hyperboreus*. Copepod egg diameters were used to calculate egg volumes for the estimation of carbon content. To assess the feeding selectivity of mackerel larvae, zooplankton collected with the 73 μm mesh were counted and identified to the lowest taxonomic level and development stages were determined when possible. This identification was made only for stations where

mackerel larvae were captured. The same criteria mentioned before were used for this identification. Zooplankton samples were subsampled with a Folsom sampler splitter and aliquots were taken with a Stempel pipette. Finally, the carbon content of each prey was estimated from specific length–weight regressions and carbon–weight ratios (Table 1).

Table 1. 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 mackerel larvae.

Taxon		Equation	Reference
Copepods			
Eggs	V	$4/3 \pi ((L/1000)/2)^3$	Kjørboe <i>et al.</i> (1985)
	C	$140 V$	
Nauplii			
<i>Acartia</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>C. finmarchicus</i>	C	$4.29 \times 10^{-6} \times L^{2.05}$	Hygum <i>et al.</i> (2000)
<i>Centropages</i> spp.	ADW	$10^{2.2357 \log L - 5.5458}$	Klein Breteler <i>et al.</i> (1982)
	DW	ADW + 7%	Båmstedt (1986)
	C	44.7% DW	Mauchline (1998)
<i>Oithona</i> spp.	DW	$2.5968 \times (L/1000)^{1.6349}$	Culver <i>et al.</i> (1985)
	C	44.7% DW	Mauchline (1998)
<i>Eurytemora</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>Metridia</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>Microcalanus</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>Microsetella</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>Pseudocalanus</i> spp.	ADW	$10^{2.2692 \log L - 5.57}$	Klein Breteler <i>et al.</i> (1982)
	DW	ADW + 7%	Båmstedt (1986)
	C	44.7% DW	Mauchline (1998)
<i>T. longicornis</i>	ADW	$10^{2.1674 \log L - 5.5336}$	Klein Breteler <i>et al.</i> (1982)
	DW	ADW + 7%	Båmstedt (1986)
	C	44.7% DW	Mauchline (1998)
<i>Tortanus</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
Copepodites			
<i>Acartia</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>Eurytemora</i> spp.	DW	$10^{2.961 \log L - 7.604}$	Middlebrook and Roff (1986)
	C	44.7% DW	Mauchline (1998)
<i>Microcalanus</i> spp.	C	$10^{3.07 \log L - 8.37}$	Uye (1982)
<i>O. similis</i>	C	$9.4676 \times 10^{-7} L^{2.16}$	Sabatini and Kjørboe (1994)
<i>Pseudocalanus</i> spp.	C	$10^{3.64 \log L - 10.156}$	McLaren (1969)
<i>T. longicornis</i>	DW	$10^{2.815 \log L - 7.181}$	Hay <i>et al.</i> (1991)
	C	44.7% DW	Mauchline (1998)
Cladocerans	C	$10^{4.15 \log L - 11.15}$	Uye (1982)
Fish larvae	DW	$10^{4.09 \log (L/1000) - 1.114}$	Laurence (1979)
	C	40% DW	Legendre and Michaud (1998)

2.2.4 Data analyses

2.2.4.1 Zooplankton assemblage

To examine the influence of various assemblages of copepod prey on the feeding of mackerel larvae, stations with at least one mackerel larva were grouped based on zooplankton species composition. Only species representing more than 0.1% of the total abundance at least at one station were used (Field *et al.*, 1982). A cluster analysis with complete linkage was performed on a Bray–Curtis similarity matrix based on the zooplankton data (Clarke, 1993). Species assemblages were calculated using the fourth-root transformation, which down-weighted the importance of abundant species, allowing rarer species to exert more influence on the calculation (Clarke and Warwick, 2001). A SIMPROF ($\alpha = 0.05$; 999 permutations) test was also performed to distinguish significant groups in the cluster analysis. A SIMPER analysis was also used to identify species that typified the assemblages. Finally, we examined species richness using Margalef's index following the formula in Magurran (1988). The calculation of the index based on zooplankton species abundance was performed on non-transformed abundance data for each station and then averaged by group. All these analyses were performed using PRIMER v6 statistical software.

2.2.4.2 Feeding selectivity

The selectivity of mackerel larvae for prey j was quantified using Chesson's (1978) α -selectivity index:

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

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 representing more than 0.8% of the total abundance in at least one larva gut were considered in the calculation of α . Digested copepods that could not be identified (about 1.8% of all prey) were removed from the calculation as well as prey that were found in the stomach but not at the station (about 2.3% of all prey). The index was computed independently for each larva and then averaged over length classes (3) and zooplankton assemblages (4). We used the formula $1/N$ to calculate a threshold value of positive selection for averaged values. Only larval abundance data obtained in the 333 μm Bongo nets was used for the feeding selectivity analysis.

2.2.4.3 Energetic index

To compare results from three studies on larval mackerel diet in the southern GSL (Ringuelette *et al.*, 2002; Robert *et al.*, 2008; this study), an energetic index (i.e., mean carbon biomass per prey) was calculated as per Robert *et al.* (2008). First, the total prey biomass found in the stomach was calculated for each larva and divided by the number of prey in the stomach. An average was then calculated per year. Unidentified digested materials were removed from the calculation as well as unidentified copepods without length measurement (about 3.3% of all prey from the three studies). For this calculation, only length classes whose diet is dominated by zooplankton were presented (< 3.5 mm; 3.5–5.4 mm and 5.5–7 mm) to avoid including fish larvae in the gut. There are nevertheless some larvae in the diet of the largest length class but our interpretation focuses on the intermediate length class (3.5–5.4 mm).

2.3 RESULTS

2.3.1 Zooplankton assemblages

The cluster analysis revealed five significant zooplankton assemblages based on zooplankton species composition (Fig. 2A). Because abundances of mackerel larvae were low, stations 5.3 and 3.3 were included in the Offshore group to obtain four distinct zooplankton assemblages. The defined groups corresponded to a spatial structure in the southern GSL: the Chaleur group was located within Chaleur Bay (Fig. 2B); the North P.E.I. group was near the New Brunswick and P.E.I. coasts, the Miscou group was situated at the mouth of Chaleur Bay, and the Offshore group stations were generally located offshore in the southern GSL. The Chaleur and North P.E.I. groups, which had inshore stations, were the shallowest assemblages, with an average depth of 32 m and 33 m, respectively. Stations from the North P.E.I. and Miscou groups had the warmest water (Table 2).

