

UNIVERSITÉ DU QUÉBEC

STRUCTURE DES COMMUNAUTÉS MÉSOZOOPLANCTONIQUES EN  
RELATION AVEC LES CONDITIONS DU MILIEU DANS LE SYSTÈME DE LA  
BAIE D'HUDSON À LA FIN DES ÉTÉS 2003 À 2006

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RAFAEL ESTRADA

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## RÉSUMÉ

Les communautés zooplanctoniques ont été étudiées pour la première fois dans trois régions hydrographiques différentes du système de la baie d'Hudson (SBH) à la fin des étés 2003 à 2006 au cours du programme MERICA-nord. Entre neuf et quatorze stations distribuées le long de différentes radiales localisées dans la baie d'Hudson (BH), le détroit d'Hudson (DH) et le bassin de Foxe (BF) ont été échantillonnées à chaque année de l'étude. Les variations concernant la biomasse du zooplancton, l'abondance, la composition et la diversité des espèces et leur relation avec les variables du milieu ont été étudiées en utilisant des techniques d'analyses multidimensionnelles (cadrage multidimensionnelle; analyse de similarité (ANOSIM); analyse de redondance). Pour toutes les années, la moyenne totale de la biomasse de zooplancton (poids humide) était de quatre fois moindres dans la BH ( $14.1 \text{ g m}^{-2}$ ) que dans le DH ( $64.2 \text{ g m}^{-2}$ ) et le BF ( $60.0 \text{ g m}^{-2}$ ). Un cadrage multidimensionnel a révélé qu'il n'y avait pas de variation interannuelle dans l'abondance relative de la communauté zooplanctonique (ANOSIM,  $R = 0.10$ ,  $p > 0.05$ ), mais qu'il y avait une variabilité interrégionale marquée entre les trois régions à l'étude (ANOSIM,  $R = 0.75$ ,  $p > 0.05$ ). La stratification de la colonne d'eau explique une grande proportion (25%) de la variabilité spatiale dans la structure de la communauté de zooplancton à l'intérieur du SBH. Les analyses de redondances démontrent que les taxons zooplanctoniques qui contribuent le plus significativement à la séparation des trois régions sont : *Microcalanus* spp., *Oithona similis*, *Oncaea borealis*, *Aeginopsis laurentii*, *Sagitta elegans*, *Fritillaria* sp., et des larves de Cnidaires, Chaetognatha et Ptéropoda dans la BH;

amphipodes hyperiides dans le BF; et *Pseudocalanus* spp. CI-CV, *Calanus glacialis* CI-CVI, *C. finmarchicus* CI-CVI, *C. hyperboreus* CV-CVI, *Acartia longiremis* CI-CV, *Metridia longa* N3-N6, CI-CIII et CVIf, *Eukrohnia hamata* et des larves d'échinodermes, de mollusques, de cirripèdes, d'appendiculaires, et de polychètes dans les sections nord-ouest et sud-est du DH. Dans la BH, les variables analysées grâce à une RDA partielle permettent de distinguer trois sous-régions à l'intérieur de la baie (i.e. les secteurs ouest, centrale et est). Chaque secteur est caractérisé par des gradients environnementaux et assemblages zooplanctoniques distincts particulièrement des nauplii et CI-CVI de *Pseudocalanus* spp., ainsi que plusieurs espèces de macrozooplancton benthique et des larves de méroplancton qui se retrouvaient davantage dans l'ouest de la BH. Dans le DH, les espèces calanoïdes (majoritairement *C. finmarchicus* et *C. glacialis*) étaient principalement observées aux stations de la rive nord associées avec les eaux arctiques et atlantiques provenant du sud-ouest du détroit de Davis. En général, les modèles d'analyse de redondance testés parmi les différentes régions du SBH, reflétaient bien le patron de circulation générale des couches de surface pour les conditions estivales en termes de variables environnementales et d'assemblages distincts de zooplancton. De façon générale, les indices de diversité ( $H'$ ,  $J'$  et  $S$ ) et la biomasse de zooplancton étaient plus faibles en milieu fortement stratifié (i.e. BH) que dans les régions plus profondes et dynamiques (i.e. BF & DH, respectivement). Les résultats obtenus dans ce travail démontrent que la structure des communautés zooplanctoniques dans les sites étudiés du SBH est influencée par la profondeur du milieu et les conditions hydrodynamiques locales qui, à travers leurs

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## LISTE DES ABRÉVIATIONS

### Abréviations en français :

SBH = Système de la baie d'Hudson

BH = Baie d'Hudson

DH = Détroit d'Hudson

BF = Bassin de Foxe

MERICA = Mers intérieures du Canada

### Abréviations en anglais :

CARC = Canadian Arctic Resources Committee

HBS = Hudson Bay System

HB = Hudson Bay

HS = Northwestern Hudson Strait (corresponding to 2003-2004 samplings)

