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CHAPITRE I
INTRODUCTION GÉNÉRALE

Le rôle des espèces marines dans l'évolution des sociétés humaines est indéniable. L'exploitation des ressources halieutiques a amené les premiers Européens à fouler la partie septentrionale de l'Amérique du Nord alors qu'ils exploitaient la zone productive des Grands bancs de Terre-Neuve. Historiquement, l'industrie de la pêche au Canada s'est imposée rapidement dans les régions côtières dès le début de la colonisation en raison d'une forte demande en poissons des pays européens. Dans toute la période précédant la Seconde Guerre mondiale, la récolte des ressources halieutiques était limitée par le nombre de pêcheurs et l'équipement utilisé. Cependant, le développement de la technologie au milieu du XXe siècle a amélioré les techniques et les équipements de récolte faisant en sorte que la pêche est graduellement passée d'une industrie limitée par les moyens techniques à une industrie limitée par la ressource exploitée (Gough, 2011).

1.1 Gestion des pêches

L'impact de la pêche moderne sur les stocks (portion exploitable d'une population), qui était jadis marginal, fait donc maintenant partie des principaux facteurs de mortalité au stade adulte et on l'estime parfois supérieur à la mortalité naturelle (Halliday & Pinhorn, 2009). Il est également important de se rappeler que même sans les impacts anthropiques, la taille des populations marines fluctue de façon importante en réaction aux variations des conditions environnementales (température, salinité, vents, courants, etc.). Ces deux facteurs ont une influence sur plusieurs aspects du développement et de la dynamique des populations en milieu marin, notamment la reproduction, l'abondance, la croissance, la distribution, les migrations, la prédation et la transmission de maladies (Adams, 1980;

Gunderson, 1980; Dominguez-Petit *et al.*, 2008; Drinkwater, 2009; Halliday & Pinhorn, 2009; Wright & Trippel, 2009). Dans le cas des poissons de fond, les facteurs environnementaux dans le nord-ouest de l'Atlantique, particulièrement le refroidissement des eaux, ont été défavorables à plusieurs espèces à l'époque même où l'effort de pêche a atteint des sommets. Ces deux phénomènes combinés ont participé à l'effondrement de plusieurs stocks à la fin du siècle dernier (Dutil *et al.*, 1998). Un des exemples les plus cités est l'effondrement de la morue franche (*Gadus morhua*) dans l'est du Canada, incluant le golfe du Saint-Laurent. Malgré l'imposition de moratoires au début des années 1990, plusieurs de ces stocks demeurent à des seuils ne permettant pas une récolte commerciale à long terme (Lilly, 2008).

La pêche, par les prises accidentelles, cause également des dommages aux populations d'espèces non commerciales. Elle détruit une partie de l'habitat par l'utilisation de chaluts qui labourent le fond marin (Kenchington *et al.*, 2006). Elle modifie la composition démographique des espèces présentes (Enberg *et al.*, 2009). Elle augmente la vulnérabilité aux variations dans les conditions environnementales (Ottersen *et al.*, 2006) et peut affecter le réseau trophique à plusieurs niveaux (Frank *et al.*, 2005; Benoit & Swain, 2008; Bundy *et al.*, 2009).

Une saine gestion des ressources devient donc essentielle si on désire une exploitation durable pour les décennies à venir. Les principales mesures de gestion utilisées sont des mesures restrictives qui visent à limiter les captures aux espèces d'intérêts commerciales. Parmi ces mesures, on peut citer des normes strictes sur les engins de pêche, des quotas de pêche par secteur et, dans certains cas extrême, un moratoire complet sur la

récolte d'une espèce. Dans la planification des détails techniques des mesures de gestion, la recherche fondamentale revêt un rôle important pour déterminer la source et l'intensité des facteurs jouant un rôle dans la survie et le recrutement des espèces.

1.2 Recrutement et stade larvaire

Afin de prévoir l'état de la ressource, les gestionnaires ont recouru à la modélisation de l'évolution des stocks. Ces modèles sont basés sur les connaissances antérieures de l'abondance des stocks et du recrutement dont les estimations sont issues en partie des pêches expérimentales et des débarquements de la pêche commerciale. Le recrutement est en grande partie lié à la survie au stade larvaire. On associe cette relation au taux de mortalité extrêmement élevé du stade larvaire qui en fait une période critique dans le cycle de vie d'une majorité de poissons osseux (Hjort, 1926; Houde, 2008; Leggett & Frank, 2008). Cette période charnière voit la poursuite du processus d'ontogénie amorcé au stade embryonnaire et le début de l'augmentation de la masse de l'organisme en réponse à l'apport de sources d'énergie et de nutriments externes. En fonction de l'espèce, l'alimentation exogène peut débuter pendant ou après la résorption du sac vitellin. L'importance de ce stade a longtemps été négligée (Cushing & Horwood, 1994). Cependant, comme mentionné par Fuiman & Werner (2002), celui-ci est sujet à un plus haut taux de mortalité parce qu'il doit supporter des contraintes similaires à celles des autres stades (juvéniles et adultes), mais avec des changements beaucoup plus rapides de tailles, de structure, de comportement et de capacité physique. De plus, le stade larvaire est caractérisé par une moins grande résistance à la famine, variant de moins de 24 heures à

quelques jours selon l'espèce. Après ce délai, une larve qui ne s'est pas alimentée est trop faible et incapable de se nourrir efficacement. Elle épuise donc ses réserves énergétiques avant de mourir (May, 1973; Houde, 2002). Les larves ont également une faible capacité natatoire et leurs déplacements sur de longues distances consistent principalement au transport passif des courants marins. Dans certains cas, on observe une migration verticale leur permettant d'accéder à des courants plus favorables (Grioche *et al.*, 2000), mais en général les courants créent une dispersion spatiale des larves pouvant les éloigner des zones productives nécessaires à leur survie (Iles & Sinclair, 1982; Fortier *et al.*, 1992). Conséquemment, et considérant le nombre de larves produites, un faible changement du taux de survie peut avoir des effets importants sur le recrutement d'une population. Ainsi, on observe régulièrement des cohortes de survie extrêmement faible chez de nombreuses espèces, même non exploitées, associées à une forte mortalité larvaire (Leggett & Deblois, 1994).

1.3 Alimentation larvaire

L'éclosion des larves de plusieurs espèces est synchronisée avec la production accrue des proies préférées. Cette synchronisation entre la production intense de proies et la présence des larves augmenterait les chances de survie selon l'hypothèse du « mismatch » (Cushing, 1990). Ainsi, une plus grande abondance de proies aura pour effet d'augmenter le taux de croissance et de diminuer la durée du stade larvaire (Chambers & Leggett, 1987). La présence de proies en grande quantité lors du stade larvaire est donc essentielle à l'émergence de fortes cohortes surtout si l'on considère que ce stade est sujet

en milieu naturel à un taux de mortalité qui avoisine les 99,99% (Anderson, 1988; Cushing, 1990; Campana, 1996; Robert *et al.*, 2008; Brochier *et al.*, 2011).

Gerking (1994) affirme que le régime alimentaire d'une espèce de poisson au stade larvaire lui confère pratiquement un statut « d'espèce distincte » si on compare sa niche alimentaire à cette période avec celle de sa phase adulte. Pour les espèces de poissons, plusieurs études ont démontré que même au stade larvaire le choix alimentaire est spécifique à certaines espèces de proies (Morote *et al.*, 2008; Robert *et al.*, 2008; Robert *et al.*, 2011). Chez certaines espèces, on peut observer la consommation de phytoplancton dans les premiers jours de l'alimentation exogène, mais l'utilisation de ce type d'aliments est généralement temporaire et l'on observe rapidement un changement d'alimentation vers la consommation de copépodes chez la plupart des espèces. Le stade de développement de copépodes sélectionné augmente avec la taille de la larve, donc avec l'augmentation de la capacité de capture et d'ingestion.

1.4 Le golfe du Saint-Laurent

Le golfe du Saint-Laurent est une zone de pêche importante qui n'a pas échappé à la chute drastique des abondances de poissons de fond à la fin du XXe siècle. Pourtant, cette région est reconnue comme une zone productive. Pendant l'hiver, la colonne d'eau est stratifiée en deux couches distinctes, une couche en surface plus froide ($< 3^{\circ}\text{C}$) et moins salée ($\approx 32,4$ psu) et une couche profonde plus chaude et plus salée ($> 3^{\circ}\text{C}$; > 34 psu) (Gilbert & Pettigrew, 1997). La couche profonde origine de l'intrusion par le détroit de Cabot des eaux du plateau continentale et du talus atlantique qui remonte les trois chenaux

du Golfe (Laurentien, Anticosti et Esquiman) (voir Figure 1, p. 14), alors que la couche de surface est constituée des eaux de ruissellement du bassin versant du Golfe et de l'estuaire du Saint-Laurent, mélangées aux eaux profondes dans les zones de remontée d'eau (Lauzier & Trites, 1957; Gratton *et al.*, 1988; Bourque & Kelley, 1995; Gilbert & Pettigrew, 1997). L'origine estuarienne et la présence de remontées d'eau profonde par forçage à plusieurs endroits rendent cette couche riche en nutriments, mais peu productive en hiver dû à un ensoleillement réduit, au couvert de glace et à l'épaisseur de la couche de mélange (De Lafontaine *et al.*, 1989; Galbraith, 2006). Cependant, au printemps, le réchauffement rapide en surface après la fonte des glaces crée une troisième couche plus chaude et moins dense qui isole la couche d'eau froide hivernale sous la surface (la couche intermédiaire froide) et qui procure, en raison de la présence de nutriments issus du mélange hivernal, les conditions idéales pour une production phytoplanctonique intense. Celle-ci est rapidement suivie d'une prolifération des espèces phytophages, principalement des copépodes (*Calanus finmarchicus*, *Temora longicornis*, *Oithona similis*, *Acartia* sp.) qui représentent environ 75% du zooplancton (de Lafontaine *et al.*, 1989). En plus de ces espèces endémiques, on observe dans le Golfe la présence d'espèces subarctiques, principalement *Calanus glacialis* et *C. hyperboreus*. Ces deux espèces de plus grande taille originaires de la mer du Labrador ont colonisé le golfe du Saint-Laurent par l'intrusion sporadique de masse d'eau à travers le détroit de Belle Isle qui, par leurs caractéristiques physico-chimiques, viennent renforcer la couche intermédiaire froide (Petrie *et al.*, 1988; Koutitonski, 1989; Smith *et al.*, 2006).

Selon ses caractéristiques géographiques et bathymétriques, le golfe du Saint-Laurent a été divisé en zones de gestion de la pêche par l'OPANO (Organisation des pêches de l'Atlantique Nord-Ouest). La région nord du Golfe, qui correspond aux divisions 4R et 4S, est caractérisée par une grande variabilité bathymétrique, une productivité primaire moins élevée et des températures plus froides comparativement à la région sud du golfe (division 4T; figure 1). Selon Frank *et al.* (2006), le nord du golfe du Saint-Laurent est également un écosystème à contrôle descendant (top down) où les espèces piscivores régularisent les populations d'espèces fourragères. Avant la réduction drastique des stocks, les espèces piscivores comme la morue franche (*Gadus morhua*), la plie canadienne (*Hippoglossoides platessoides*) et la limande à queue jaune (*Limanda ferruginea*) étaient susceptibles, par leur alimentation, de réguler dans cette région les populations de différentes espèces fourrages dont font partie les lançons (lançon d'Amérique, lançon du Nord ; *Ammodytes* spp.), la stichée arctique (*Stichaeus punctatus*) et la lompenie-serpent (*Lumpenus lampraeformis*) (Martell & McClelland, 1994; Bundy *et al.*, 2009; Morissette *et al.*, 2009). Cependant, en comparant les abondances d'ichtyoplancton avant et après la période d'effondrement des stocks, Bui et collaborateurs (2010) ont démontré que les abondances de larves de lançons (*Ammodytes* spp.) sont restées stables malgré cette forte réduction des principaux prédateurs, alors que, les larves d'autres espèces fourrages, principalement la stichée arctique (*Stichaeus punctatus*) et la lompenie-serpent (*Lumpenus lampraeformis*), ont augmenté en abondance en accord avec l'hypothèse de Frank et collaborateurs (2006) sur le contrôle par les prédateurs de l'écosystème du Nord du Golfe du Saint-Laurent.

Actuellement, le cycle de vie et l'alimentation du lançon (*Ammodytes* sp.) sont relativement bien connus puisque certaines espèces, abondante à travers les zones tempérées de l'hémisphère nord, font l'objet d'une pêche commerciale dans l'Atlantique Nord-Est. Néanmoins, la majorité des études publiées sont axées sur le stade adulte et très peu décrivent en détail l'alimentation au stade larvaire. De plus, la communauté zooplanctonique varie de façon importante suivant la région étudiée, rendant difficile la comparaison de la sélection alimentaire des larves entre régions. À l'opposé, la stichée arctique et la lompénie-serpent sont des espèces qui ont été très peu étudiées et la presque totalité des connaissances porte également sur le stade adulte. De plus, l'alimentation au stade larvaire n'a jamais été détaillée pour les espèces consommées et se limite, dans les meilleurs cas, aux stades de croissance des copépodes (pour la stichée arctique seulement). Sans des connaissances plus approfondies, on peut difficilement expliquer les liens trophiques de ces populations en milieu naturel.