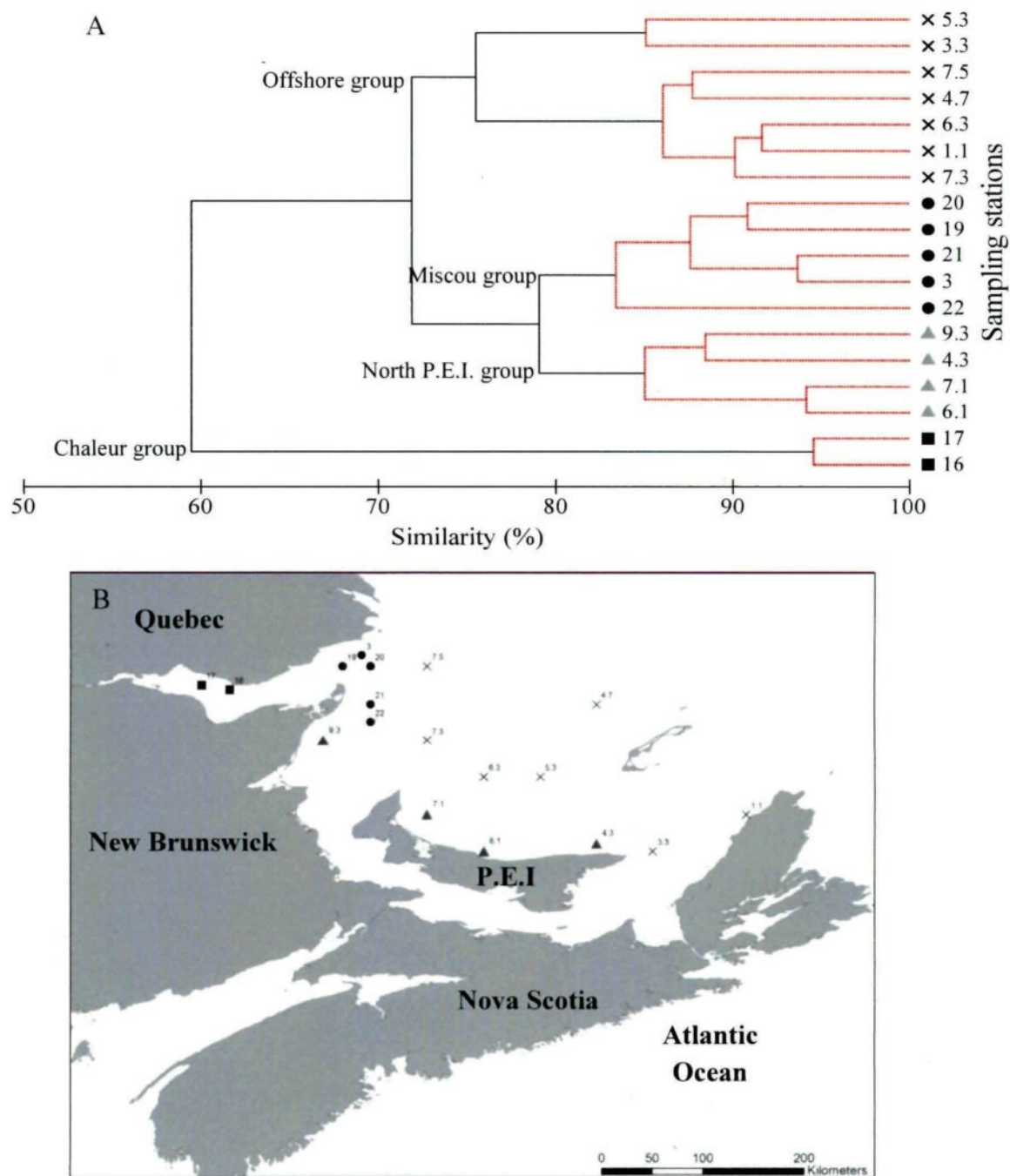


Figure 2. (A) Dendrogram from the complete-linkage cluster analysis on stations. Bold lines indicate significant divisions according to the SIMPROF test; corresponding station group are noted. (B) Location of stations with zooplankton samples in the southern Gulf of St. Lawrence. Grey and dark symbols were sampled in 2008 and 2010, respectively.

In all assemblages, copepod eggs and *Oithona* spp. nauplii (mainly *O. similis*) were the most abundant groups, reaching particularly high densities in the Chaleur assemblage (Fig. 3A,B). The abundances of copepodite and nauplius stages of *Oithona* spp., *Pseudocalanus* spp., and copepod eggs in the Chaleur group were by far the highest of all assemblages, reaching more than 1 272 000 individuals·m⁻², 1 259 000 ind·m⁻², and 429 000 ind·m⁻², respectively. The Chaleur group was also characterized by the greatest abundance of both stages of the copepod *Acartia* spp., bivalve larvae, and gastropod eggs. The abundance of *T. longicornis*, especially copepodite stages, was also highest in the Chaleur group but was dominant only in the North P.E.I. group, which included only inshore stations. The North P.E.I. group had the highest number of cnidarians and was the only assemblage to contain fish eggs and cirripedians. The Miscou group, located at the mouth of Chaleur Bay, was characterized by the greatest abundance of *Microsetella* spp. nauplii of all the assemblages and had a high abundance of *Pseudocalanus* spp. nauplii. The abundance of *C. finmarchicus* nauplius stages was low, with none in the Chaleur group and a gradient toward the Offshore group, which had the highest abundance. The abundance of *C. finmarchicus* copepodites was higher than for nauplius stages and tended to increase steadily from inshore to offshore stations. This trend was also observed for other *Calanus* species. The Offshore group was also dominated by a great number of appendicularians. The Offshore group had the highest species richness of all assemblages, with over 27 species, while the Chaleur group was composed of only 16 (Table 2).