HSS = Southeastern Hudson Strait Section (corresponding to 2005-2006 samplings)

FB = Foxe Basin

NMDS = Non-metric multidimensional scaling

ANOSIM = Analysis of similarity

RDA = Redundancy analysis

pRDA = Partial redundancy analysis

SD = Standard deviation

CV = Coefficient of variation

Depth = Bottom depth

UMT = Upper mean temperature

LMT = Lower mean temperature

UMS = Upper mean salinity

LMS = Lower mean salinity

Flu0-100 = Integrated fluorescence form 0 to 100 m

Strat = Stratification index

WM = wet mass



## 1. INTRODUCTION GÉNÉRALE

### 1.1. LE CHANGEMENT CLIMATIQUE DANS LE SYSTÈME DE LA BAIE D'HUDSON

Au cours du dernier siècle, le climat de la terre a connu un réchauffement d'environ  $0,6^{\circ}\text{C}$  qui est non seulement relié à des événements naturels comme les variations du rayonnement solaire ou de l'activité volcanique, mais plus potentiellement à l'augmentation des concentrations de gaz à effets de serre d'origine anthropique (IPCC 2001, 2007). L'Arctique est l'une des régions où les changements climatiques provoquent actuellement des bouleversements importants (Serreze et al., 2000). En effet, les données satellitaires de 1978 à 2003 montrent une diminution moyenne de la couverture de la glace de mer de 2-3% par décennie, ce qui correspond à  $350\,000\text{ km}^2$  par année (Comiso et Parkinson, 2004). Dans ce contexte, le système de la baie d'Hudson (SBH) n'est pas une exception puisqu'il est considéré comme une région très sensible aux variations climatiques (Laidre et Haide-Jorgensen, 2005). Dans la région de la baie d'Hudson (BH), la glace de mer s'y forme en novembre et demeure typiquement jusqu'au mois de juin (Gough et Wolfe, 2000). Dans le SBH, la répartition et l'étendue de la glace de mer étaient relativement constantes à la mi-juillet entre 1971 et 1992 (Fig. 1). Toutefois, les conditions de la glace de mer ont été beaucoup plus variables et démontrent une tendance à la diminution depuis 1993. De plus, Markus et al. (2009) ont récemment démontré que la saison libre de glace dans SBH a été rallongée de plus de 20 jours entre 1992 et 2007, ce qui représente l'augmentation la plus élevée pour les régions arctiques. D'après les simulations de modèles climatiques globaux,

la multiplication anticipée par deux des concentrations atmosphériques de CO<sub>2</sub> entraînera la disparition quasi totale de la glace de mer dans la BH (Gough et Wolfe, 2001).

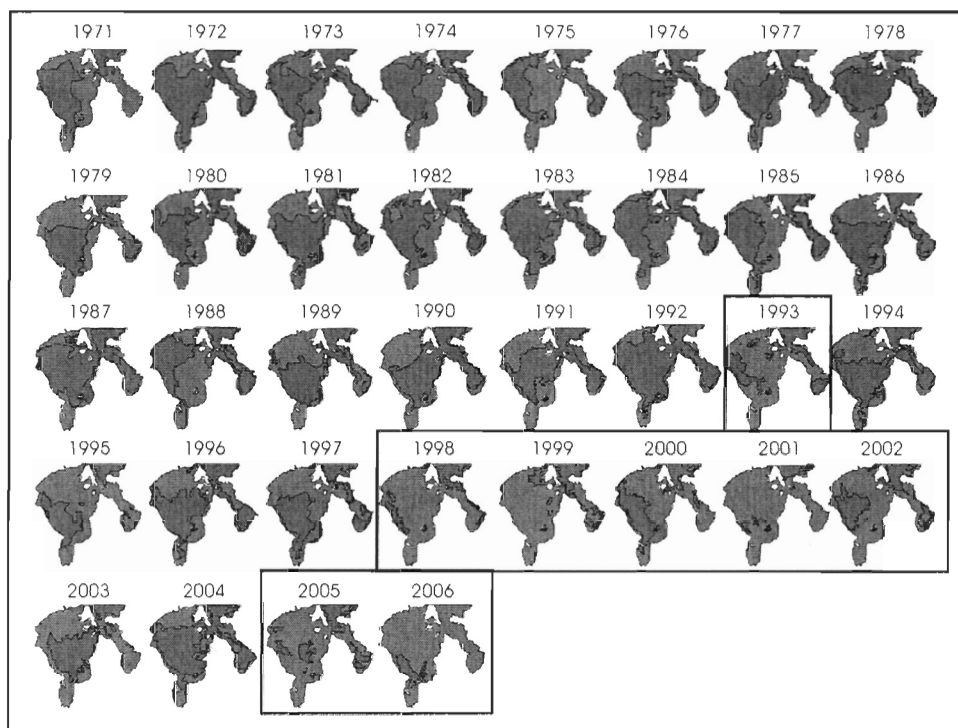


Figure 1. Couvertures historiques de glace de mer à la mi-juillet dans le SBH de 1971 à 2006 (M. Harvey; données non publiées).