1.5 Objectif

L'objectif de mon étude est donc de parfaire les connaissances sur l'alimentation du stade larvaire du lançon, de la stichée arctique et de la lompénie serpent à travers quatre sous-objectifs. (i) Décrire la communauté zooplanctonique du milieu étudié. (ii) Décrire le régime alimentaire des trois espèces de larves. (iii) Déterminer la sélectivité alimentaire des larves. (iv) Comparer les niches alimentaires pour déterminer la possibilité d'interactions de compétitions dans le nord du golfe du Saint-Laurent entre ces trois espèces.

CHAPITRE II

ZOOPLANKTON PREY SELECTION AMONG THREE DOMINANT ICHTHYOPLANKTON SPECIES IN THE NORTHWEST GULF OF ST LAWRENCE

2.1 Introduction

Before the collapse of Atlantic cod (*Gadus morhua*) and the decline of other fisheries [e.g., redfish (*Sebastes* spp.), American plaice (*Hippoglossoides platessoides*)] in the early 1990s, the Gulf of St. Lawrence (GSL) was considered a top-down controlled ecosystem (Frank *et al.*, 2005; Savenkoff *et al.*, 2007). The main fish prey of these top predators include capelin (*Mallotus villosus*), sandlance (*Ammodytes* spp.), Atlantic mackerel (*Scomber scombrus*), arctic shanny (*Stichaeus punctatus*) and snakeblenny (*Lumpenus lampretaeformis*) (Lilly and Fleming, 1981; Scott and Scott, 1988; Morissette *et al.*, 2003; Savenkoff *et al.*, 2004). According to the theory of population dynamics, a decrease in the main predators is presumed to be followed by an increase in the abundance of their prey in a top-down controlled ecosystem (Peckarsky *et al.*, 2008). However, a recent comparison of the ichthyoplankton communities for the years before and after the Atlantic cod collapse in the northwest GSL showed no indication of changes in the average abundance of sandlance larvae (Bui *et al.*, 2010). On the other hand, the same study showed that larval stages of forage species such as arctic shanny and snakeblenny have increased in abundance in the ichthyoplankton community, suggesting—as expected—an increase in abundance of these populations following the release of predation pressure.

Top-down forcing is not the only way that species abundance is regulated in an ecosystem, for instance, bottom-up effects caused by limited prey abundance have been observed in various aquatic ecosystems (Blanco *et al.*, 2003; Brown-Saracino *et al.*, 2007; Grabowski *et al.*, 2009). Gliwicz (2002) pointed out that predation and starvation mechanisms underling top-down and bottom-up effects are fundamentally different but

usually work in conjunction to limit species abundance. Hence, lowering the impact of one regulating agent can increase the importance of the other in community structuring. Since ichthyoplankton growth relies mainly on copepod density, changes in copepod abundance can modify energy transfer pathways in the community, potentially favouring one species over another through competition.

During early life, the transition from endogenous to exogenous feeding is known to be a critical period for larval fish; the high mortality rate have a direct implication on recruitment (Cushing, 1975; Fuiman and Werner, 2002; Houde, 2008). The feeding habits of sandlance larvae have been studied (Fortier *et al.*, 1992; Simonsen *et al.*, 2006; Malzahn and Boersma, 2009), but except for the study by Monteleone's (1986), none has given special attention to discriminating between copepod species and developmental stages in the diet. Monteleone's (1986) study took place in Long Island Sound, where sandlance actively prey on *Temora longicornis*, the most abundant copepod species in this region (Kane and Prezioso, 2008). However, that ecosystem has marked oceanographic and biological differences compared with the northwest GSL, which shows a zooplankton community typical of the sub-arctic northwest Atlantic dominated by *Calanus* species both in abundance and biomass and high abundance of much smaller *Oithona* (De Lafontaine *et al.*, 1991; Plourde *et al.*, 2002; Harvey and Devine, 2009). In the GSL, Fortier *et al.* (1992) partially described the larval diet of arctic shanny, but indicated developmental stages only, without giving prey species identification; hence, very little is known about the feeding ecology of arctic shanny and snakeblenny larvae. Furthermore, since many studies have indicated that larval feeding selectivity and copepod escape response are dependent on

species and developmental stage (Fields and Yen, 1997; Buskey *et al.*, 2002; Visser, 2007; Robert *et al.*, 2008), the detailed identification of prey species should be considered in the evaluation of feeding selectivity by fish larvae.

The objectives of our study were therefore to improve our knowledge of the feeding ecology and to examine the interactions among the larvae of three important forage fish species, sandlance, arctic shanny, and snakeblenny, in order to better identify the role trophodynamics processes can play in structuring the ichthyoplankton community in the northwest GSL ecosystem. We compared larval diet, feeding selectivity, and feeding niche overlap on the basis of zooplankton species and developmental stage identification. Moreover, the last published review presenting the plankton communities of the northern GSL was by De Lafontaine *et al.* (1991). Therefore, we also present some new information about the zooplankton community composition of the northwest GSL, which had not been well documented to date.

2.2 Method

2.2.1 Study site

The GSL is a semi-closed sea where exchange with the North Atlantic Ocean is limited to the Strait of Belle Isle in the northeast and the Cabot Strait in the southeast (Figure 1). In winter, the GSL is composed of two distinct water layers: a cold and relatively fresh surface layer is present on top of a saltier and warmer bottom layer. After ice melt in early spring, a third layer is formed when surface temperature increases rapidly and traps colder water underneath. This cold intermediate layer persists until fall (Gilbert

and Pettigrew, 1997) and can be reinforced by water from the Labrador Shelf entering through the Strait of Belle Isle (Galbraith, 2006).

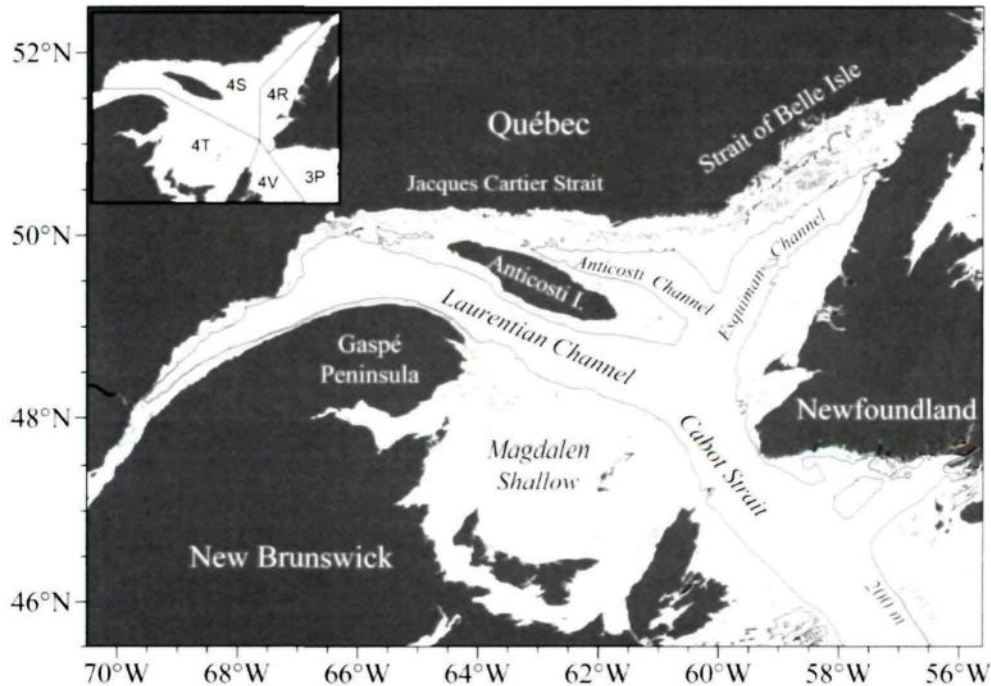


Figure 1. Map of the Gulf of St. Lawrence with channels and bounding regions. The insert map shows the NAFO divisions of the gulf.

The GSL is divided in two major regions, the northern GSL [Northwest Atlantic Fisheries Organization (NAFO) division 4R, 4S] and the southern GSL (NAFO division 4T), which differ in water depth (Dutil *et al.*, 2011), biological community composition, and overall productivity (Plourde and McQuinn, 2010); there is also limited exchange between them (Morissette *et al.*, 2009). The northwest GSL is delimited by the Laurentian Channel (south and west) and Esquiman Channel (east). Due to its location and current dynamics, the northwest GSL is more affected by intrusions of subarctic water from the

Labrador Shelf (especially in the northeast) than is the rest of the GSL (Galbraith, 2006). Ice melt or advection to the southeast and high nutrient concentrations in the upper layer in the spring following convection from the previous fall create the conditions that promote intense phytoplankton blooms (Le Fouest *et al.*, 2010) and copepod reproduction when stratification occurs in late spring. This highly productive period is concurrent with the hatching of many fish species that use copepods from all development stage as a main food source.

2.2.2 Sampling

Samples were collected in the northwest GSL on board the research vessel *Coriolis II* over a short period, between 12 and 17 May 2008, to limit temporal variation. The study area, composed of 34 stations (Figure 4), was chosen based on documented ichthyoplankton abundance (Bui *et al.*, 2010). At each station, physical and chemical variables (temperature, salinity, *in situ* fluorescence) were obtained with a Sea-Bird SBE Seacat 19 CTD lowered at a speed of 1 m s^{-1} from the surface to within ~ 5 m of the seabed. Water samples were taken near-surface (~ 4 m), at 10 m intervals down to 60 m, and at ~ 5 m above the seabed, whenever possible. Two 100 ml subsamples from each depth were filtered under vacuum on 25 mm GF/F filters and promptly frozen at -80°C to prevent pigment decomposition.

Ichthyoplankton was collected using double-oblique tows with a bongo sampler (61 cm in diameter) equipped with 333 μm mesh nets and flowmeters at the mouth to calculate filtered water volumes. At every sampling station, tows were carried out from the

surface to 50 m and from the surface to 150 m at a tow speed of $\sim 1 \text{ m s}^{-1}$. For every bongo tow, one collected sample was preserved in a formaldehyde–seawater solution (4%) and the other in pure ethanol. Zooplankton was sampled by vertical tows using a conical zooplankton net (50 cm in diameter) equipped with a 73 μm mesh net carried out from 50 m to the surface. Zooplankton samples were preserved in a formaldehyde–seawater solution (4%).

2.2.3 Laboratory procedures

In the laboratory, chlorophyll *a* concentration was determined using the standardized Welschmeyer (1994) method described in Mitchell *et al.* (2002). The relationship between chlorophyll *a* concentration and the corresponding *in situ* fluorescence was used to convert CTD fluorescence data into chlorophyll *a* concentrations.

All ichthyoplankton was removed from the bongo samples (both ethanol- and formaldehyde-preserved) and identified under a binocular microscope (Leica Mz 12.5) to the species level using larva meristic characteristics described by Fahay (2007). The three dominant species were sandlance (66.05%), arctic shanny (8.90%), and snakeblenny (4.45%). These three species were selected for digestive tract content analysis. To compare prey lengths with the lower jaw lengths of the larvae, calibrated pictures of all larvae were taken through the binocular microscope and measurements were evaluated with the Sigma Scan Pro v5 software (Systat Software, Inc., Chicago, IL, USA). Prey items in larval digestive tracts were identified to the lowest taxonomic level possible at x400 magnification. Unidentified nauplii and copepods were assigned to the species/stage in

proportion to the relative abundance of identified prey items in their group (Robert *et al.*, 2011). Phytoplankton cells were not counted, but their presence was noted and considered for further calculations.

Zooplankton identification and enumeration were made on subsamples from a Folsom splitter (van Guelpen *et al.*, 1982) after removal of appendicularians and gelatinous organisms > 1 cm. Identification of the zooplankton developmental stage and species was done using a binocular microscope to measure prosome or total length and check for specific morphological characteristics. Nauplii species were identified using morphological characteristics and by comparison of total length along the central axis. *Pseudocalanus* spp., *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* nauplii total lengths were also compared with data compiled from copepods sampled by vertical net at stations of the Atlantic Zone Monitoring Program (1996–2006) and during the annual summer bottom-trawl survey for fish stock evaluation in the northern GSL (Therriault *et al.*, 1988; Mitchell *et al.*, 2002; Harvey and Devine, 2009). Length ranges used to discriminate species are reported in Table I and length distributions from historical data are presented by developmental stage and species in Figure 2. However, *C. hyperboreus* and *C. glacialis* nauplii were pooled to reduce potential identification error caused by overlapping lengths, since this is the main discriminating criteria used to identify these species. Copepod eggs were assigned to species using the following diameter values (reported in McLaren *et al.*, 1988, and Castellani *et al.*, 2005): *C. finmarchicus* for eggs between 135 and 165 μm , *C. glacialis* for eggs between 165 and 195 μm , and *C. hyperboreus* for eggs between 195 and 250 μm . Copepod eggs with diameters < 135 μm can be assigned to more than one

species, mainly *Oithona similis* and *T. longicornis*, and are therefore identified as copepod eggs < 135 μm .