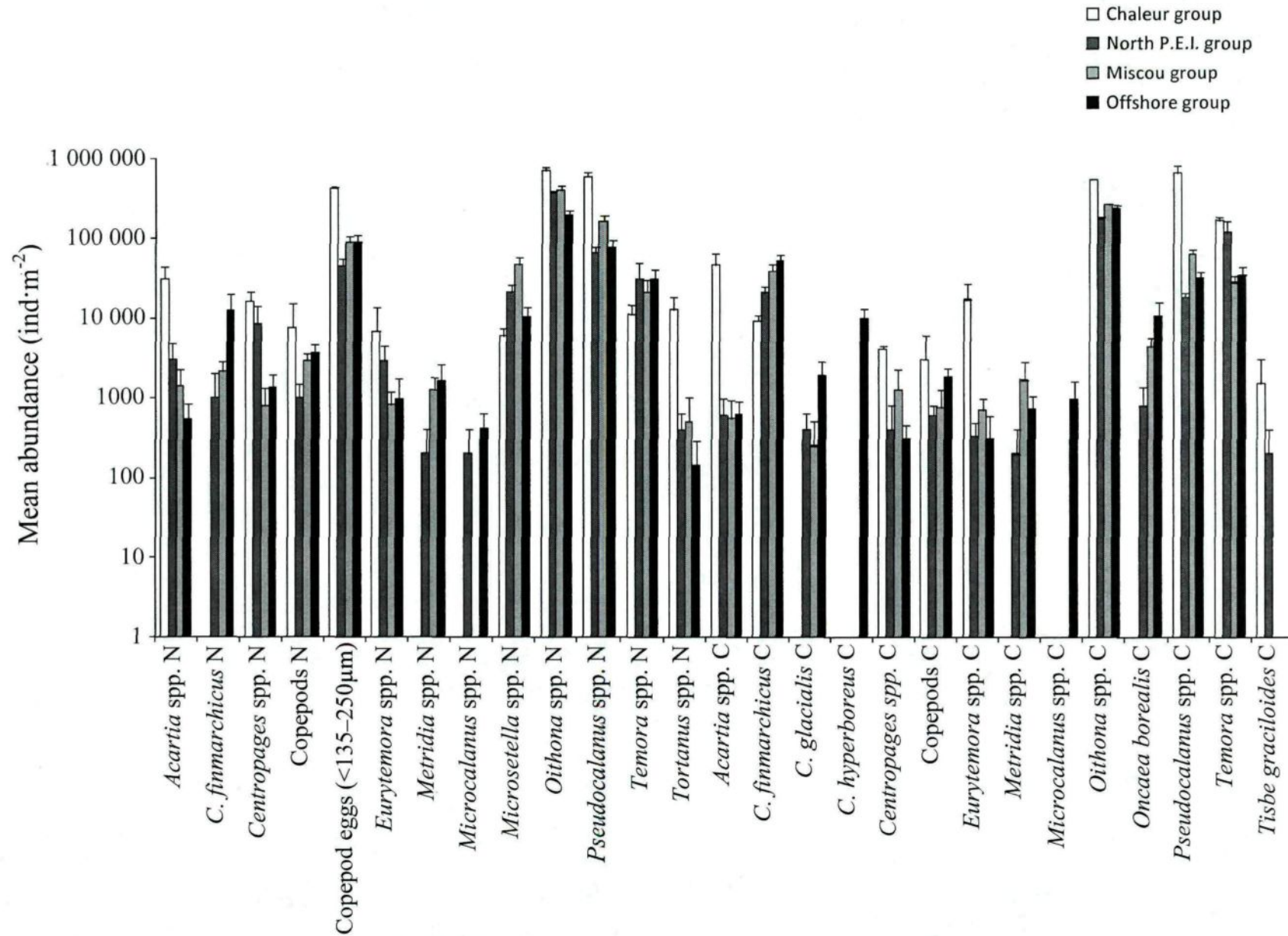


Figure 3a. Mean $\log_{10}$ -transformed abundance of zooplankton taxa (N: nauplii and C: copepodites) in the four zooplankton assemblages. Standard errors are shown.

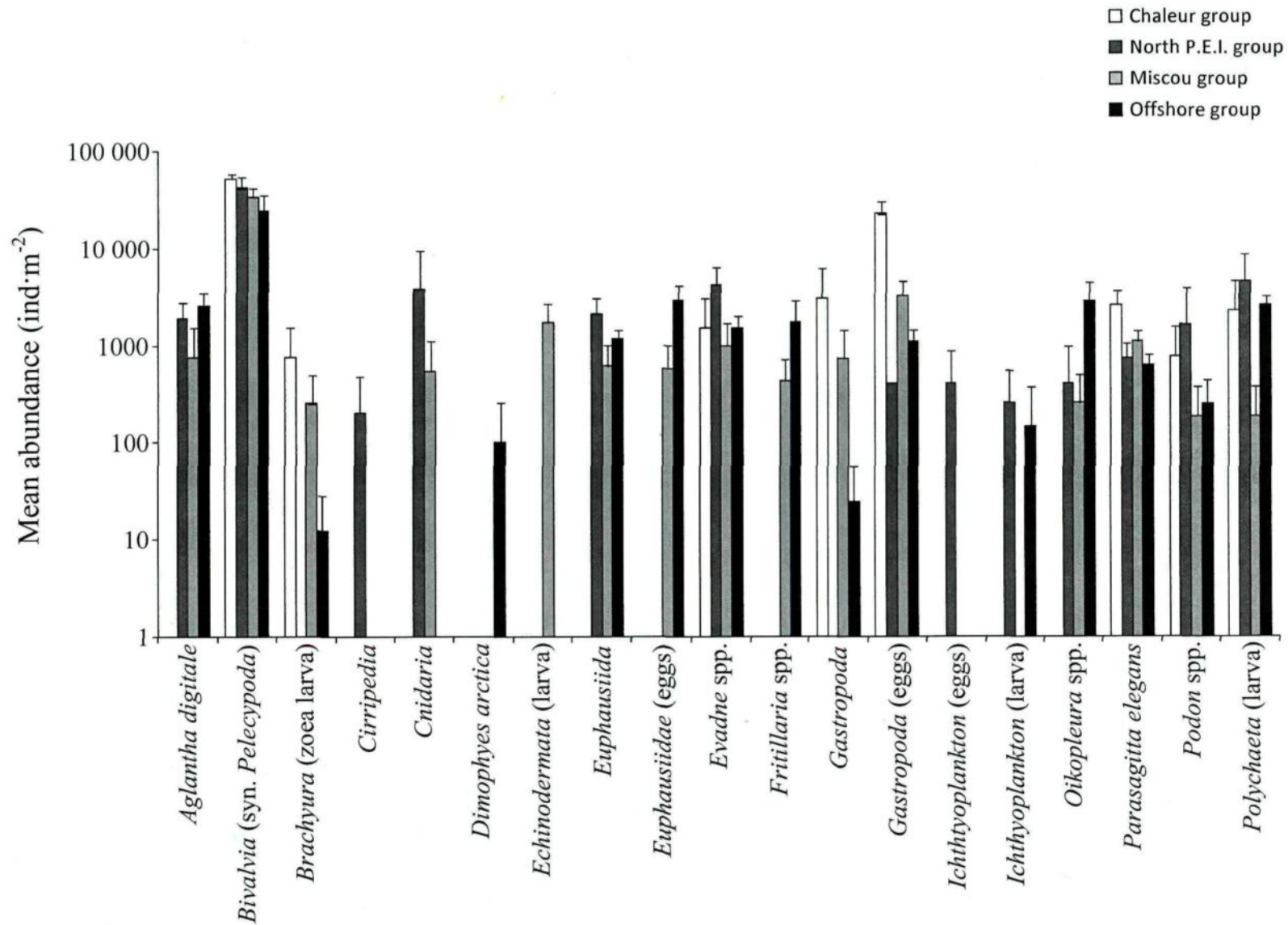


Figure 3b. Mean $\log_{10}$ -transformed abundance of other zooplankton taxa in the four zooplankton assemblages. Standard errors are shown.

The SIMPER analysis showed that the discriminating species between all zooplankton assemblages were very similar (Table 2). Only six groups (*Oithona* spp., *Pseudocalanus* spp., *Temora* spp., *Microsetella* spp., copepod eggs < 135 μ m, and *C. finmarchicus*) had a strong effect on station groupings. The zooplankton assemblage in the Chaleur group was dominated by *Oithona* spp. and *Pseudocalanus* spp., which contributed 74.8% to the average similarity. The North P.E.I. group was dominated by *Oithona* spp. and *T. longicornis*, with contributions to the average similarity of 64.1% and 11.8%, respectively. The zooplankton assemblage in Miscou group was dominated by *Oithona* spp. and *Microsetella* spp., which contributed 71.0% to the average similarity. The Offshore group was dominated by *Oithona* spp. and *Pseudocalanus* spp., with contributions to the average similarity of 62.5% and 12.7%, respectively. The contribution of *C. finmarchicus* was only important for the Offshore group, with a relatively low contribution compared to other zooplankton species. Species that contributed the most to the dissimilarity between groups were *Pseudocalanus* spp., *Microsetella* spp., and *Oithona* spp. Total zooplankton abundance was highest in the Chaleur and Miscou groups, which also had the lowest diversity.