Ces changements climatiques du milieu auront, sans aucun doute, des conséquences sur la structure et le fonctionnement de l'écosystème marin du SBH (Stirling et al., 1999). Des recherches réalisées de 1981 à 2002 sur le Guillemot de Brünnich (*Uria lomvia*) ont montré un changement dans l'alimentation des oisillons (Gaston et al., 2003). Durant la période étudiée, la principale source de nourriture pour les oisillons est passée de la morue arctique (*Boreogadus saida*) au capelan (*Mallotus villosus*) et au lançon (*Ammodytes* spp.). Gaston et al. (2003) ont remarqué que le déclin de la morue arctique (une espèce qui est fortement associée à la glace de mer pour son alimentation et pour fuir les prédateurs) et l'augmentation dans l'abondance du capelan et du lançon (deux espèces qui sont plus abondantes dans les eaux avec peu ou sans couvert de glace estival) étaient associés avec un réchauffement général des eaux de la BH.

De plus, Gaston et Woo (2008) ont rapporté la présence récente de Petit pingouin (*Alca torda*) dans la région de la BH. Cette espèce a été aperçue à l'île de Coats qui est située à 300 km plus à l'ouest du site de nidification connu pour cette espèce. L'arrivée de cet alcidé coïncide avec l'augmentation de capelans et de lançons dans l'alimentation des oisillons de Guillemots de Brünnich au même site d'étude. De plus, la disparition du Petit pingouin est constatée lorsque le lançon (sa proie préférentielle dans le Canada atlantique) disparaît également. Cette corrélation entre la présence de lançons et de Petit pingouins suggère un lien entre l'arrivée de cet oiseau et l'augmentation de l'abondance de lançon dans ces eaux.

La morue arctique se nourrit principalement de copépodes et d'amphipodes planctoniques, d'amphipodes associés à la glace et de mysidacés. Cette espèce est le principal lien entre les niveaux trophiques inférieurs et les prédateurs supérieurs (e.g. les oiseaux et les mammifères marins) (Hop et al., 1997; Sæther et al., 1999). Le capelan et le lançon sont tous les deux des espèces planctonophages dont la diète est composée de copépodes (principalement de *Calanus finmarchicus*, mais aussi de *C. hyperboreus*) (Scott, 1973; Astthorsson et Gislason, 1997).

## 1.2. LE ZOOPLANCTON ET LES CHANGEMENTS CLIMATIQUES

Le SBH est considéré comme un “point chaud” pour la conservation marine par le Comité des Ressources Arctiques Canadiennes (CARC), en regard de l'importance de la biodiversité et l'influence de la dynamique de ses eaux sur tout l'ensemble du système (Beckmann, 1994). Ce système possède une grande richesse faunique, des microalgues à l'ours polaire. L'ours polaire dépend fortement de la glace de mer pour chasser et se nourrir de phoques au cours de la période hivernale et printanière. De plus, il symbolise ce système en étant au sommet du réseau alimentaire (Gough et Wolfe, 2001). Les microalgues qui croissent à la base de la glace de mer au printemps et dans la colonne d'eau (phytoplancton) (Horner, 1985) sont la principale source de nourriture pour la faune benthique et plusieurs espèces zooplanctoniques comme le copépode *Calanus glacialis* (Runge et Ingram, 1991). Le zooplancton est le principal phytophage dans la chaîne alimentaire océanique. Il joue un rôle primordial dans le transfert d'énergie entre les producteurs primaires et les

consommateurs des niveaux trophiques supérieurs. De plus, les organismes zooplanctoniques jouent un rôle clé dans la pompe biologique, puisqu'ils transportent une part importante du carbone fixé par le phytoplancton au fond des océans par leur production de péloles fécales (Richardson, 2008).

Le zooplancton est reconnu comme un bio-indicateur très sensible aux changements climatiques, car il répond rapidement aux variations de températures et des systèmes de courants océaniques en modifiant sa répartition spatiale (Hays et al., 2005).

Jusqu'à ce jour, la dynamique du zooplancton dans le SBH est encore peu connue. Peu de recherches portant sur l'abondance et la composition spécifique du zooplancton, en fonction des variables du milieu, ont été publiées. Le zooplancton a été étudié au sud (Grainger et Sween, 1976), au sud-est (Hsiao et al., 1983), à l'est (Rochet et Grainger, 1987) et au nord-ouest et nord-est (Roff et al., 1980) de la BH. La première étude décrivant simultanément l'abondance et la composition du zooplancton dans différentes régions de la BH et du DH a été effectuée par Harvey et al. (2001). Cette étude a été réalisée en septembre 1993 et couvrait un large secteur situé entre la baie James au sud de la BH et la baie d'Ungava dans le DH. Des études ont été également réalisées à l'est (Taggart et al., 1989 ; Hudon et al., 1993), à l'ouest (Percy et al., 1992), et pour l'ensemble (Grainger, 1990) du détroit d'Hudson (DH) et dans le bassin de Foxe (BF) (Grainger, 1962).