Table I. Total length measure ranges used to distinguish between *Pseudocalanus* spp., *C. finmarchicus*, and *C. glacialis/hyperboreus* nauplii.

Naupliar stage	<i>Pseudocalanus</i> spp.	<i>C. finmarchicus</i>	<i>C. glacialis/hyperboreus</i>
	< (mm)	(mm)	> (mm)
N1	0.170	0.170–0.210	0.210
N2	0.200	0.200–0.220	0.220
N3	0.270	0.270–0.310	0.310
N4	0.320	0.320–0.400	0.400
N5	0.400	0.400–0.480	0.480
N6	0.460	0.460–0.600	0.600

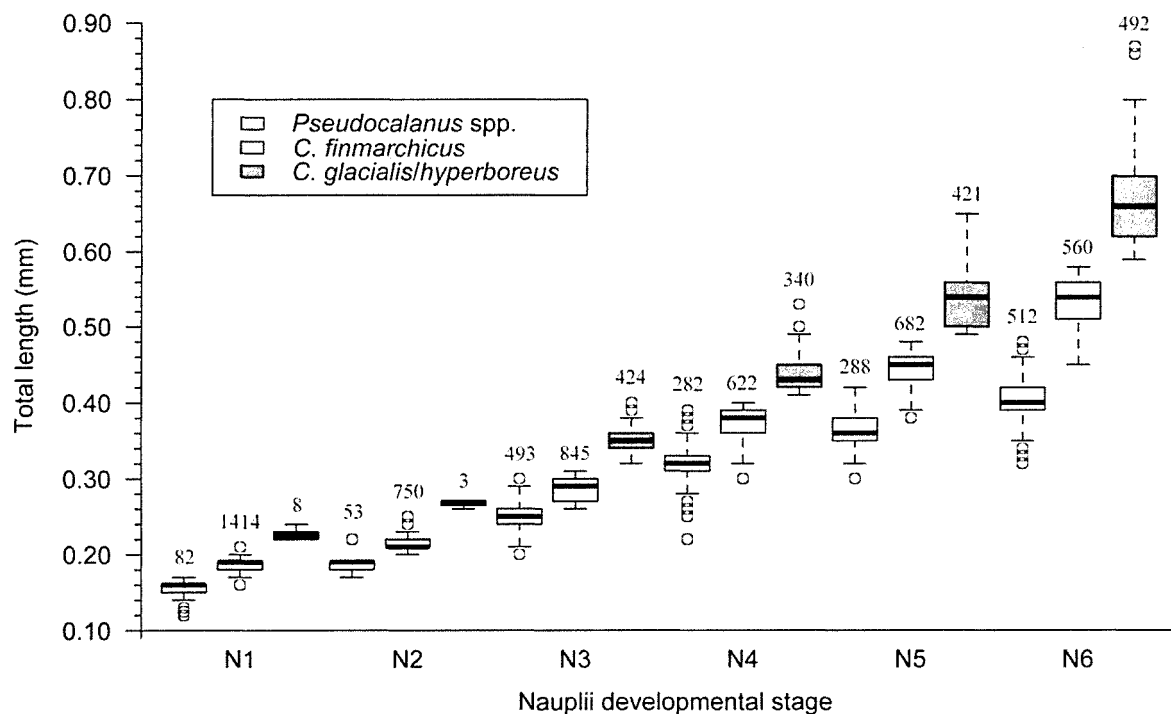


Figure 2. Whisker plot of prosome length distribution of historical data (1996–2006) for *Pseudocalanus* spp., *C. finmarchicus*, and *C. glacialis/hyperboreus* nauplii. Open circles indicate outliers to the recorded values. Numbers indicate count of nauplii in each class.

2.2.4 Data analysis

To define habitats with similar feeding potential, we grouped stations based on zooplankton species assemblages. Only species representing $> 0.1\%$ of the total station abundance for at least one station were used. A CLUSTER analysis with complete linkage was performed on a Bray-Curtis similarity matrix based on untransformed zooplankton data (Clarke, 1993). By using untransformed data, very abundant species may have too much influence on the analysis, but it is justified in our study by the low differences in the mean abundances of the main species among stations. A SIMPROF test ($\alpha=0.05$; 999 permutations) was also performed to distinguish significant groups in the CLUSTER analysis. After comparison, species that represented a major contribution to the group clustering were determined by one-way SIMPER analysis on species abundance. The CLUSTER analysis, SIMPROF test, and SIMPER analysis were performed with the PRIMER v6 statistical software (PRIMER-E Ltd, Plymouth, UK).

Mean values (0–50 m layer) of salinity, depth, temperature, chlorophyll *a*, and species abundances were compared among groups of stations with a Student's *t*-test. The normality condition was assessed visually for each group with box plots (Quinn and Keough, 2002). Comparisons that failed a Levene test of equality of variance were tested with a Welch's *t*-test (Welch, 1947).

Differences in feeding incidence among species was compared within each station group with Pearson's chi-square test. Gut content and zooplankton data were used to calculate the Chesson α electivity index (Chesson, 1983) for each group to compare feeding selectivity of sandlance, arctic shanny, and snakeblenny, for each prey type *j*:

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

where (d_j/p_j) is the ratio of the relative abundance of prey j in the diet and in the environment, $\sum(d_i/p_i)$ is the sum of this ratio for all prey types, and N is the number of prey types considered. The index was calculated for each individual larva and then averaged for each species in each group. The value $1/N$ was used as a threshold value of positive selection. Since the Chesson α -electivity index was used to compare feeding selectivity among species, prey types present in the diet of at least one of the three larva species were used in the calculation of all threshold values.

In order to compare feeding niche overlap between species in each group and in different length classes, the Schoener index (Schoener, 1968) was used because it is known to be free of assumptions about competition processes, it facilitates intercommunity comparisons, and it is not affected by arbitrary prey species classification applied by the observer that may not be distinguished by the larvae (Abrams, 1980). This index was calculated as:

$$C_{jk} = (1 - \frac{1}{2} \sum |P_{ij} - P_{ik}|) \cdot 100 \quad (2)$$

where C_{jk} is the feeding niche overlap between species j and k , and P_{ij} and P_{ik} are, respectively, the relative abundance of prey type i in the diets of species j and k . The overlap is complete when $C_{jk} = 100$ and absent when $C_{jk} = 0$.

2.3 Results

2.3.1 Zooplankton assemblages

The CLUSTER analysis and SIMPROF test based on the zooplankton data discriminated five groups of stations (a–e) (Figure 3). Four stations (1, 3, 4, 33) were removed from subsequent analyses because their low abundance of fish larvae did not allow a reliable investigation of the diet. These stations are in group e, at the western end of Anticosti Island, and are associated with a specific oceanographic feature of the GSL

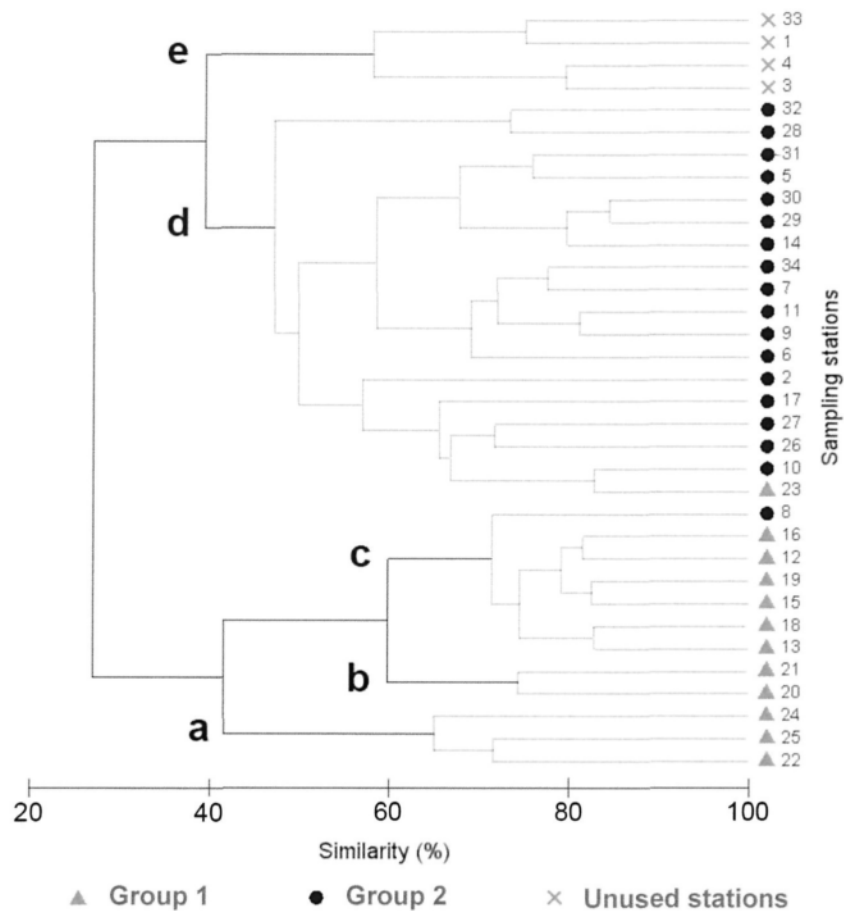


Figure 3. Result of the CLUSTER analysis of similarities and corresponding station grouping. Bold lines indicate significant divisions according to the SIMPROF test (999 permutations; $\alpha = 0.05$); corresponding station groups are labeled **a** to **e**.

previously described by Sevigny *et al.* (1979) known as the Anticosti gyre. Based on the high similarity of zooplankton assemblages among most stations (>40%), groups a, b, and c were pooled to form station group 1. For convenience, group d will be referred to hereafter as group 2. Because most stations included in each group were also geographically close, station 8 was reassigned to group 2 and station 23 to group 1 (Figure 4). This reassignment did not change the conclusions of the statistical tests and had a very limited impact on the calculated values of selectivity and niche overlap. According to the SIMPER analysis, *Fritillaria* sp., *O. similis* nauplii, and bivalvia larvae were the principal contributors (contribution to average similarity 51.75%) to group 1 assemblage and *O. similis* nauplii, *Fritillaria* sp., *C. glacialis*, and *C. finmarchicus* eggs (contribution to average similarity 52.99%) to group 2 assemblage (Table II).

Table II. Relative contribution of zooplankton species to station groups 1 and 2 from the SIMPER analysis.

Stations group	Ave. similarity	Dominant species	Mean abundance (Nb. 10 m ⁻²)	Contrib. (%)
Group 1	66.44%	<i>Fritillaria</i> sp.	164510.65	31.67
		<i>Oithona similis</i> (N1–N6)	78448.35	12.81
		Bivalvia	54783.13	7.27
		<i>Oithona similis</i> (CI–CV)	42203.55	6.82
		<i>Calanus glacialis</i> eggs (165–195 µm)	40370.09	6.52
		<i>Calanus finmarchicus</i> eggs (135–165 µm)	34971.56	5.51
		<i>Calanus finmarchicus</i> (N1–N6)	25159.15	5.29
		<i>Calanus hyperboreus</i> eggs (195–250 µm)	27204.82	4.67
		<i>Calanus glacialis/hyperboreus</i> (N1–N6)	19539.94	3.59
		<i>Pseudocalanus</i> spp. (N1–N6)	23359.65	3.27
		<i>Metridia</i> spp. (N1–N6)	13233.17	2.13
		Polychaeta	11331.81	1.84
Group 2	63.87%	<i>Oithona similis</i> (N1–N6)	61873.64	15.40
		<i>Fritillaria</i> sp.	62196.19	14.27
		<i>Calanus glacialis</i> eggs (165–195 µm)	71601.17	13.69
		<i>Calanus finmarchicus</i> eggs (135–165 µm)	59027.25	9.63
		<i>Calanus finmarchicus</i> (N1–N6)	37784.00	8.86
		<i>Oithona similis</i> (CI–CV)	33123.96	8.28
		<i>Calanus hyperboreus</i> eggs (195–250 µm)	38276.32	7.25
		<i>Calanus glacialis/hyperboreus</i> (N1–N6)	15694.76	4.14
		<i>Oithona similis</i> (CVI female)	11609.09	2.85
		<i>Pseudocalanus</i> spp. (N1–N6)	15830.57	2.82
		Bivalvia	10276.43	2.12
		Polychaeta	8799.48	1.73