Table 2. Key characteristics of the four zooplankton assemblages.

Zooplankton assemblages				
Assemblage parameters	Chaleur group	North P.E.I. group	Miscou group	Offshore group
Physicochemical parameters				
Average depth ($\pm$ SE) (m)	32 $\pm$ 1	33 $\pm$ 5	66 $\pm$ 13	75 $\pm$ 9
Sea-surface temperature ($\pm$ SE) ($^{\circ}$ C)	13.4 $\pm$ 0.5	15.3 $\pm$ 0.6	14.3 $\pm$ 0.4	13.6 $\pm$ 0.5
Sea-surface salinity ($\pm$ SE)	27.1 $\pm$ 0.1	26.0 $\pm$ 0.3	27.7 $\pm$ 0.1	27.9 $\pm$ 0.5
Biological parameters				
Total zooplankton abundance ($n \cdot m^{-2}$)	3 528 045	1 011 767	1 422 076	880 163
Species richness (Margalef's index)	0.80	1.07	0.93	1.26
Species typifying assemblage	<i>Oithona</i> spp.	<i>Oithona</i> spp.	<i>Oithona</i> spp.	<i>Oithona</i> spp.
(contribution to average similarity (%))	38.09	64.10	50.47	62.52
	<i>Pseudocalanus</i> spp.	<i>Temora</i> spp.	<i>Microsetella</i> spp.	<i>Pseudocalanus</i> spp.
	36.73	11.79	20.57	12.73
	Copepod eggs <135 μ m	<i>Pseudocalanus</i> spp.	<i>Pseudocalanus</i> spp.	<i>C. finmarchicus</i>
	12.41	8.62	15.94	6.58
	<i>Temora</i> spp.	<i>Microsetella</i> spp.	Copepod eggs <135 μ m	<i>Temora</i> spp.
	4.97	5.70	4.99	6.31

The Offshore group was the only assemblage to contain mackerel larvae from the three length classes (Fig. 4). The Miscou group had larvae from the bigger length class only and larvae from this group had the highest mean standard length with 7.30 mm. The North P.E.I. group had smaller larvae than other groups with a mean standard length of only 3.57 mm. Finally, the Chaleur group was dominated by larvae bigger than 5.4 mm.

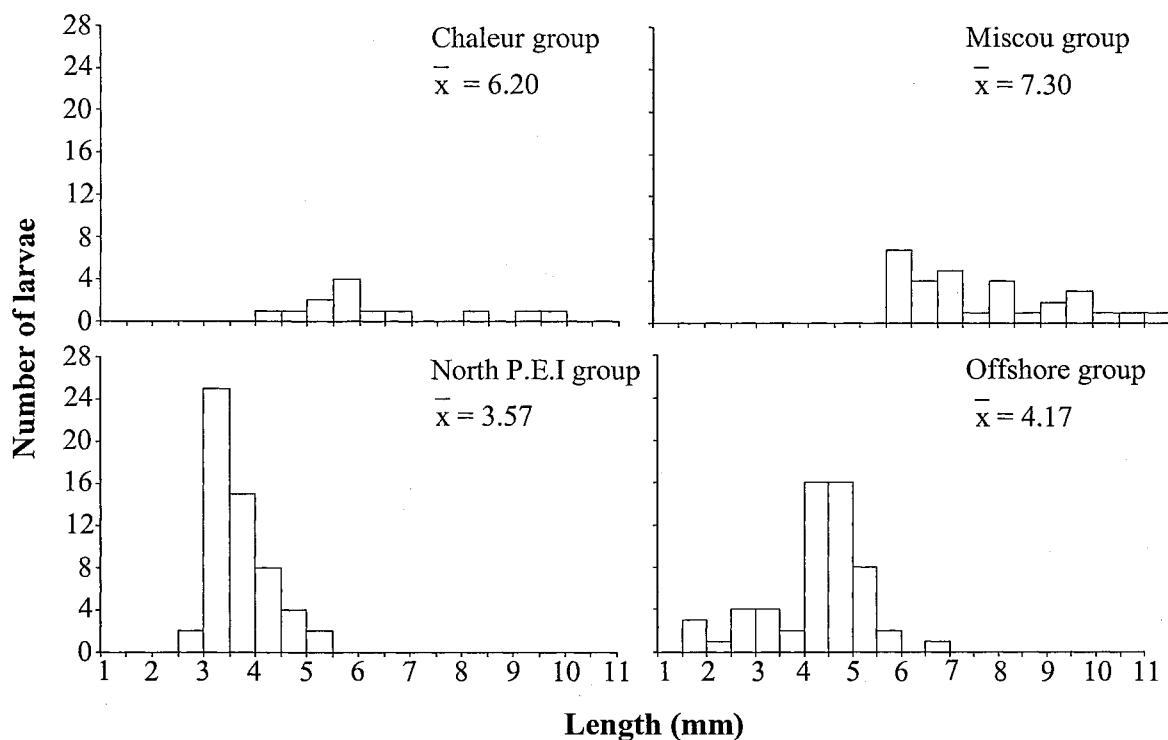


Figure 4. Standard lengths by zooplankton assemblage of mackerel larvae analyzed for stomach content analysis.

2.3.2 Diet composition

Oithona spp. nauplii (mostly *O. similis*) were the main prey of small mackerel larvae (< 3.5 mm), making up 85 to 100% of prey numbers in the diet (Table 3). As shown by the low feeding incidence, mackerel at this size did not eat a wide variety of prey. The carbon weight of the stomach content of these larvae was also dominated by *Oithona* spp. nauplii, which made up 92 to 100% of the biomass (Table 4). Of all length classes, larvae < 3.5 mm had the lowest mean carbon ingested, with an average of only 0.15 μgC per larva.

Mackerel larvae ≥ 3.5 mm long had a more diverse diet than smaller larvae; it was mainly composed of *Oithona* spp. nauplii, *Pseudocalanus* spp. nauplii, and both

developmental stages of *Temora* spp. (Table 3). *Oithona* spp. nauplii made up a significant fraction of the diet of larger larvae in all assemblages and were the main prey for 3.5–5.4 mm larvae in the North P.E.I. group and for larvae > 5.4 mm in the Offshore group, with 72 and 75% of the diet in numbers, respectively. However, *Oithona* spp. nauplii represented a small fraction of the total carbon ingested in larger larvae, contributing only 0.74–36% of the biomass (Table 4). *Pseudocalanus* spp. nauplii were the main prey of the two larger length classes of mackerel larvae in the Chaleur group, contributing from 34 to 82% of the diet in numbers and from 15 to 92% in biomass. In other assemblages, *Pseudocalanus* spp. was not the most important prey: *Temora* spp. nauplii was the main prey of 3.5–5.4 mm larvae in the Offshore group while *Temora* spp. copepodites was the main prey for larvae > 5.4 mm in the Miscou group. In general, *Temora* spp. contributed a significant fraction of the diet for the other length classes and assemblages. Except for the Chaleur and Miscou groups, *Temora* spp. nauplii and, especially, copepodites were the most important prey in terms of carbon for larvae ≥ 3.5 mm. The carbon content of larvae > 5.4 mm from the Chaleur and Miscou groups was mostly dominated by fish larvae (mainly smaller mackerel larvae; 46 and 73%, respectively). *Pseudocalanus* spp. nauplii were the main prey in terms of carbon for 3.5–5.4 mm larvae in the Chaleur group. The consumption of copepodite stages and larger prey such as *C. finmarchicus* nauplii, cladocerans, and fish larvae tended to increase with length classes (Tables 3 and 4).