### 1.3. OBJECTIFS DE L'ÉTUDE

La variabilité spatiale et interannuelle du zooplancton dans les trois régions hydrographiques du SBH n'a jamais été étudiée. Le programme nommé MERICA-nord (études des MERs Intérieures du Canada) a été développé par le ministère des Pêches et Océans Canada de la Région Québec afin de suivre, comprendre et prédire les changements climatiques et ses effets sur la productivité et la biodiversité qui surviendront au cours des prochaines années dans le SBH (Saucier et al., 2003). Dans ce contexte, l'objectif principal de ce travail est de décrire la structure de la communauté zooplanctonique, son abondance, sa biomasse et sa répartition dans les trois régions du SBH et ses relations avec les conditions environnementales (i.e. l'indice de stratification, la température et la salinité des couches de surface, la température et la salinité des couches profondes, la fluorescence intégrée de 0 à 100 m et la profondeur du milieu) lors de quatre années d'échantillonnage qui se sont déroulées à la fin des étés 2003 à 2006. Un deuxième objectif vise à identifier des tendances linéaires possibles entre la biomasse et indices de diversité du zooplancton et les gradients physiques qui pourraient être influencés par les changements climatiques.

#### 1.4. LE SYSTÈME DE LA BAIE DE HUDSON

Le système de la baie d'Hudson (SBH) se situe dans les régions arctiques et subarctiques du Canada, entre 50 - 70°N et 95 - 65°O (Fig. 2). Il comprend : la baie d'Hudson (BH), le détroit d'Hudson (DH) et le bassin de Foxe (BF) qui forment probablement, l'un des plus grands estuaires nordiques (Prinsenber, 1984).

Cette région est connectée à l'est, aux eaux de l'océan Atlantique par la mer du Labrador (via le DH) et dans le nord avec les eaux arctiques provenant du détroit de Fury et Hecla (via le bassin de Foxe) (Prinsenber, 1986b). Le SBH est principalement influencé par trois types d'eau : l'écoulement des rivières, l'eau de mer provenant de l'océan Arctique et l'eau de mer du courant de l'île de Baffin (Straneo et Saucier, 2008). L'eau de la fonte de glace de mer serait la source la plus importante d'eau douce dans le cycle saisonnier de cette région, notamment dans le BF (Jones et Anderson, 1994). Le BF a une profondeur ne dépassant pas 100 m pour les régions à l'est et de 200 m pour la région située au sud dans le canal de Foxe (Prinsenber, 1986c). La BH a une profondeur moyenne de 125 m caractérisée par une topographie du fond variable moins accidentée dans le sud et très accidentée dans le nord; ce qui lui donne une forme rectangulaire de 925 par 700 km, en ignorant les zones peu profondes du sud-est (Jones et Anderson, 1994; Prinsenber, 1986b). Le BF et la BH sont tous deux connectés à la partie profonde du DH qui est un canal étroit (70-150 km) et long (~750 km) d'une profondeur moyenne entre 300 et 400 m (Drinkwater, 1986). Normalement, le nord du BF est recouvert de glace de la mi-



octobre au mois de septembre, tandis que la BH est entièrement couverte de glace lors de l'hiver et libre de glace au mois d'août et septembre (Prinsenber, 1986c; Wang et al., 1994). Le DH est couvert de glace au  $\sim 3/4$  de l'année et commence normalement à être libre de glace à partir du début du mois d'août jusqu'à la fin octobre (Percy, 1990). Selon la répartition de la salinité estivale et les patrons de morcellement de la glace dans le BF, il y a une circulation cyclonique dans la région nordique du bassin avec un fort courant vers le sud ( $0.6 \text{ m s}^{-1}$ ) le long de la péninsule de Melville. De plus, il y a dans la partie sud du bassin un apport d'eau provenant du DH le long de la péninsule de Foxe et une sortie d'eau le long de l'île de Southampton (Prinsenber, 1986c) (Fig. 2, coin supérieur droit). Les eaux de fond du BF ont une salinité plus élevée (causée par la libération de l'eau salée lors de la production et le vieillissement de la glace de mer) que les eaux provenant de l'océan Arctique par le détroit de Fury et Hecla et les eaux de fond provenant de l'est du DH. La couche supérieure d'eau saumâtre (salinité  $[S] = 33.1$ ) du BF a une épaisseur approximative de 25 m (Jones et Anderson, 1994). La température moyenne des eaux de surface est de  $\sim 3 \text{ }^\circ\text{C}$  et est plus chaude dans la région du canal de Foxe (Prinsenber, 1986c).