N: nauplia; developmental stages 1 to 6

C: copepodite; developmental stages I to VI

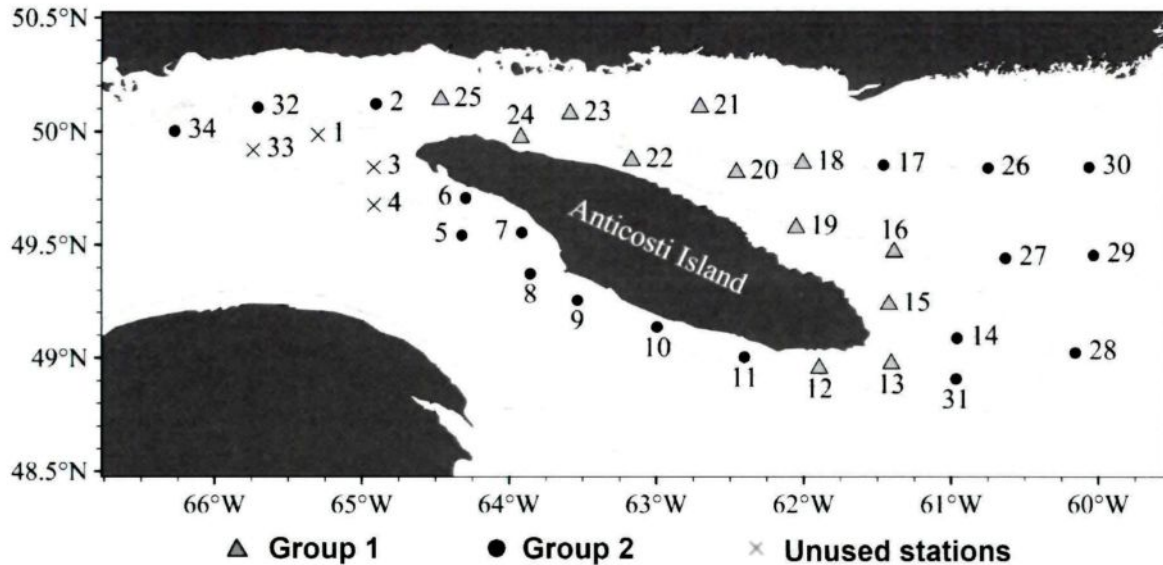


Figure 4. Location of stations sampled in May 2008 in the northwest Gulf of St. Lawrence and final group designations. Because most stations included in each group were also geographically close, station 8 was reassigned to group 2 and station 23 to group 1.

2.3.2 Station group characterization

The Welch's *t*-test revealed a significant difference between the two groups of stations for salinity in the 0–50 m layer ($t=2.4669$; $df=20.3$; $p=0.023$) for an average value of 31.83 (SE=0.06) in group 1 and 31.09 (SE=0.23) in group 2. No significant differences were found for mean temperature ($t=-1.4784$; $df=28$; $p=0.151$), chlorophyll *a* ($t=0.9017$; $df=28$; $p=0.375$), and water depth ($t=-1.709$; $df=28$; $p=0.099$).

For group 1 stations, the 73 μm vertical net captured an average of 5.92×10^6 ind. 10 m^{-2} compared with 4.97×10^6 ind. 10 m^{-2} for group 2 stations (excluding ichthyoplankton). Overall, the community was dominated by copepods. After sorting copepod abundances by species (mainly *O. similis*, *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*) and developmental stage (eggs, nauplii, copepodites, and adults), the community in group 1 was

dominated by the larvacean *Fritillaria* sp. (25.9%), *O. similis* nauplii (12.9%) and copepodite (4.6%), and bivalvia larvae (8.9%) (Figure 5). The group 2 community was dominated by *C. glacialis* eggs (14.9%), followed by *Fritillaria* sp. (13.0%) and *O. similis* nauplii (12.2%).

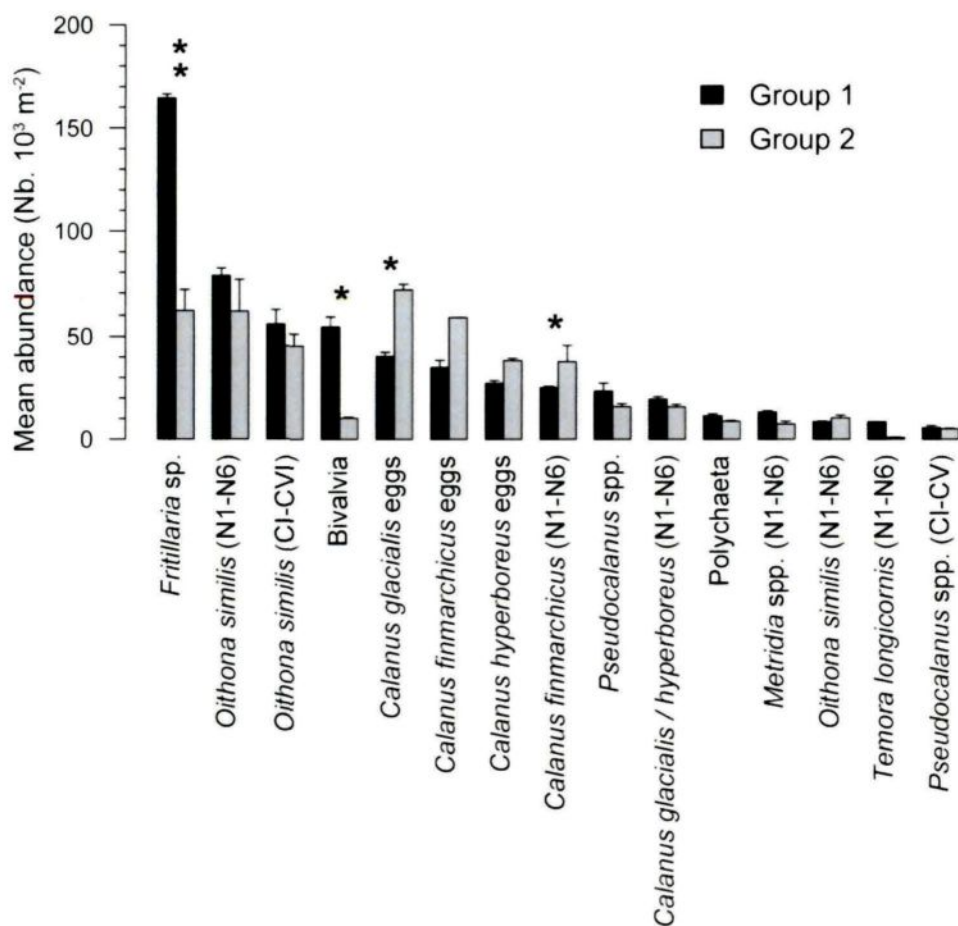


Figure 5. Mean abundance for the 15 most abundant zooplankton species from the vertical net for station group 1 (black) and 2 (grey). Error bars show one standard error of the mean. Asterisks indicate significant differences between station groups (* p < 0.05 and ** p < 0.0001).

In both groups, *O. similis* was characterized by an abundance of nauplii, followed by copepodites and adult females (Figure 5). For this species, egg abundance could not be estimated because of their small size and because females usually carry them in sacs attached to the urosome until the nauplii hatch. *Calanus finmarchicus* and *C. glacialis* eggs were almost twice as abundant in group 2 compared with group 1. *Calanus hyperboreus* eggs in group 2 were also more abundant compared with group 1, but showed clearly lower abundance than *C. finmarchicus* and *C. glacialis* eggs in both groups. *Calanus finmarchicus* nauplii stage structure was characterized by an abundance of N3 in group 2; N3 were still more abundant in group 1, but the overall mean abundance of the various naupliar stages were more similar (Figure 6). *Calanus finmarchicus* CI were dominant in both groups, but adults (CVI) were equally abundant in group 2. *Calanus glacialis/hyperboreus* nauplii were dominated by older stages (N5 and N6) in group 1, but N3 were more abundant in group 2. In both groups, *C. glacialis* CI were more abundant. Stage II *C. hyperboreus* copepodites were most abundant in both groups.

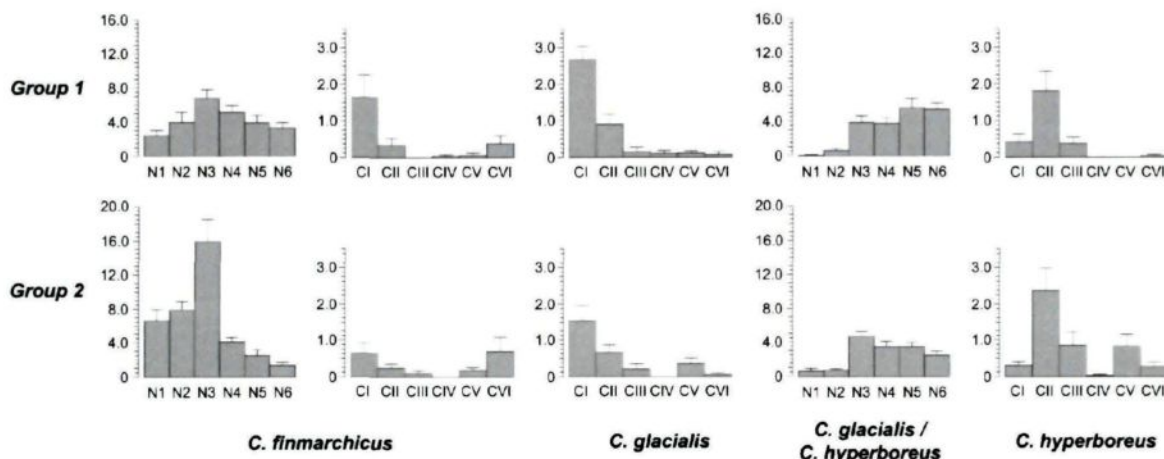


Figure 6. Mean abundance (Nb. 10^3m^{-2}) of the copepods *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* broken down by nauplii (N1 to N6) and copepodite (CI to CVI) developmental stages for the two groups of stations. *C. glacialis* and *C. hyperboreus* nauplii were combined because they cannot be distinguished. Note the different scale for nauplii and copepodites. Error bars show one standard error of the mean.

Sandlance was the dominant larval fish species at 29 of the 34 stations, with the highest abundance at station 25 (108 larvae 10m^{-2}). Mean abundances was 19.20 (SE=9.92) larvae 10m^{-2} and 9.34 (SE=2.76) larvae 10m^{-2} in group 1 and 2, respectively, Sandlance was abundant at most stations except in the Anticosti Channel region and at the east end of Anticosti Island (Figure 7A). Arctic shanny larvae were mainly present between the north shore and Anticosti Island (Figure 7B). The highest abundance observed was 12 larvae 10m^{-2} at station 22, and average abundances were 3.58 (SE=1.19) larvae 10m^{-2} and 0.65 (SE=0.27) larvae 10m^{-2} in group 1 and 2, respectively. Snakeblenny larvae were mainly present in the Anticosti Channel and at the east end of the Anticosti Island (Figure 7C). The highest abundance observed was 5 larvae 10m^{-2} at station 26. The average

abundances of larvae were 1.47 (SE=0.42) larvae 10 m^{-2} and 0.59 (SE=0.32) larvae 10 m^{-2} , in group 1 and 2, respectively.

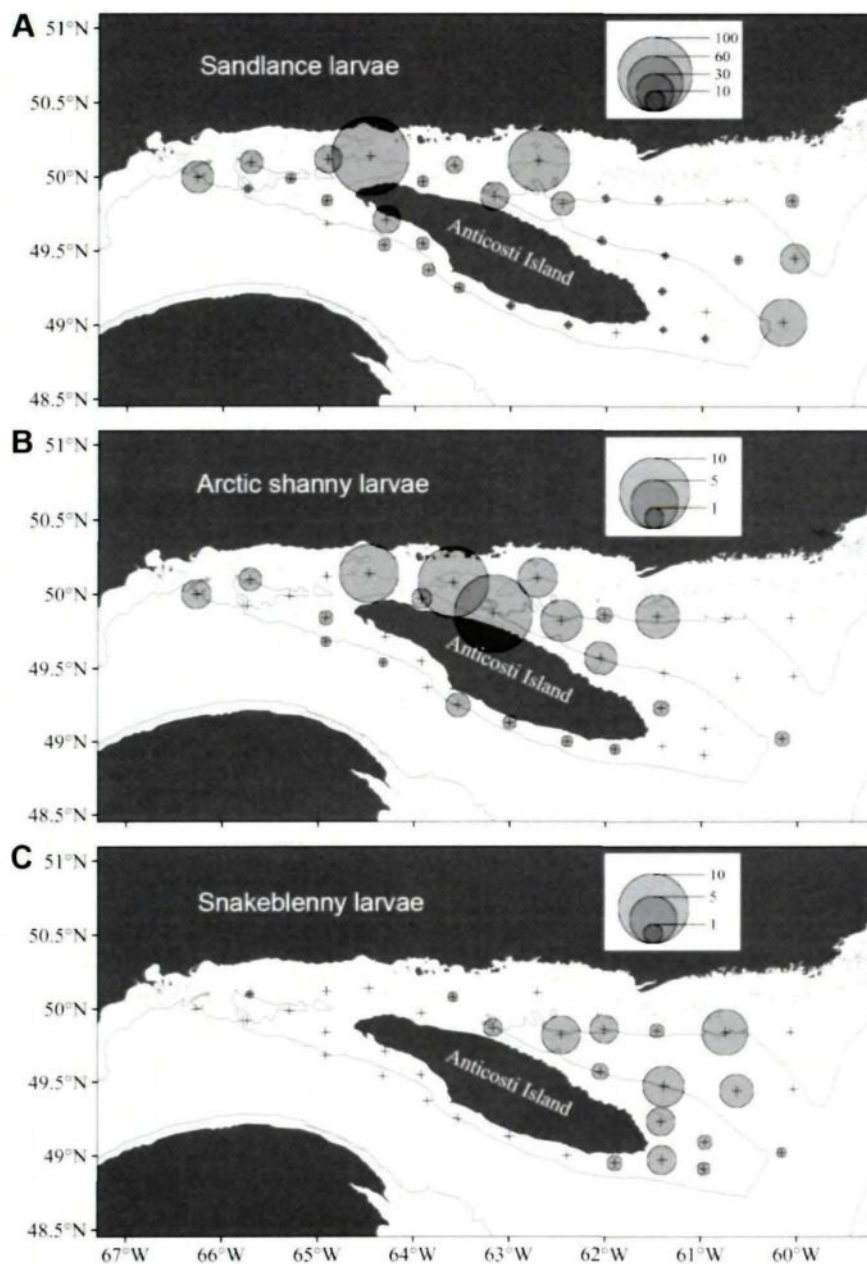


Figure 7. Distribution and abundance (Nb. 10 m^{-2}) of the three most important ichthyoplankton species present in May 2008 in the northwestern Gulf of St. Lawrence. Note the different scale for sandlance larvae.