Larvae 3.5–5.4 mm long in the Offshore group had the highest feeding incidence (90%), the highest mean number of prey (6.3), and the highest mean carbon ingested (3.17 μg). For larvae > 5.4 mm, the mean carbon ingested tended to decrease from the Chaleur

group to the Offshore group along with the feeding incidence, which reached its maximum (100%) in the Chaleur group. However, the mean number prey ingested was not correlated to the mean carbon ingested.

Table 3. Diet composition of larval mackerel expressed as the percent contribution in numbers of the different prey taxa by length class and zooplankton assemblage.

Prey taxon	Length class (mm)							
	< 3.5		3.5–5.4			> 5.4		
	North P.E.I. group	Offshore group	Chaleur group	North P.E.I. group	Offshore group	Chaleur group	Miscou group	Offshore group
Copepods								
Eggs	—	—	—	—	0.83	—	—	—
Nauplii								
<i>Acartia</i> spp.	3.03	—	—	—	—	—	0.70	—
<i>Calanus finmarchicus</i>	—	—	—	—	2.08	7.55	6.99	—
<i>Centropages</i> spp.	3.03	—	9.09	1.33	1.25	—	—	—
<i>Oithona</i> spp.	84.85	100	9.09	72.00	22.82	20.76	20.28	75.00
<i>Eurytemora</i> spp.	3.03	—	—	—	—	—	—	—
<i>Metridia</i> spp.	—	—	—	—	0.42	1.89	0.70	—
<i>Microcalanus</i> spp.	—	—	—	—	0.83	3.77	—	—
<i>Microsetella</i> spp.	—	—	—	1.33	0.42	—	—	—
<i>Pseudocalanus</i> spp.	—	—	81.82	5.33	13.70	33.96	6.99	—
<i>Temora</i> spp.	—	—	—	9.33	31.12	7.55	13.29	25.00
<i>Tortanus</i> spp.	3.03	—	—	—	—	1.89	0.70	—
Copepodites								
<i>Acartia</i> spp.	—	—	—	—	—	—	0.70	—
<i>Eurytemora</i> spp.	—	—	—	—	2.50	—	0.70	—
<i>Microcalanus</i> spp.	—	—	—	—	—	—	0.70	—
<i>Oithona similis</i>	—	—	—	—	0.83	—	1.40	—
<i>Pseudocalanus</i> spp.	—	—	—	—	0.42	—	5.59	—
<i>Temora longicornis</i>	—	—	—	8.00	22.00	15.09	32.87	—
Non-identified copepods	—	—	—	2.67	—	—	5.59	—
Cladocerans	—	—	—	—	—	3.77	0.70	—
Fish larvae	—	—	—	—	—	3.77	2.10	—
Others ^a	3.03	—	—	—	0.83	—	—	—
Number of larva analyzed	27	12	4	29	42	9	30	3
Number of fish with ≥ 1 prey	13	1	3	17	38	9	22	2
Feeding incidence (%)	48.00	0.08	75.00	59.00	90.00	100.00	73.00	67.00
Mean number of prey	2.5	2.0	3.7	4.4	6.3	5.9	6.5	2.0

^a Includes Ostracoda and Bivalves

Table 4. Diet composition of larval mackerel expressed as the percent contribution in carbon (μg) of the different prey taxa by length class and zooplankton assemblage.

Prey taxon	Length class (mm)							
	< 3.5		3.5–5.4			> 5.4		
	North P.E.I. group	Offshore group	Chaleur group	North P.E.I. group	Offshore group	Chaleur group	Miscou group	Offshore group
Copepods								
Eggs	—	—	—	—	0.30	—	—	—
Nauplii								
<i>Acartia</i> spp.	1.41	—	—	—	—	—	0.01	—
<i>Calanus finmarchicus</i>	—	—	—	—	3.55	2.33	4.70	—
<i>Centropages</i> spp.	2.15	—	6.97	1.23	0.48	—	—	—
<i>Oithona</i> spp.	92.16	100.00	1.13	31.18	3.21	0.74	0.83	35.92
<i>Eurytemora</i> spp.	2.31	—	—	—	—	—	—	—
<i>Metridia</i> spp.	—	—	—	—	0.04	0.04	0.10	—
<i>Microcalanus</i> spp.	—	—	—	—	0.05	0.11	—	—
<i>Microsetella</i> spp.	—	—	—	0.17	0.02	—	—	—
<i>Pseudocalanus</i> spp.	—	—	91.91	11.33	15.31	14.89	3.05	—
<i>Temora</i> spp.	—	—	—	12.00	18.31	1.63	2.23	64.08
<i>Tortanus</i> spp.	1.98	—	—	—	—	0.04	0.02	—
Copepodites								
<i>Acartia</i> spp.	—	—	—	—	—	—	0.30	—
<i>Eurytemora</i> spp.	—	—	—	—	10.35	—	0.11	—
<i>Microcalanus</i> spp.	—	—	—	—	—	—	0.18	—
<i>Oithona similis</i>	—	—	—	—	1.02	—	0.35	—
<i>Pseudocalanus</i> spp.	—	—	—	—	0.26	—	10.33	—
<i>Temora longicornis</i>	—	—	—	44.10	47.11	7.14	31.33	—
Cladocerans	—	—	—	—	—	0.62	0.13	—
Fish larvae	—	—	—	—	—	72.46	46.33	—
Number of larva analyzed	27	12	4	29	42	9	30	3
Mean carbon ingested (μg)	0.16	0.14	2.08	0.72	3.17	11.65	11.18	0.29

2.3.3 Feeding selectivity

Most mackerel larvae positively selected nauplius stages of *Oithona* spp. and *Temora* spp. Small larvae selected almost exclusively small *Oithona* spp. nauplii. Except for the Chaleur group, *Temora* spp. nauplii were positively selected by larger mackerel larvae (≥ 3.5 mm); this was especially true in the Offshore group, which had a Chesson α index of 0.44. In all assemblages and length classes, mackerel larvae exhibited negative selectivity against *Pseudocalanus* spp. nauplii, except for the 3.5–5.4 mm larvae from the Chaleur group. However, mackerel larvae from this length class and assemblage had the same Chesson α index for the three species due to small sample size. Larvae fed little on *C. finmarchicus*, but the selectivity for this prey was significantly positive in the Miscou group for larger larvae. Fish larvae, *Centropages* spp. nauplii, and *Temora* spp. copepodites were also positively selected by mackerel larvae > 5.4 mm in the Miscou group. Only larvae > 5.4 mm selected for copepodite stages and fish larvae.