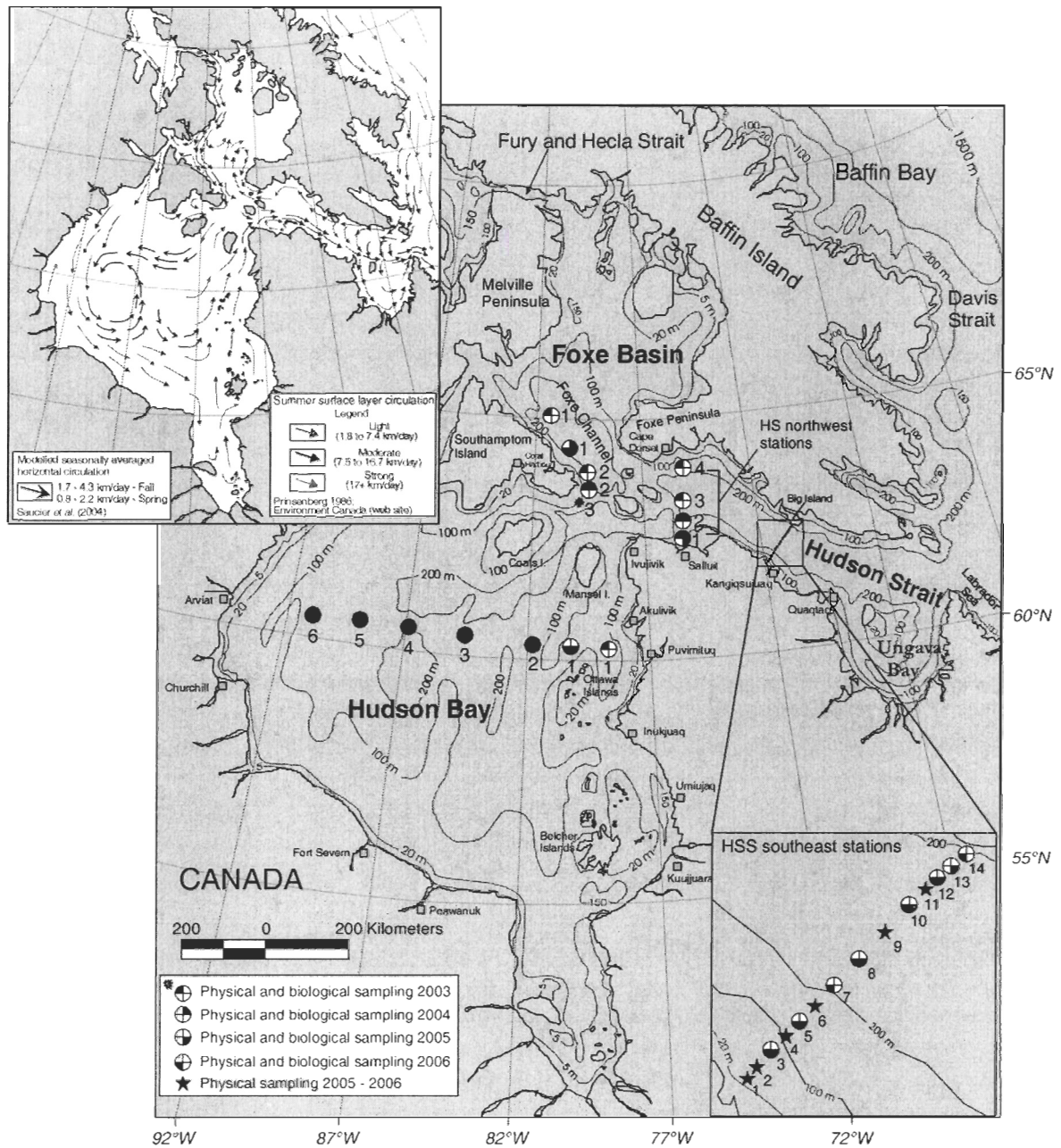


Figure 2. Localisations des stations d'échantillonnage dans le SBH pendant le programme MERICA-nord 2003-2006. En médaillon, le patron de circulation générale de la couche de surface pour les conditions estivales dans le bassin de Foxe, la baie d'Hudson et le détroit d'Hudson (adapté de Prinsenber, 1986b; Saucier et al., 2004); Environnement Canada).  
 \* Station (FB3) visitée seulement en 2003.