2.3.4 Feeding niche description

Prey size and lower jaw length showed approximately the same range of values for sandlance and arctic shanny (Figure 8A) while snakeblenny jaw lengths were longer, with some overlap with larger sandlance larvae but none with arctic shanny. Accordingly, the prey size range of snakeblenny was also wider but still overlapped with those of sandlance and arctic shanny. Snakeblenny prey size also increased with increasing jaw length; no such relationship was seen for sandlance and arctic shanny for length ranges observed in this study. A comparison of total length distribution frequencies of larvae revealed a narrow range for arctic shanny compared with sandlance and snakeblenny, limited length overlap between snakeblenny and sandlance, and no overlap between snakeblenny and arctic shanny (Figure 8B–D).

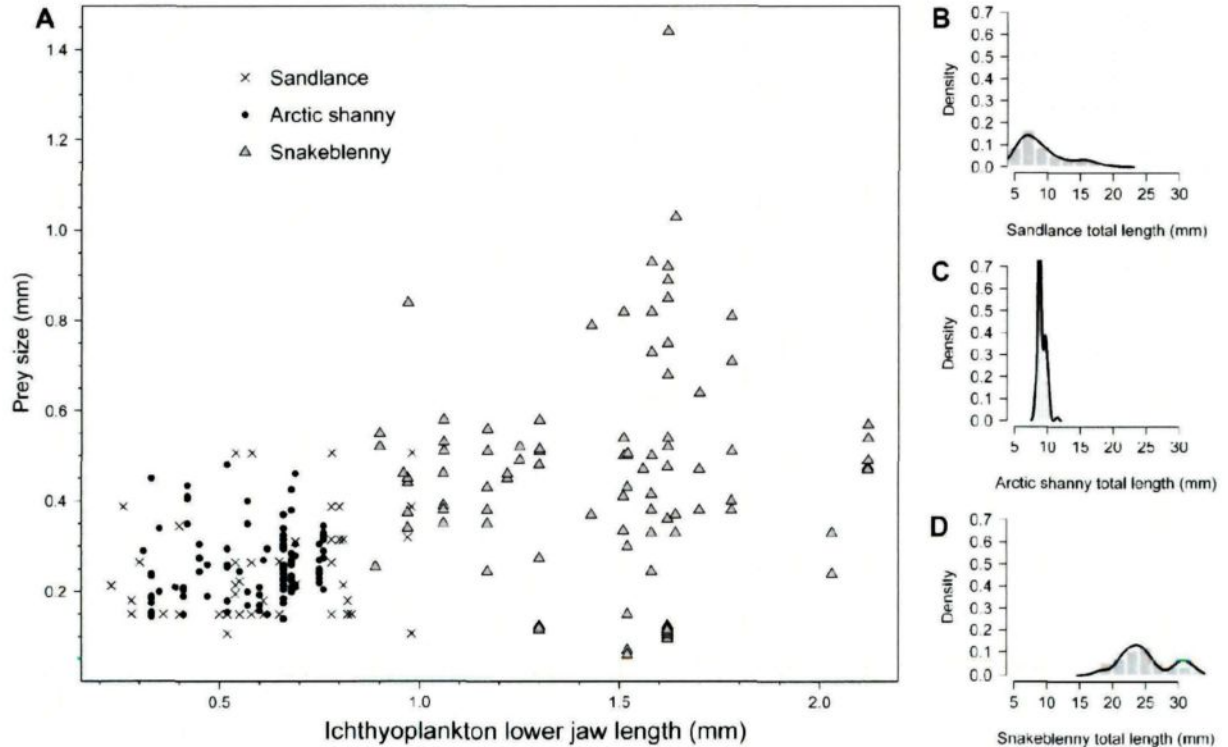


Figure 8. (A) Relationship between larval lower jaw length and prey size for the three most abundant species in the northwest Gulf of St. Lawrence. (B,C,D) Length distributions of larvae are presented by species.

The combined sandlance diet for both groups is composed of 18 prey types and is dominated by *C. finmarchicus* eggs. The digestive tract content of sandlance in group 2 also contained a high proportion of *C. glacialis/hyperboreus* N6 (Table III), but this value is driven by one unusual sandlance larva where this prey type accounted for 67% of the diet. For this species, phytoplankton was found in the gut of 18 larvae ranging from 4.87 mm to 15.58 mm in total length (Table III). In four of these larvae, other prey types (copepod eggs and nauplii) were present in the digestive tract. The arctic shanny diet is composed of 19 prey types: dominated by *C. finmarchicus* N3 and *C. glacialis/hyperboreus* N4 in group 1 while in group 2, the diet is characterized by less diversity and different prey

types, mainly *O. similis* nauplii and *C. finmarchicus* eggs (Table III). For this species, phytoplankton was found in the gut of five larvae, ranging from 7.97 mm to 9.04 mm in total length (Table III). For three of these larvae, other prey types (copepod eggs and nauplii) were present in the digestive tract. The snakeblenny diet is composed of 13 prey types; primarily *C. hyperboreus/glacialis* N6 and copepodites in both station groups, but *C. finmarchicus* eggs were also present in group 1 only. Like arctic shanny, the number of prey types is lower in snakeblenny from group 2 (Table III). The feeding incidence is lower for sandlance, especially in group 1, than for snakeblenny and arctic shanny. For all three species, the feeding incidence is significantly different among species in group 1 ($p < 0.0001$) and 2 ($p = 0.009$).

Table III. Diet composition and feeding incidence for the selected ichthyoplankton species in each group.

Prey item	Sandlance (%)		Arctic shanny (%)		Snakeblenny (%)	
	grp. 1	grp. 2	grp. 1	grp. 2	grp. 1	grp. 2
Eggs						
Eggs <135 µm	2.63	1.09	3.13	-	30.91	-
<i>C. finmarchicus</i> (135–165 µm)	55.26	18.48	2.08	17.86	0.91	-
<i>C. glacialis</i> (165–195 µm)	7.89	1.09	3.13	10.71	-	-
<i>C. hyperboreus</i> (195–250 µm)	2.63	-	-	7.14	-	-
>250 µm	-	-	-	-	0.91	-
Nauplii						
<i>Acartia</i> spp. (N1–N6)	4.51	4.76	-	-	-	-
<i>Oithona similis</i> (N1–N6)	4.51	2.38	3.74	21.43	-	-
<i>Pseudocalanus</i> sp. (N1)	-	-	1.87	-	-	-
<i>Pseudocalanus</i> sp. (N3)	4.51	-	1.87	-	-	-
<i>Pseudocalanus</i> sp. (N5)	-	-	-	5.36	-	-
<i>Pseudocalanus</i> sp. (N6)	-	2.38	1.87	-	-	-
<i>Metridia longa</i> (N6)	4.51	-	-	-	-	-
<i>C. finmarchicus</i> (N1)	-	-	3.74	-	-	-
<i>C. finmarchicus</i> (N2)	-	-	1.87	-	-	-
<i>C. finmarchicus</i> (N3)	-	11.89	24.32	-	-	-
<i>C. finmarchicus</i> (N4)	-	-	7.48	5.36	-	-
<i>C. finmarchicus</i> (N5)	-	2.38	7.48	10.71	2.03	-
<i>C. finmarchicus</i> (N6)	-	-	1.87	-	8.14	-
<i>C. glacialis/hyperboreus</i> (N2)	-	-	3.74	-	-	-
<i>C. glacialis/hyperboreus</i> (N3)	9.02	7.13	5.61	-	-	-
<i>C. glacialis/hyperboreus</i> (N4)	4.51	11.89	16.84	10.71	-	-
<i>C. glacialis/hyperboreus</i> (N5)	-	9.51	9.35	10.71	2.03	1.96
<i>C. glacialis/hyperboreus</i> (N6)	-	19.02	-	-	30.52	68.53
<i>Temora longicornis</i> (N5)	4.51	-	-	-	-	-
<i>Eurytemora</i> sp. (N6)	-	2.38	-	-	-	-
Copepodites						
Copepodite (ND)	-	3.26	-	-	19.09	16.39
<i>Microcalanus</i> sp. (CVIF)	-	-	-	-	0.91	-
<i>Pseudocalanus</i> sp. (CV)	-	-	-	-	-	1.64
<i>Pseudocalanus</i> sp. (CVIF)	-	-	-	-	1.82	1.64
<i>C. glacialis</i> (CII)	-	-	-	-	0.91	-
Euphausiacea nauplii						
Euphausiacea (N1–N6)	-	-	-	-	1.82	9.84
<i>Nb. of prey in guts</i>	39	87	96	28	110	61
<i>Nb. of larvae</i>	60	52	32	10	17	11
<i>Nb. of feeding larvae</i>	16	20	22	6	15	10
<i>Nb. of larvae with empty gut</i>	44	29	10	4	2	1
<i>Mean nb. of prey per feeding larvae</i>	2.43	4.83	4.36	4.67	7.86	6.10
<i>Nb. of prey types ingested</i>	11	14	17	9	12	6
<i>% larvae with phytoplankton</i>	11.7%	17.3%	15.6%	0.0%	0.0%	0.0%
<i>Feeding incidence (with phytoplankton)</i>	33.3%	53.8%	75.0%	60.0%	88.2%	90.9%

N: nauplia; developmental stages I to 6

C: copepodite; developmental stages II, V, VI

F: female

ND: not determined

Feeding incidence includes the presence of phytoplankton in the digestive tract.

The Chesson α index calculated for group 1 stations (Figure 9A) revealed strong positive selectivity by sandlance for *C. finmarchicus* eggs. For arctic shanny, the index showed a weak positive selectivity for *C. finmarchicus* N3 and *C. glacialis/hyperboreus* N4 and N5. The index for snakeblenny showed selectivity for *C. glacialis/hyperboreus* N6, copepodites, and *C. finmarchicus* N6.

The Chesson α index calculated for group 2 stations (Figure 9B) also revealed strong positive selectivity by sandlance for *C. finmarchicus* eggs, with an additional low but positive selectivity for *C. finmarchicus* N3. In the case of arctic shanny, the positive selectivity was weak for *C. glacialis/hyperboreus* N4, *C. finmarchicus* eggs, and very weak for *C. glacialis/hyperboreus* N5, *Pseudocalanus* spp. N5, and *C. glacialis* and *C. hyperboreus* eggs. Snakeblenny was again selecting *C. glacialis/hyperboreus* N6 and copepodites, but not *C. finmarchicus* N6, as was the case in group 1.