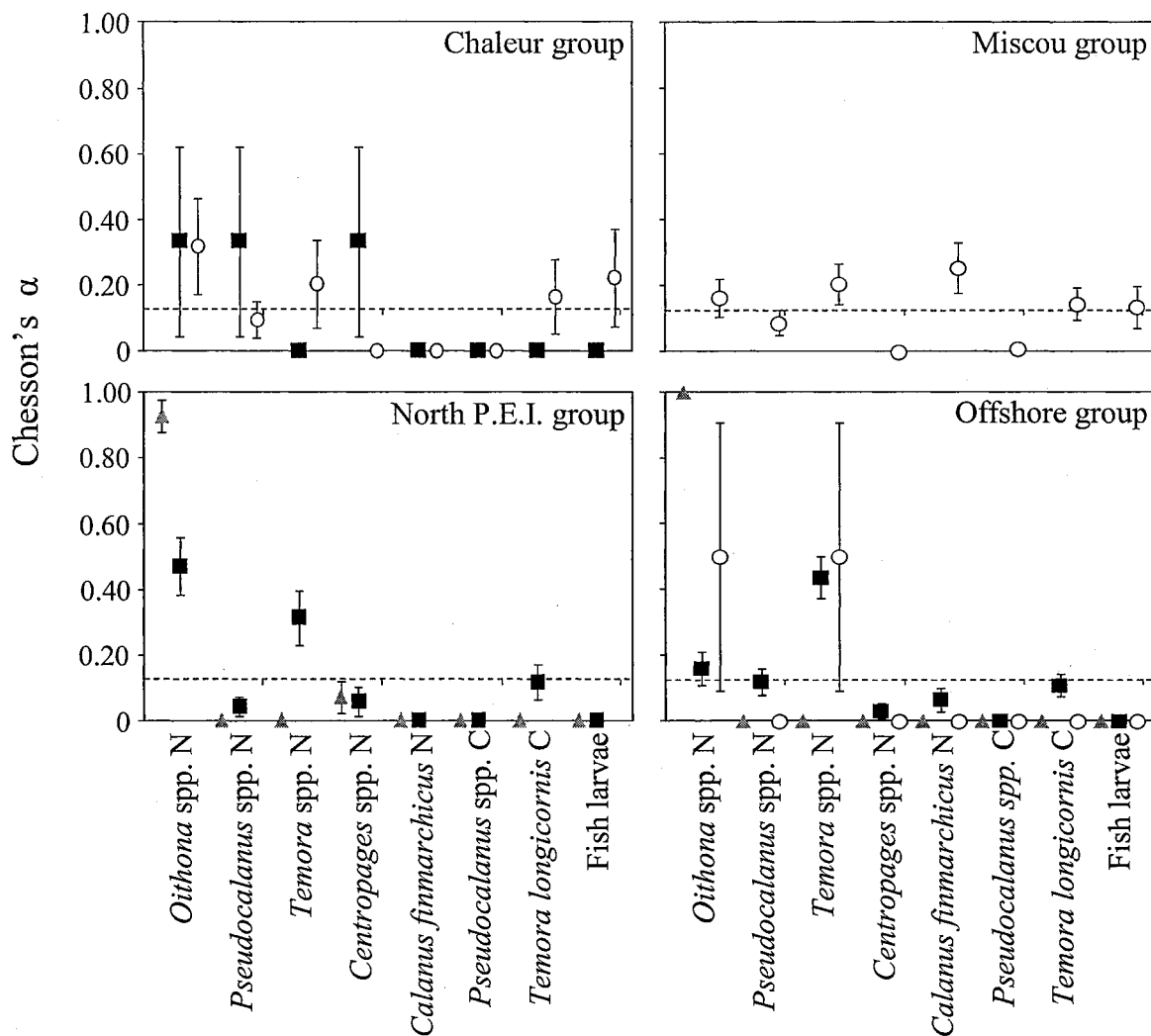


Figure 5. Chesson's α selectivity index of mackerel larvae for assemblages and for length classes < 3.5 mm (grey triangles), $3.5-5.4$ mm (black squares), and > 5.4 mm (white circles). The dotted lines indicate minimum threshold values ($1/N$) for random selection, as described by Chesson (1978). Errors bars represent standard errors.

2.3.4 Energetic index

The energetic index, expressed as mean biomass per prey, was calculated for each year analyzed in the three studies on larval mackerel diet in the southern GSL (Ringuette *et al.*, 2002; Robert *et al.*, 2008; this study). In general, the mean biomass per prey tended to increase with larval mackerel length, reaching a maximum of 6.39 μgC per prey in 1997 for larvae 5.5–7 mm (Table 5). This trend is less pronounced for larger larvae from 1982 to 1996, which reached a maximum of only 2.12 μgC per prey in 1982. Small larvae from 2008 had the lowest energetic index, with a range of values of only 0.05–0.07 μgC per prey. In contrast, larvae < 3.5 mm from 1998 had the highest energetic index, with a maximum of 2.55 μgC per prey. The range of biomass per prey values for 3.5–5.4 mm larvae were similar among the three studies, ranging from 0.01 to a maximum of 5.17 μgC per prey in 1999. Both strong year-classes (1982 and 1999) were characterized by a high energetic index for this length class. Larvae of 5.5–7 mm in length from 1997 had the highest energetic index for this length class, with a maximum of 5.17 μgC per prey.

Table 5. Comparative energetic index ((mean) range of biomass [μgC] per prey values) between the three studies on the diet of larval mackerel in the southern Gulf of St. Lawrence (Ringuette *et al.*, 2002; Robert *et al.*, 2008; and this study).

Length class (mm)				
	<3.5	3.5–5.4	5.5–7	
1982*	(0.11) 0.05–0.14	(0.36) 0.02–2.12	(0.54) 0.20–0.89	Ringuette <i>et al.</i> 2002
1985	(0.27) 0.13–0.76	(0.25) 0.04–0.49		
1987	(0.20) 0.07–0.39	(0.20) 0.05–0.50	(0.44) 0.14–0.75	
1996	(0.09) 0.01–0.17	(0.23) 0.01–1.05	(0.33) 0.03–1.28	
1997		(0.33) 0.03–0.74	(0.45) 0.12–4.10	Robert <i>et al.</i> 2008
1998	(0.50) 0.03–2.55	(0.37) 0.09–2.76	(0.49) 0.08–5.17	
1999*		(0.39) 0.07–5.17	(3.17) 0.18–6.39	
2000		(0.21) 0.05–0.45	(0.31) 0.06–1.73	
2008	(0.07) 0.05–0.07	(0.38) 0.06–1.55	(0.22) 0.07–0.38	Present study
2010		(0.38) 0.07–0.64	(0.60) 0.07–1.66	

*Strong year-class

2.4 DISCUSSION

The principal objective of this study was to examine the influence of various assemblages of copepod prey on the feeding of Atlantic mackerel larvae in the southern GSL. This study was also an attempt to clarify inconsistencies in the literature on the role of preferred prey in the feeding and recruitment of mackerel larvae in the GSL.