Dans la BH, les données de bouteilles de dérive et la répartition spatiale de la salinité et de la température indiquent une circulation cyclonique dans la couche de surface ( $0.05 \text{ m s}^{-1}$ ). La masse d'eau sortant le long de la côte est de la baie est relativement chaude et de faible salinité (Prinsenber, 1983; 1986a). Des simulations numériques récentes suggèrent qu'en absence de glace de mer, les eaux de la baie expérimenteraient de plus fortes activités de tourbillons en surface. Ces tourbillons seraient associés 1) aux forçages synoptiques du vent et à la présence d'un gyre cyclonique à grande échelle dans la partie ouest de la BH, et 2) aux plus forts courants à l'automne ( $0.02\text{-}0.05 \text{ m s}^{-1}$ ) qui sont deux fois plus élevées que ceux du printemps (Saucier et al., 2004) (Fig. 2, coin supérieur gauche). La circulation générale dans la baie causée par le vent et les courants de densité résultants de la dilution par les eaux de ruissellement des rivières. Ces eaux proviennent d'une grande aire de drainage ( $3.1 \times 10^6 \text{ km}^2$ ) avec un débit annuel moyen de  $2.1 \times 10^4 \text{ m}^3 \text{ s}^{-1}$  (Prinsenber, 1986b; 1988). Durant l'été, la BH est stratifiée verticalement avec une forte pycnocline allant de 15 à 25 m; les températures des eaux de surface atteignent  $12 \text{ }^\circ\text{C}$  et les eaux profondes  $-1.7 \text{ }^\circ\text{C}$ ; la salinité de surface s'étend de 10 à 30 près des rivières majeur au centre et au nord-est de la BH, respectivement (Roff et Legendre, 1986). Les eaux profondes de la BH, lesquelles circulent elles aussi d'une façon cyclonique, sont le produit des eaux froides de surface de l'océan Arctique entrant 1) par le DH par l'ouest (via le détroit de Fury et de Hecla, au nord du BF); 2) par le DH par l'est (qui coule vers l'ouest par le biais d'une extension du courant de Baffin); 3) et par les eaux plus chaudes et plus salées de l'Atlantique entrant en profondeur par le DH (Barber, 1967).

Dans le DH, la circulation de surface a trois principaux patrons : 1) un courant entrant au SBH se dirigeant vers le nord-ouest le long de la rive sud de l'île de Baffin; 2) un courant sortant du SBH se déplaçant vers le sud-est le long de la rive nord du Québec, et qui éventuellement contribue au courant du Labrador; et 3) dans la moitié orientale du détroit, un écoulement à contre-courant vers le sud s'ajoutant au courant sortant du SBH (Drinkwater, 1986; LeBlond et al., 1981) (Fig. 2, coin supérieur gauche). Selon Straneo et Saucier (2008), les afflux d'eaux douces ( $S = 33$ ) du DH au SBH apportent  $\sim 44$  mSv (milli Sverdrup); ces écoulements d'eau hors du détroit de Davis sont donc des eaux arctiques qui circulent pour atteindre l'Atlantique Nord subpolaire. D'autre part, l'écoulement sortant du DH, apporte de l'eau douce et froide du SBH, le long de la côte du Québec, vers la mer du Labrador; ce flux s'étend de 40 à 50 km des côtes, avec des vitesses de  $1 \text{ m s}^{-1}$  (Straneo et Saucier, 2008). Les sorties d'eaux du DH, transportent deux types de masses d'eau : des eaux plus douces ( $S = < 33$ ) et très stratifiées sont acheminées entre juin et mars, et des eaux plus salées ( $> 33$ ) et moins stratifiées sont acheminées sous les eaux douces, lors de la période de la sortie des eaux douces entre mars et juin. Il est estimé que 15% du volume et 50% de l'eau douce du courant du Labrador proviennent du DH (Straneo et Saucier, 2008). Cela influence grandement les propriétés et l'écosystème le long du plateau du Labrador (Straneo et Saucier, 2008). De façon globale, les marées de grandes amplitudes dans le DH (qui augmentent de 2 m à l'est de l'entrée à plus de 3,4 m près de Big Island, et qui décroissent à l'entrée ouest) et les forts courants tidaux (jusqu'à  $2\text{-}3 \text{ m s}^{-1}$ ) produisent un mélange vertical intense, qui à une forte influence sur la stratification verticale de la colonne d'eau, de la température de l'eau et de la salinité ainsi que sur la productivité

biologique locale dans différentes régions du détroit (Drinkwater, 1986; Drinkwater et Jones, 1987).

**2. LATE SUMMER ZOOPLANKTON COMMUNITY STRUCTURE,  
ABUNDANCE AND DISTRIBUTION IN THE HUDSON BAY SYSTEM AND  
THEIR RELATIONS WITH ENVIRONMENTAL CONDITIONS, 2003-2006**