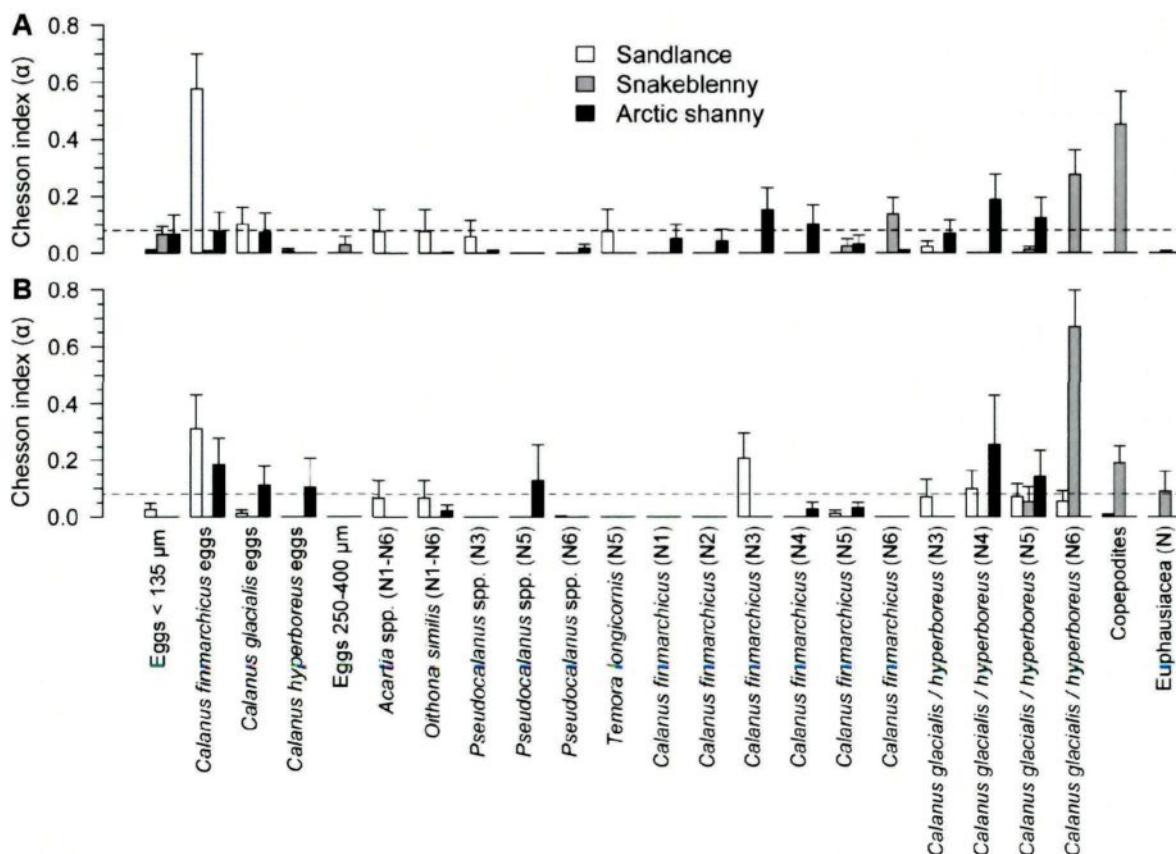


Figure 9. Chesson selectivity index calculated for station group 1 (A) and 2 (B) for sandlance, arctic shanny, and snakeblenny. Dotted lines indicate the threshold value for a random selection, as described by Chesson (1983). Error bars show standard error of the mean.

The Schoener C index between station groups (Table IV) indicates a moderate feeding niche overlap between sandlance and arctic shanny in group 1 (24.2%) and a higher overlap in group 2 (44.5%). The overlap between sandlance and snakeblenny is very low in group 1 (3.8%) and moderate in group 2 (23.5%). Niche overlap between arctic shanny and snakeblenny is low in group 1 (10.0%) and very low in group 2 (2.0%).



Table IV. Comparison of feeding niche overlap between station groups.

<i>Ichthyoplankton species</i> <i>Station group</i>	Sandlance		Snakeblenny		Arctic shanny	
	1	2	1	2	1	2
Sandlance	1	-				
	2	41.9	-			
Snakeblenny	1	3.8	27.6	-		
	2	0.0	23.5	54.0	-	
Arctic shanny	1	24.2	49.6	10.0	2.0	-
	2	36.2	44.5	5.0	2.0	41.9
<i>Nb. of larvae (n)</i>	15	21	10	15	11	17

Schoener C index value (in %) calculated between species and by groups; interspecies comparisons in the same group are shown in bold.

Comparing the feeding niche overlap index between species based on length classes (Table V) indicates a moderate diet overlap between arctic shanny and sandlance larvae < 12 mm (< 8 mm: 19.9%; 8–12 mm: 23.9%) and high overlap between arctic shanny and sandlance larvae > 12 mm (12–16 mm: 43.2%; > 16 mm: 37.8%). It also indicates a moderate overlap between arctic shanny and snakeblenny < 28 mm (< 23 mm: 19.8%; 23–28 mm: 28.6%), and very low overlap between sandlance < 12 mm and snakeblenny (all classes); the overlap became high when comparing sandlance in the 12–16 mm range and snakeblenny (< 23 mm: 36.0%; 23–28 mm: 43.9%; > 28 mm: 34.8%). In the case of sandlance longer than 16 mm, the overlap index is low with snakeblenny > 28 mm (15.7%) and moderate with snakeblenny < 28 mm (< 23 mm: 19.1%; 23–28 mm: 21.1%).

Table V. Comparison of feeding niche overlap between length classes.

<i>Ichthyoplankton species</i> <i>Length class (mm)</i>	Sandlance				Snakeblenny			Arctic shanny	
	<8	8–12	12–16	>16	<23	23–28	>28	8–12	
Sandlance	<8	-							
	8–12	56.2	-						
	12–16	34.5	24.2	-					
	>16	61.0	47.6	52.7	-				
Snakeblenny	<23	0.0	0.0	36.0	19.1	-			
	23–28	1.7	4.6	43.9	21.1	58.6	-		
	>28	0.0	2.9	34.8	15.7	76.8	66.7	-	
Arctic shanny	8–12	19.9	23.9	43.2	37.8	19.8	28.6	12.1	-
<i>Nb. of larvae (n)</i>	8	13	10	5	12	8	5	28	

Schoener C index value (in %) calculated between species class length. Interspecies comparisons >20% are shown in bold.

2.4 Discussion

The objectives of this study were to describe the feeding niches and feeding competition occurring at the larval stage among three major forage fish species in the northwest GSL. To fulfill these objectives, we used a diet description that included the identification of zooplankton developmental stages to the species level.

The selectivity index demonstrates that sandlance larvae are actively preying on *C. finmarchicus* eggs while arctic shanny are preying on eggs and nauplii of *C. finmarchicus*, and nauplii of *C. glacialis/hyperboreus*. The larger snakeblenny larvae, predominantly prey on bigger copepod nauplii (stage N6) and copepodite stages. The

feeding overlap index indicates a similarity in sandlance and arctic shanny diets within each station group and also between groups. The diet similarity between sandlance and snakeblenny is greater in group 2 and with sandlance in the 12–16 mm range. There is little diet similarity between arctic shanny and snakeblenny between station groups and length classes.

2.4.1 Zooplankton community

The northwest GSL is an important commercial fishing ground, but the zooplankton community has rarely been described, especially in the region between Anticosti Island and Québec's north shore. Although large zooplankton species, e.g., mysids and euphausiaceans, are surely under-represented in samples from the vertical net used (73 μm ; 50 cm in diameter), it is adequate to sample potential ichthyoplankton prey items, like *Calanus* spp. nauplii and eggs (Nichols and Thompson, 1991). Copepods and nauplii discrimination of *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* have always been problematic due to morphological similarity and total length overlap. Based on molecular analysis, Parent *et al.* (2011) reported that for stage CV size overlap range from 0% to 24% for these species in the GSL but in our analysis copepodite stages were seldom consumed by sandlance and arctic shanny in this study. Lindeque *et al.* (2006) state that *C. finmarchicus* and *C. glacialis* nauplii can be distinguish only from molecular analysis but historical data indicate that total length can be used to distinguish between nauplii species in the studied region (Plourde, S., unpublished data). Although this criteria may lead to some misidentification, especially near the limits of the length range used, most

nauplii length fall next to the mean value and are likely assigned to the right species. A similar problem occurs with identification of some copepod eggs. In the study area, it is unlikely to observe *C. hyperboreus* eggs in May as this species mainly lay eggs from late December to late March in the region (Plourde *et al.*, 2003), but misidentification would have a limited impact on our results due to the very low abundance of eggs identified to this species in the larvae digestive tracts.

The multivariate analysis revealed important differences in the zooplankton community between station groups 1 and 2. This distinction is partly caused by the abundance of larvacean of the genus *Fritillaria*. According to Choe and Deibel (2008), high abundances of *Fritillaria borealis* in Conception Bay (east coast of Newfoundland) usually follow the spring phytoplankton bloom and are positively correlated with temperature and negatively correlated with salinity. However, this species is considered euryhaline, and tolerance ranges are reported to vary greatly (Tomita *et al.*, 2003; Schulz and Hirche, 2007; Blachowiak-Samolyk *et al.*, 2008; Choe and Deibel, 2008; Spinelli *et al.*, 2009). In our study area, the difference in mean salinity between station groups cannot explain the important difference in *Fritillaria* sp. abundance between the groups. When examined in more detail, *Fritillaria* sp. was especially abundant at stations north of Anticosti Island (group 1) and rare at stations located at the eastern limit of the sampling area (see Figure 5).

The remaining distinction between the station groups was mainly related to abundances of copepod nauplii and eggs (e.g., *O. similis*, *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*), which are actively preyed on by ichthyoplankton. In the northwest GSL, abundances of *O. similis* nauplii and copepodites were higher at the end of the Anticosti

Channel. The relatively high abundance of this species throughout the region is also in accordance with a previous study suggesting that *O. similis* is well represented in most marine environments around the world (Gallienne and Robins, 2001). Our results indicate that *O. similis* nauplii are abundant in the arctic shanny diet, but only in station group 2. However, the Chesson selectivity index indicates that this prey item is not selected by arctic shanny and seems to be more an alternate prey. It is possible that the lower carbon or energy content related to the small size of *O. similis* nauplii explains this observation, but further investigations are needed.

Large copepod species like *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* represent major food sources for the larval fish species in our study. The cold arctic water present in the GSL originating from the Labrador Current is a suitable habitat for the various endemic arctic copepod species, primarily *C. glacialis* and *C. hyperboreus* (Johns *et al.*, 2001; Head *et al.*, 2003; Pepin *et al.*, 2011). By using time series from the Continuous Plankton Recorder (1958–2006), Head and Pepin (2010) and Pershing *et al.* (2010) demonstrated that a change occurred in the surface zooplankton community off eastern Newfoundland and on the Scotian Shelf, approximately at the moment of the fisheries collapse in the early 1990s. However, no clear sign of similar changes have been reported for the GSL: Harvey and Devine (2009) indicate the near stability of the zooplankton community since the beginning of the decade, except in Cabot Strait and in the estuarine region of the GSL for *C. hyperboreus* abundance.

2.4.2 Feeding ecology of larval fish

Sandlance larvae are known to show a relatively poor foraging capability but can already feed on copepod nauplii after hatching as observed by Monteleone and Peterson (1986) in mesocosm. Accordingly, sandlance larvae in the wild must hatch at the time of high primary production, when copepod reproduction in the ecosystem is enhanced. These conditions enable larvae to survive the first-feeding stage, which is known to experience the highest mortality rate in most fish species (Cushing, 1990; Fortier *et al.*, 1992). As observed by Malzhan and Boermas (2009), sandlance faced with competition or periods of lower productivity may be forced to shift their diet to a potentially lower quality food source like phytoplankton. This induces a decrease in nutritional condition, which has a negative impact on larval survival and ultimately recruitment (Malzahn *et al.*, 2007). In our study, phytoplankton cells were observed in the digestive tracts of sandlance larvae, which could have been due to competition for preferred prey or limited copepod production in the GSL. Moreover, feeding incidence was consistently lower (especially in group 1) and larvae with phytoplankton in their digestive tract were longer than observed in previous studies (Monteleone and Peterson, 1986; Fortier *et al.*, 1992).

Our study is the first to present detailed larval feeding niches and the relative diet overlap for the forage species arctic shanny and snakeblenny. Both the overlap index (station groups and length classes) and the relative diet composition show that snakeblenny and sandlance share some prey types in their diets, but the selectivity index shows a clear distinction between the selected prey of snakeblenny and sandlance in both station groups. It is important to note that the Schoener overlap index does not take into account relative

prey abundances in the environment and that part of the overlap may be opportunistic catches by larvae looking for preferred prey. Snakeblenny can eat bigger prey than sandlance or arctic shanny, thus exploiting a niche less or not at all exploited by the other two species, resulting in lower competition. Moreover, Munk *et al.* (2003) also reported that snakeblenny are larger than other ichthyoplankton species in similar environments. This could be an evolutionary trait improving survival by the use of a feeding niche with fewer competitors. Unfortunately, hatch size is unknown for this species, and this could be used to determine whether larval growth rate is higher or if fish are more developed at hatching, which would give some insight about survival strategies of early-stage snakeblenny. Nevertheless, the spatial distribution of snakeblenny larvae in 2008 had limited overlap with sandlance and arctic shanny, which makes it a less likely competitor of those species.