Our results demonstrated that *O. similis* and *T. longicornis* nauplii were very important in the diet of larval mackerel in the southern GSL and were generally positively selected by larvae. *Oithona* spp. nauplii were the most abundant copepod prey in all zooplankton assemblages in the southern Gulf; this was also observed around the Îles-de-la-Madeleine by Robert *et al.* (2008). In addition, they were the copepod prey the most consumed by mackerel larvae, especially those < 3.5 mm. This is the first study to show strong predation of mackerel larvae on *Oithona* spp. nauplii and a positive selection for this prey in the GSL, since previous studies (Ringuette *et al.*, 2002; Darbyson *et al.*, 2003; Robert *et al.*, 2008) generally reported low predation on *Oithona* spp. nauplii and negative selection for this prey. However, *Oithona* spp. nauplii represented only a small fraction of the total carbon ingested by mackerel larvae, except in larvae < 3.5 mm for which the carbon content was dominated by this small copepod prey.

Consistent with previous studies on adult mackerel diet (Grégoire and Castonguay, 1989; Darbyson *et al.*, 2003), *Temora* spp. was also an important prey in the diet of mackerel larvae in terms of numbers and carbon content, bypassing *Pseudocalanus* spp. *Temora* spp. was generally positively selected by mackerel larvae, as they were eaten in greater proportion compared with their abundance at the station. *Pseudocalanus* spp.

nauplii were the most important prey in the gut content of mackerel larvae in only one assemblage (*i.e.*, the Chaleur group, larvae 3.5–5.4 mm) and were generally selected against by larvae. These results differ from Robert *et al.* (2008), who demonstrated a dominance of *Pseudocalanus* spp. nauplii in the diet of larvae < 7 mm and a strong selectivity for this prey. Similar to the findings of Robert *et al.* (2008), we found that mackerel larvae in all assemblages did not feed much on *C. finmarchicus*, although this prey was selected for by larvae > 5.4 mm in the Miscou group. The low incidence of *C. finmarchicus* nauplii in the gut content of mackerel larvae can be attributed to their low abundance in the southern GSL for the two years of sampling used in this study compared to other years (Castonguay *et al.*, 1998). *C. finmarchicus* abundance was high only in offshore stations and consisted mostly of copepodite stages, which are too large to be consumed by small mackerel larvae (< 5.4 mm). These differences in the abundance of *C. finmarchicus* between years can be explained by the fact that while *Calanus* spp. are relatively rare in the southern GSL, this group is very abundant in this region during some years, especially for offshore stations (Runge *et al.*, 1999; Locke, 2002; Castonguay *et al.*, 2008). Years of high abundance could be due to low RIVSUM (index of river discharge from the St. Lawrence River and its major tributaries) that promotes the invasion of *C. finmarchicus* from source regions in deeper areas of the northwest GSL into the western part of the southern GSL (Runge *et al.*, 1999).

Scombrid fish exhibit an early feeding shift from planctivory to piscivory during ontogeny: young larvae feed primarily on copepod nauplii and eggs while bigger larvae feed on copepodite stages and fish larvae (Last, 1980; Grave, 1981; Hunter, 1981; Fortier

and Villeneuve, 1996; Hillgruber and Kloppmann, 2001). As larvae grow, prey size increases, so larvae can increase their growth rate and therefore their chances of survival. Robert *et al.* (2008) also observed a shift in selection from *Pseudocalanus* spp. and *Temora* spp. nauplii to large cladocerans and fish larvae starting from ~7 mm in body length. Consistent with these results, larger prey such as *C. finmarchicus* nauplii, cladocerans, and fish larvae (mainly mackerel larvae) were eaten by larvae > 4.5 mm. The consumption of *C. finmarchicus* nauplii increased constantly with length. Fish larvae were only observed in the gut content of bigger larvae (> 9 mm) and were generally the only prey present in the stomach, contributing most of the total carbon content of these larvae.

Ringuette *et al.* (2002) observed that *Pseudocalanus* spp. and *C. finmarchicus* nauplii accounted for most of the gut content of mackerel larvae in the GSL while Robert *et al.* (2008) found that *Pseudocalanus* spp. was strongly selected by mackerel larvae around Îles-de-la-Madeleine. Our results highlight the importance of *O. similis* in the diet of mackerel larvae in the GSL. These different results suggest that *Oithona* spp. nauplii seem to become more important in the diet when there is not a great abundance of large copepods such as *Pseudocalanus* spp. or *C. finmarchicus*, as observed in this study. In contrast, when there is a great abundance of large copepod prey, mackerel larvae seem to prefer them, as observed in Ringuette *et al.* (2002), Robert *et al.* (2008), and for Chaleur group in this study. In fact, in this study, the abundance of the small copepod *Oithona* spp. was greater than the abundance of mackerel larvae classical prey (*C. finmarchicus*, *Pseudocalanus* spp. and *T. longicornis*) except for the Chaleur group where *Pseudocalanus* spp. was dominant. In contrast, the approximate abundance of classical prey, extracted from Robert *et al.* 2008,

was greater than abundance of *Oithona* spp. Moreover, the comparison of female abundance from Ringuette *et al.* 2002 and this study shows that the exceptional recruitment year of 1982 had much more *C. finmarchicus* and *Pseudocalanus* spp. female than in this study. In fact, for both species, the abundance in 1982 was between 0 and more than 10 000 $\text{no}\cdot\text{m}^{-2}$ while for this study, the abundance varied from 40 to 830 $\text{no}\cdot\text{m}^{-2}$ and 2 900 to 10 700 $\text{no}\cdot\text{m}^{-2}$, for *C. finmarchicus* and *Pseudocalanus* spp. females respectively. These findings agree with the optimal foraging theory, which stipulates that organisms should maximize their net energy intake per unit time of foraging (MacArthur and Pianka, 1966). In other words, the selectivity for prey reflects the optimum ratio between energy gain and energy spent for the capture of prey. *Pseudocalanus* spp. and *C. finmarchicus* are known to be the most energetically valuable prey for mackerel larvae (Robert *et al.*, 2008) and should be preferred by larvae when they are abundant. However, in years of low abundance, feeding selectively on these large prey should become too expensive for larvae since they spend more time searching for these prey. This may explain why the ubiquitous *Oithona* spp. can become a profitable prey for small mackerel larvae, even though they have a lower carbon content. The small *Oithona* spp. and the medium-sized *T. longicornis* can be considered important alternative prey for mackerel larvae in terms of energy gain.