## ABSTRACT

Zooplankton communities were examined for the first time in three different hydrographic regions of the Hudson Bay system (HBS) in early August-early September from 2003 to 2006. Sampling was conducted at fifty stations distributed along different transects located in the Hudson Bay (HB), Hudson Strait (HS) and Foxe Basin (FB). The variations in zooplankton biomass, abundance, taxonomic composition and diversity in relation to environmental variables were studied using multivariate [non-metric multidimensional scaling, one-way analysis of similarity (ANOSIM) and redundancy analysis (RDA)] techniques. During all sampling years, the average total zooplankton biomass (expressed in wet mass) was, on average, 4 times lower in HB ( $14.1 \text{ g m}^{-2}$ ) than in HS ( $64.2 \text{ g m}^{-2}$ ) and FB ( $60.0 \text{ g m}^{-2}$ ). Clustering samples by their relative species compositions revealed no interannual variation in zooplankton community (ANOSIM test,  $R = 0.10$ ,  $p > 0.05$ ), but did reveal a markedly interregional variability between the three regions (ANOSIM test,  $R = 0.75$ ,  $p \leq 0.001$ ). Water column stratification explained the greatest proportion (25 %) of this spatial variability in the structure of zooplankton communities within the HBS. According to the RDAs, the zooplankton taxa that contribute most significantly to the separation of the three regions are: *Microcalanus* spp., *Oithona similis*, *Oncaea borealis*, *Aeginopsis laurentii*, *Sagitta elegans*, *Fritillaria* sp., and larvae of Cnidaria, Chaetognatha and Pteropoda in the HB; hyperiid amphipods in the FB; and *Pseudocalanus* spp. CI-CV, *Calanus glacialis* CI-CVI, *C. finmarchicus* CI-CVI, *C. hyperboreus* CV-CVI, *Acartia longiremis* CI-CV, *Metridia longa* N3-N6, CI-CIII and

CVIif, *Eukrohnia hamata*, larvae of Echinodermata, Mollusca, Cirripedia, Appendicularia, and Polychaeta in the northwestern and southeastern HS sections. In the HB, the environmental variables analysed in a partial RDA allowed to distinguish three regions inside the bay transects (HB West, Central, and East) with different environmental gradients and zooplankton assemblages with *Pseudocalanus* spp. naupliar and CI-CVI, and macrozooplankton benthic and meroplankton larvae showing higher occurrence in western HB. In the HS, *Calanoid* species (mainly *C. finmarchicus* & *C. glacialis*) were mainly observed in the northern shore stations associated with the weakly stratified Arctic-North Atlantic waters coming from southwestern Davis Strait (inflow). In general, the RDA models tested among the regions of the HBS were very consistent with its general surface layer circulation pattern for the summer condition in terms of environmental variables and distinct zooplankton assemblages. Overall, both the zooplankton biomass and diversity indices ( $H'$ ,  $J'$  and  $S$ ) were lower in the most stratified environment (i.e. HB) than in the deeper and more dynamic regions (i.e. FB & HS, respectively). The results of this work show clearly that the structure in zooplankton communities is influenced by the hydrodynamic conditions in the HBS that, through their actions on temperature, salinity, stratification, mixing conditions and depth strata, lead to the spatial differentiation of these communities.



## INTRODUCTION

Estuarine systems in general are highly dynamic and display distinctive physical and chemical features that influence planktonic organisms in different ways (Sterza and Fernandes, 2006). Salinity, more than any other variable, determines the diversity in estuaries (which decreases with distance from the sea) and distribution of zooplankton within estuaries (Litle, 2000; Johnson and Allen, 2005). However, current systems could play a major role in zooplankton distribution within a geographic area carrying species that might be tolerant or not (Lance, 1963) to the changing conditions of the water masses they are living in.

In these estuarine environments, it is common to find a sequence of zooplankton assemblages along the salinity gradient with: i) euryhaline-freshwater species (at the riverine end); ii) then estuarine species followed by euryhaline marine species (further downstream); iii) stenohaline marine species (at the marine zone) (Litle, 2000). This reflects the horizontal distribution of zooplankton species classically observed in estuarine systems. In fact, brackish waters contain a mixture of typically brackish zooplankton plus some particularly tolerant marine and fresh water species with more limited estuarine distribution (Johnson and Allen, 2005).

In temperate ecosystems, the establishment of the seasonal thermocline significantly modifies the structure of the water column from mixed conditions in winter to strongly

stratified conditions in summer-autumn (Ramfos et al., 2006). In estuaries, the stratification is an universal feature produced by the combined effects of temperature and salinity differences in the water column and its intensity depends strongly in the amount of freshwater input and on the intensity of wind and tidal mixing (Johnson and Allen, 2005).

The Hudson Bay system (HBS) is located in the Arctic and sub-Arctic regions of Canada. It is formed by: the Hudson Bay (HB), the Hudson Strait (HS) and the Foxe Basin (FB), which together make up one of the largest northern estuaries (Prinsenber, 1984). Briefly, HB is one of the biggest inland seas in the Northern Hemisphere ( $830 \times 10^3 \text{ km}^2$ ) (Prinsenber, 1984). This region is characterised by a great fresh water input coming from the surrounding rivers and also by the seasonal sea-ice melting, which give it estuary-like characteristics: a two water layer circulation pattern separated by a strong pycnocline located between 5 and 25 m (Roff and Legendre, 1986). The massive intrusions of continental waters drive a horizontal cyclonic circulation pattern on the surface layer of the HB, which is characterized by fresher and less dense waters than those entering between Southampton and Coats Islands. The fresh surface waters mix with the numerous local river plumes and slowly circle the bay before exiting by the southern shore of the HS towards the Labrador Sea (Pett and Roff, 1982).