Our results demonstrate that arctic shanny and sandlance tend to feed on the same prey types and sizes. However, a slightly lower selectivity index in both station groups and a relatively higher number of prey types in station group 1 seem to indicate that arctic shanny can feed on a wider range of prey types than sandlance. This could mean that arctic shanny is less to be affected by abundances fluctuations of a specific prey, giving a competitive advantage over sandlance larvae. Arctic shanny also present evidence of adjusting feeding selectivity in an environment where the abundance of copepod eggs (*C. finmarchicus* and *C. glacialis*) increases (group 2; see Figure 5): we observed that under such conditions arctic shanny feed less on *C. finmarchicus* nauplii and select more the eggs

of this species. A shift in the diet is also observed, but less pronounced, in sandlance larvae, which actively selected the more abundant *C. finmarchicus* N3 in group 2.

2.4.3 Feeding and ichthyoplankton community structure

Considering the ichthyoplankton community of the northwest GSL, the increase in the abundance of some species of larvae observed by Bui *et al.* (2010) may reflect an increase in the adult populations from lower predation pressure following the fisheries collapse in the 1990s, but our study also suggests that species-specific responses among forage fish species may involve factors such as (i) the relatively higher feeding rates of arctic shanny and snakeblenny larvae compared with competitors (e.g., sandlance), (ii) the use by snakeblenny larvae of a feeding niche with fewer competitors, and (iii) the higher adaptability of arctic shanny larvae in the ecosystem due to a more generalist feeding behaviour.

Our results support the hypothesis that interspecific competition for zooplankton prey among ichthyoplankton species plays a role in the resilience of specific taxa and in structuring the community in the northwest GSL. Interspecific competition might have limited the possibility of an increase in sandlance abundance after the removal of their main predator in the northern GSL. Indeed, arctic shanny larvae seem to have a better foraging capability than sandlance, which could explain their rise in abundance. Our study also supports the suggestion of Robert *et al.* (2008) that investigations of fish recruitment and population dynamics should emphasize hypotheses that include larval feeding and accurate prey species descriptions.

CHAPITRE III
CONCLUSION GÉNÉRALE

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Ce mémoire a été réalisé dans le but d'améliorer les connaissances sur la communauté d'ichtyoplancton du nord-ouest du golfe du Saint-Laurent, et ce pour plusieurs raisons. Cette région, relativement peu connue, possède des caractéristiques physiques et biologiques distinctes qui limitent l'inférence faite à partir des rares études effectuées sur les espèces choisies dans d'autres régions, notamment sur les espèces de proies sélectionnées. Les relations trophiques à l'intérieur de la communauté zooplanctonique, la biologie et le cycle de vie de plusieurs espèces sont également peu documentées. L'objectif de mon étude était d'améliorer les connaissances sur l'alimentation du lançon, de la stichée arctique et de la lompenie serpent au stade larvaire en décrivant la communauté zooplanctonique du milieu étudié et le régime alimentaire des trois espèces de larves, et en déterminant la sélectivité alimentaire des larves pour comparer les possibilités d'interactions de compétitions dans le nord du golfe du Saint-Laurent des trois espèces.

Néanmoins, les résultats obtenus indiquent que la communauté zooplanctonique est divisée en deux régions distinctes. La première, située au nord et à la pointe est de l'île d'Anticosti, se distingue par une forte abondance de *Fritillaria* sp. et de larves de bivalves. La deuxième région, de part et d'autre de la première et au sud de l'île, se distingue par la présence d'oeufs de *C. glacialis* et de nauplii de *C. finmarchicus*. Dans les deux régions on observe la présence des copépodes *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Metridia* spp., *O. similis*, *Pseudocalanus* spp. et *T. longicornis* à différents stades de développement.

L'alimentation des lançons et de la stichée arctique est surtout caractérisée par l'utilisation des oeufs de *C. glacialis* et des nauplii de *C. finmarchicus* et *C. glacialis/hyperboreus* à différents stade de développement. De plus, l'indice C de

Schoener indique un potentiel élevé de compétition entre le lançon et la stichée arctique qui occupent une niche alimentaire similaire. Néanmoins, la stichée arctique, malgré une distribution de taille plus restreinte, consomme une plus grande variété de types de proies. Les données recueillies suggèrent donc un mode d'alimentation similaire, mais plus généraliste de la part des larves de stichée arctique par rapport aux larves de lançons. Dans une perspective où les proies préférées seraient en quantité limitées, ceci permettrait aux larves de stichée arctique de survivre plus facilement puisqu'elles ont une plus grande possibilité d'adaptation lors de changement dans la communauté zooplanctonique. Ceci pourrait également expliquer les variations d'abondances de certaines espèces fourragères, comme la stichée arctique, observées après l'effondrement des stocks commerciaux, mais d'autres facteurs ont probablement aussi joué un rôle important sur ces changements. Par exemple, la consommation de lançons au stade adulte par différentes espèces de prédateurs dont les populations sont en augmentation comme les pinnipèdes et certaines espèces d'oiseaux piscivores marins peut avoir eu un impact sur le nombre d'oeufs produit en réduisant le nombre de géniteurs. Les conditions climatiques sont également reconnues pour avoir des impacts sur la survie et le recrutement des espèces marines, mais actuellement ce genre d'interactions a principalement été mis en évidence pour des espèces plus connues, liées directement à la pêche commerciale, plutôt que les espèces fourrages, ce qui rend difficile toutes interprétations sans introduction d'un biais important.

De son côté, la lompénie-serpent, dont l'alimentation diffère de façon importante lorsqu'on la compare à celle des lançons et de la stichée arctique, ne semble pas en compétition avec ces deux espèces, du moins au stade larvaire. Une différence de taille

importante qui se traduit par la possibilité d'ingérer de plus grandes proies explique en grande partie cette observation. Néanmoins, l'absence de compétition apparente entre la lompénie et les deux autres espèces dans cette étude n'exclut en rien la possibilité d'une compétition avec d'autres espèces non étudiées ici ou les espèces étudiées mais à des périodes du développement différentes.

Il est important cependant de prendre compte des limites de cette étude. (i) Les échantillons ont été récoltés sur une seule année et des variations inter annuel, par exemple au niveau de la production zooplanctonique peuvent créer des situations où la compétition interspécifique est négligeable. De plus, (ii) il est impossible, comme dans la plupart des études en milieu naturel, de déterminer si le phytoplancton était consommé de façon volontaire ou non par les larves de lançon. (iii) Étant donné le nombre de larves récoltées, une interprétation des résultats par classe de tailles est plus risqué, particulièrement pour le lançon. (iv) La différence de tailles importantes des larves de lompénie serpent fait en sorte que cette espèce ne semble pas contribuer ou être affecté par les effets de la compétition. Cependant, il est pensable de croire que cette espèce interagit de manière plus importante avec d'autres espèces qui n'ont pas été étudiées ici.

Néanmoins, les résultats obtenus nous orientent sur de nouvelles questions quant aux conséquences de changements dans la communauté zooplanctonique du nord-ouest du golfe du Saint-Laurent. Quels seraient les impacts sur l'ichtyoplancton de l'augmentation d'une espèce de proie par rapport à une autre? Quelles sont les implications sur d'autres espèces qui sont actuellement moins abondantes? Comment la sélection d'un type de proie favorise-t-elle la survie par rapport à une autre? Les réponses à ces questions restent en

suspend, mais on peut espérer qu'une poursuite de la recherche dans cette région permettra d'y répondre.

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ANNEXE

4.1 Propos

Cette annexe contient des informations complémentaires concernant la distribution spatiale des principales espèces de zooplancton présent dans les échantillons de filet verticaux à la mi-mai 2008 dans le nord-ouest du golfe du Saint-Laurent. Ces cartes ont été produites à l'aide du logiciel libre d'accès R (www.r-project.org) et du supplément PDSmapping (www.dfo-mpo.gc.ca/Library/285683.pdf) pour décrire la distribution géographique de ces espèces. Dans le cas des copépodes, les abondances sont regroupées en stade de développement (oeufs, nauplii et copépodites) puisqu'ils représentent une part importante de l'alimentation des lançons, de la stichée arctique et de la lompénie serpent.

4.2 Espèce absente de l'alimentation

Les régions du détroit de Jacques-Cartier, du sud et de la pointe est de l'île d'Anticosti semblent particulièrement importantes pour les larves de lançons et de stichée arctique où leurs abondances sont plus importantes (Figure 9). À cet égard, les abondances de *Fritillaria* sp. sont également plus élevées dans cette région (Figure A1-A). On note également une certaine importance de cette espèce dans les stations entourant la pointe sud-est (station 8). Les larves de bivalves quant à elles sont plus abondantes dans la partie ouest du chenal d'Anticosti (Figure A1-B). Les polychètes, beaucoup moins abondants, ont une distribution qui semble relativement aléatoire dans toute l'aire d'étude (Figure A1-C).

4.1 Copépodes

Les abondances du copépode *O. similis* sont proportionnellement similaires lorsque

l'on compare les stades nauplii et copépodites (Figure A2). Celles-ci sont plus élevées du côté est, de part et d'autre de l'île. Les oeufs et nauplii de *C. finmarchicus* sont plus abondants à l'ouest et à l'est de l'île ainsi qu'aux stations situées au sud-ouest de l'île (Figure A3). La distribution des copépodites de cette espèce semble aléatoire. Les oeufs de *C. glacialis* sont plus importants près des pointes est et ouest de l'île et au banc Beaugé, entre les chenaux d'Anticosti et d'Esquiman (Figure A4-A). La distribution des oeufs de *C. hyperboreus* peut être biaisée par le critère d'identification utilisé, néanmoins les oeufs de cette taille sont plus abondants au banc Beaugé, à la pointe est de l'île et près de la pointe sud-ouest (Figure A4-B). Les abondances combinées de nauplii de *C. glacialis* et *C. hyperboreus* sont relativement semblables dans toute la zone d'étude (Figure A4-C). Les abondances de copépodites *C. glacialis* sont plus élevées le long de la côte du Québec et à la pointe est de l'île (Figure A4-D) alors que celles de *C. hyperboreus* sont plus importantes au sud-ouest de l'île (Figure A4-E).

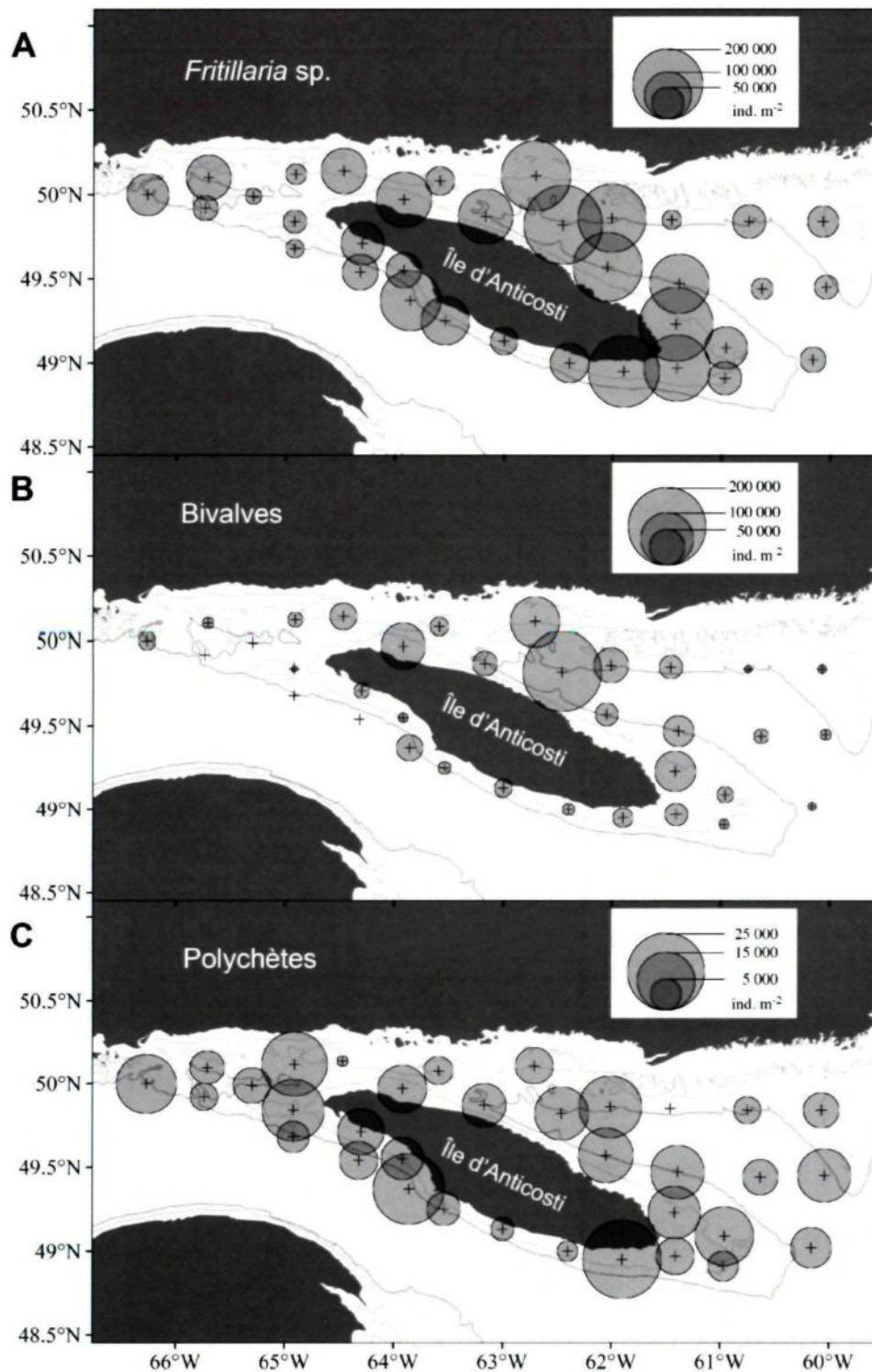


Figure A1. Abondance de *Fritillaria* sp. (A), larves de bivalves (B) et de polychètes (C) par station échantillonnée en mai 2008 dans le nord-ouest du golfe du Saint-Laurent.