Therefore, when the abundance of large copepods is high, mackerel larvae seem to specialize and prey preferentially on the more abundant and valuable large copepod prey, possibly forming a search image (e.g., Ishii and Shimada, 2010). In fact, when a particular prey is very abundant, predators will encounter and eat this prey more often and will therefore develop a preference for this prey through a cryptic image representing that prey

called the search image (Ishii and Shimada, 2010). In contrast, larvae switch to an opportunistic generalist feeding behaviour when large copepods are less abundant, consuming energetically favourable prey if they are encountered more frequently than energetically inferior prey, but without actively selecting these prey types (Graeb *et al.*, 2005). This switching feeding behaviour has already been observed for sea bream (*Archosargus rhomboidalis*) and lined sole (*Achirus lineatus*) (Houde and Schekter, 1980). Thus, we hypothesize that it is probably a high abundance of large copepods, and especially female copepods, producing an exceptionally high abundance of large nauplii throughout the southern GSL, rather than a high abundance of small copepods, that will produce exceptional mackerel year classes in Canada. This idea is supported by Runge *et al.* (1999), who showed that the strong mackerel recruitment of 1982 occurred in a period where the biomass of large ($> 1000 \mu\text{m}$, mainly *Calanus finmarchicus*) zooplankton was the highest of the decade. High biomass of large zooplankton also prevailed in the GSL in 1999, which coincided with the strong year-class of the other decade studied (Castonguay *et al.*, 2008).

Concerning the comparative energy index, our results showed no specific trend between the mean biomass per prey and the years analyzed for the three studies. The only exception is for the strong year-classes of 1982 and 1999, where the mean biomass per prey for 3.5–5.4 mm larvae were higher than other years. We suggest that a high energy index is a necessary condition but is not sufficient to produce an exceptional year-class: a good energy index will not necessarily give rise to a good year-class. This result agrees with Castonguay *et al.* (2008), who observed strong relationships between different variables analyzed and the two years of high recruitment and poor relationships for the other years.

Our results show the importance of *O. similis* and *T. longicornis* in the diet of larval Atlantic mackerel in the southern GSL, which contrasts with previous studies. These contrasting results indicate that it is difficult to generalize on the importance of either copepod species in determining the recruitment of Atlantic mackerel. We suggest that it is an exceptionally high availability of large copepod prey such as *Pseudocalanus* spp. or *C. finmarchicus* nauplii throughout the southern GSL rather than a high availability of small copepod prey that will produce an exceptional mackerel year-class. These results concerning the preferred prey of mackerel larvae should be used to adjust the predictive model of mackerel recruitment based on *Pseudocalanus* spp., *Temora* spp., and *C. finmarchicus* egg production.

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CHAPITRE III

CONCLUSION GÉNÉRALE

Cette étude a été réalisée dans le but de vérifier l'influence de différents assemblages zooplanctoniques sur l'alimentation des larves du maquereau bleu, dans le sud du golfe du Saint-Laurent. Ce projet se voulait aussi une tentative de résoudre les désaccords dans la littérature quant au rôle des proies préférentielles dans l'alimentation et le recrutement du maquereau bleu pour ultimement ajuster les modèles prédictifs du recrutement de ce poisson d'importance commerciale.

Les résultats obtenus ont démontré l'importance des stades nauplii des copépodes *O. similis* et *T. longicornis* dans l'alimentation des larves de maquereau bleu du sud du golfe du Saint-Laurent. Ces proies étaient consommées en grand nombre par les larves de maquereau bleu et étaient généralement positivement sélectionnées par les larves. Le copépode *O. similis* était le plus abondant dans le golfe du Saint-Laurent et était aussi le copépode le plus consommé par les larves de maquereau bleu, spécialement les larves plus petites que 3.5 mm. Cette étude est la première à démontrer une prédation importante des larves de maquereau bleu sur les stades nauplii du copépode *O. similis* et à démontrer une sélection positive pour ces petites proies. Toutefois, la contribution du copépode *O. similis* à la biomasse totale ingérée par les larves de maquereau bleu était plutôt faible, à l'exception des plus petites larves. Le copépode *Temora* spp. était également une proie importante dans la diète des larves de maquereau bleu en termes de nombre et de biomasse, surpassant le copépode *Pseudocalanus* spp. Ce dernier était important pour la diète des larves d'un assemblage seulement et était généralement négativement sélectionné par les larves. Le copépode *C. finmarchicus*, pratiquement absent du sud du golfe en 2008 et 2010 a, quant lui, été consommé en faible proportion par les larves de maquereau bleu.

Ces résultats sont très différents de ceux obtenus lors d'études précédentes sur l'alimentation des larves de maquereau bleu dans le sud du golfe du Saint-Laurent. Les divergences des résultats entre ces études montrent qu'il est difficile de généraliser sur l'importance de l'une ou l'autre des espèces de copépodes préférentiels dans le recrutement du maquereau bleu. Toutefois, une hypothèse concernant le comportement alimentaire des larves de maquereau bleu peut tout de même être émise considérant les résultats obtenus dans cette étude. En effet, les stades nauplii du copépode *O. similis* semblent être plus importants dans la diète des larves de maquereau bleu lorsqu'il n'y a pas ou peu de grosses proies copépodes comme *Pseudocalanus* spp. ou *C. finmarchicus*. Par contre, lorsqu'il y a une forte abondance de grosses proies copépodes, les larves de maquereau bleu semblent s'y intéresser davantage. Ainsi, à forte abondance de grosses proies, les larves de maquereau bleu semblent opter pour un comportement alimentaire spécialiste, se nourrissant préférentiellement sur les proies abondantes et favorables énergétiquement. Au contraire, à faible abondance de grosses proies, les larves semblent adopter un comportement alimentaire opportuniste généraliste, puisqu'elles consomment des proies énergétiquement favorables, seulement si elles sont rencontrées plus fréquemment que les proies avec moins de valeur énergétique, mais ne sélectionnent pas activement ce type de proies. De ce fait, nous suggérons qu'il s'agit probablement d'une disponibilité exceptionnelle de grosses proies (*Pseudocalanus* spp. ou *C. finmarchicus*) dans le sud du golfe du Saint-Laurent comparativement aux petites proies de copépodes qui produira une classe d'âge exceptionnelle de maquereau bleu, peu importe l'espèce de copépode. Les résultats de cette étude devraient être considérés pour ajuster le modèle prédictif du

recrutement du maquereau bleu basé sur l'abondance des œufs des copépodes *Pseudocalanus* spp., *C. finmarchicus* et *T. longicornis*. En effet, il faudrait pour l'avenir, tenir compte du copépode *Oithona* spp. dans le modèle de prédiction du recrutement du maquereau bleu. Il serait plus juste de relier l'indice du recrutement du maquereau bleu à un ratio grosse proie (*Pseudocalanus* spp. + *Calanus finmarchicus* + *Temora longicornis*) versus petite proie (*Oithona* spp.) au lieu d'utiliser la production d'œufs des trois copépodes préférentiels du maquereau bleu. D'ailleurs, il serait intéressant de vérifier la validité de la supposition selon laquelle le produit de l'abondance des femelles et du taux de production d'œufs spécifique à une espèce est un bon estimé de la production des proies. Dans le cas contraire, il faudrait plutôt utiliser l'abondance relative pour le calcul du ratio.

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