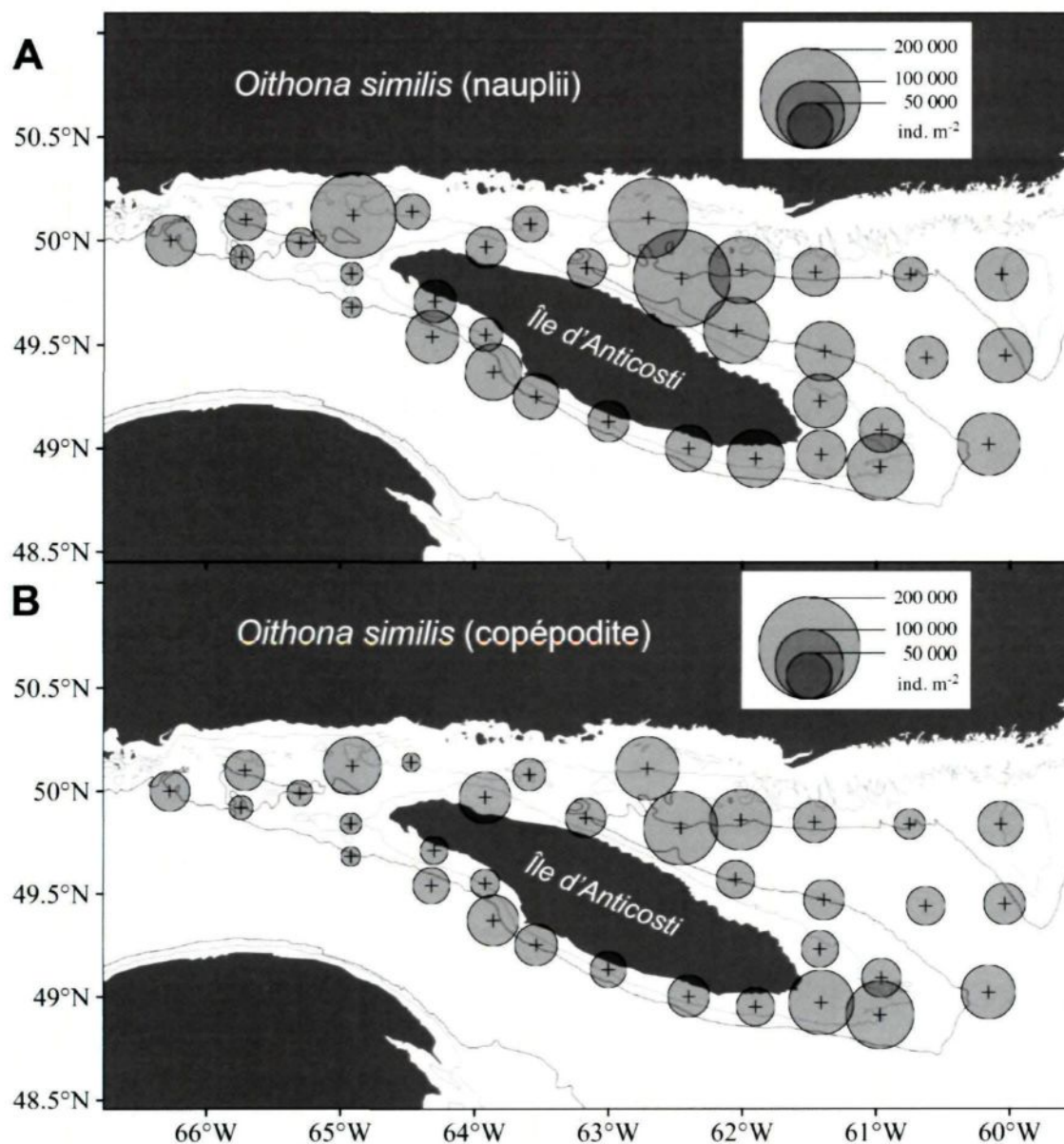


Figure A2. Abondance d'*O. similis* aux stades nauplii (N1-N6) (A) et copépodites (CI-CVI) (B) par station échantillonnée en mai 2008 dans le nord-ouest du golfe du Saint-Laurent.

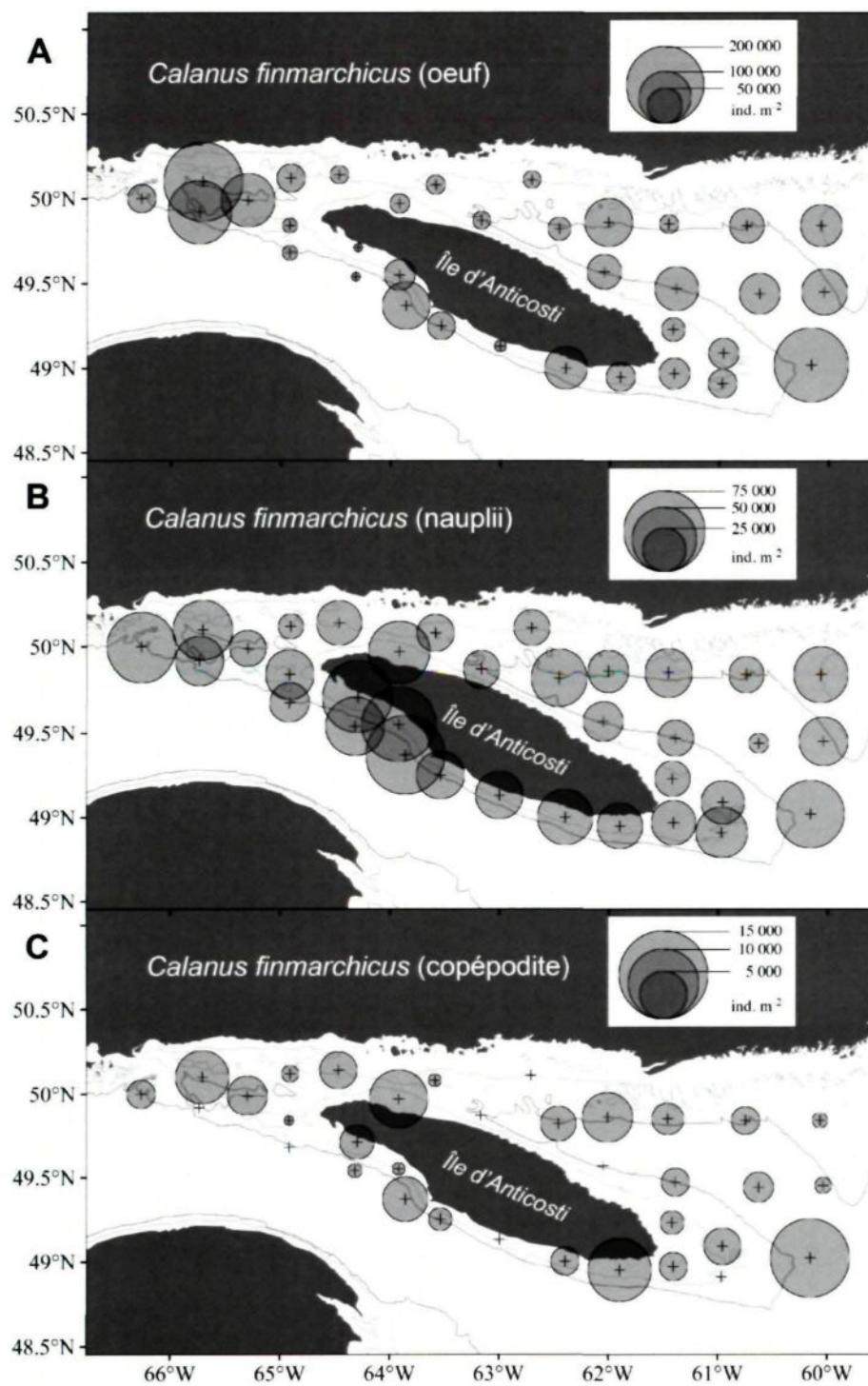


Figure A3. Abondance de *C. finmarchicus* aux stades oeuf (A), nauplii (N1-N6) (B) et copépodites (C1-CVI) (C) par station échantillonnée en mai 2008 dans le nord-ouest du golfe du Saint-Laurent.

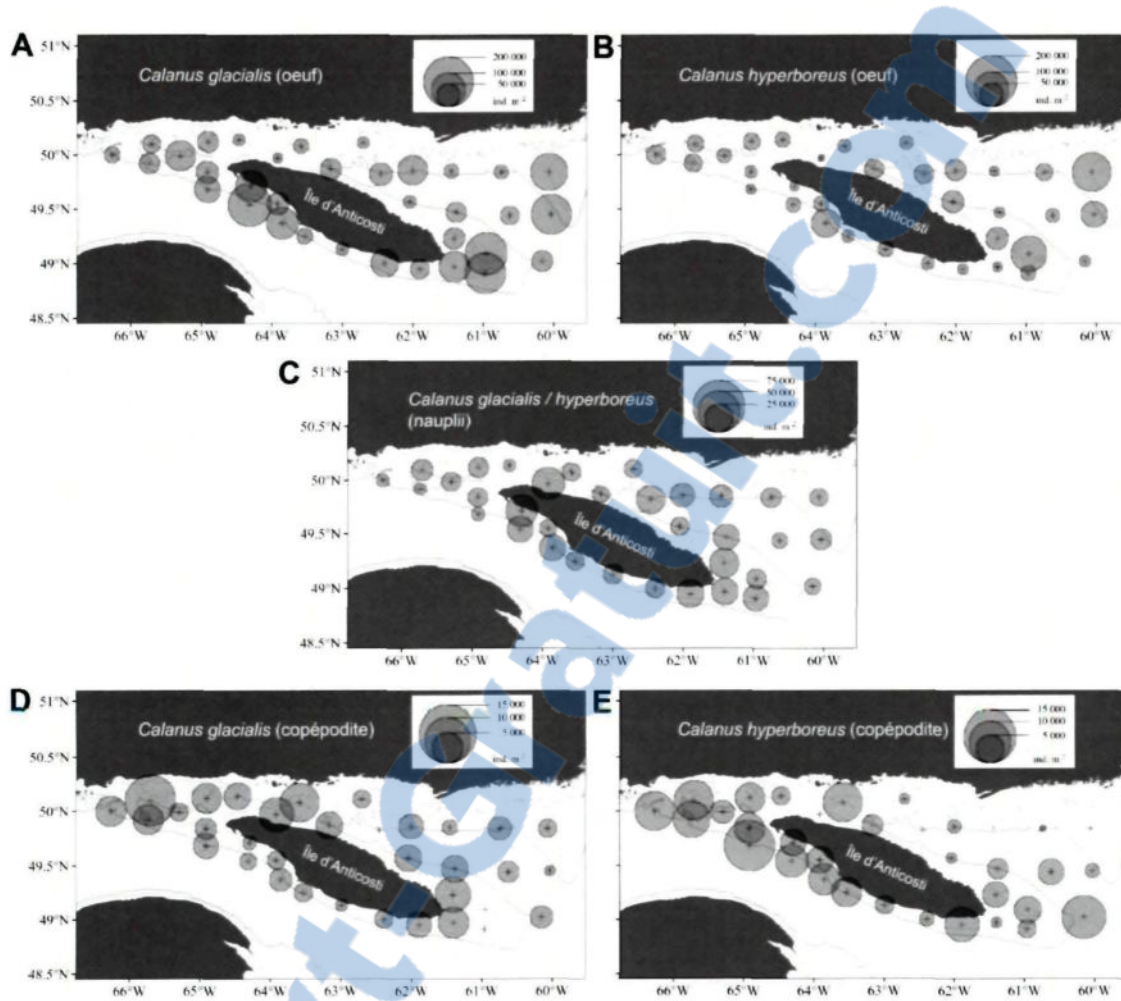


Figure A4. Abondance de *C. glacialis* et *C. hyperboreus* aux stades oeuf (A, B), nauplii (C) et copépodites (CI-CVI) (D, E) par station échantillonnée en mai 2008 dans le nord-ouest du golfe du Saint-Laurent.