Earlier studies showed that the horizontal distribution of the macro- and mesozooplankton in the HBS can be influenced by the local environmental gradients and water mass circulation. For example, Grainger (1962) distinguished two groups of

zooplankton in the FB. The first one with species showing the influence of arctic waters entering the basin from the north (i.e. the copepods *C. glacialis*, *C. hyperboreus*, and the amphipod *Themisto libellula*, amongst others), and the second constituted of subarctic species introduced from the south (i.e. *C. finmarchicus*, *Themisto abyssorum*). Rochet and Grainger (1987) identified different zooplankton assemblages in eastern HB waters accordingly to the salinity gradients and water masses present there. In their study, the zooplankton component (e.g. the cnidarians *Aglantha digitale* and *Aeginopsis laurentii*) in the eastern part of the bay showed clearly the influence of arctic waters all over the area, whereas zooplankton indicative of estuarine conditions (e.g. the copepods *Centropages abdominalis* and *Eurytemora herdmani*) were confined to the southeastern HB area where low salinities prevail.

More recently Harvey et al. (2001) identified four different zooplankton assemblages within the environmental gradients recorded, salinity in particular, over a large sector close to the shores extending from the entrance of James Bay, south of HB, to the southeastern HS shore. In their study, the euryhaline copepods *Acartia longiremis* and *Centropages hamatus* represented the first group in the less saline waters of southeastern HB, while the higher zooplankton biomasses, featured by *Calanus finmarchicus* and *C. glacialis*, characterized a more saline surface water portion at the end of the HS transect.

During the last century, the oceanic and terrestrial planet surfaces have warmed (about 0.6 °C) mainly due to the increase of the greenhouse effect gases coming from

human origin activities (IPCC, 2001, 2007). The Arctic is one of the regions where climate changes are currently causing serious damages (Serreze et al., 2000). In this context, the HBS is no exception since, it is considered as a very sensitive region to climate variations (Laidre and Heide-Jørgensen, 2005).

According to the Canadian first-generation coupled general circulation model (CGCM I), the doubling of the CO<sub>2</sub> atmospheric concentrations will involve the quasi total disappearance of sea-ice in the HB (Gough and Wolfe, 2001), which could have important consequences over the local biota and the entire ecosystem (Stirling et al., 1999). The temporal change in the sea-ice cover in the HBS during mid-July from 1971 to 2006 is shown in Fig. 1 of the general introduction (chapter 1.1). Between 1971 and 1992, the spreading and extension of the sea-ice cover were relatively constant. But since 1993, sea-ice conditions have been more variable and instable (Fig. 1) showing a trend toward earlier melt onset in spring and also later freeze-up in fall (Markus et al., 2009). Overall, the melt season in HB has lengthened by almost 20 days from 1992 to 2007 (Markus et al., 2009). These changes in sea-ice dynamics suggest that the HBS are already responding to climate warming with potential consequences on the water properties and circulation, the freshwater transport towards the Labrador Sea, and the biological productivity of this arctic/subarctic system (Saucier et al., 2004).

Apart from playing a fundamental role in marine food webs, zooplankton has been recognized as a bioindicator of climate changes, because it responds quickly to temperature

as well as oceanic current variations by modifying its spatial distribution (Hays et al., 2005; Richardson, 2008). Information on zooplankton dynamics in the HBS is scarce. Only a few papers on specific zooplankton groups in relation to the local physical variables, limited to some regions of the HB, FB and HS specifically, have been published (Grainger, 1962, 1990; Grainger and McSween, 1976; Roff et al., 1980; Hsiao et al., 1984; Rochet and Grainger, 1988; Taggart et al., 1989; Percy et al., 1992; Hudon et al., 1993; Harvey et al., 2001). The spatial and interannual zooplankton variation for three different hydrographic regions of the HBS has never been studied. The MERICA (*MERs Intérieures du Canada*) program has been developed by the DFO Quebec Region to follow, understand, and predict the future climate changes and their effects on the productivity and biodiversity of the HBS (Saucier et al., 2003).

In this context, the main objective of this work is to describe the zooplankton community structure, abundance, biomass and distribution in the HBS and its relationship with the environmental conditions during late summers of 2003 to 2006. A second objective is to identify possible linear trends between zooplankton distribution and physical gradients that may be influenced by climate changes. This will allow us to propose different scenarios on the potential effects of climate changes on the zooplankton communities in sub-arctic regions. Our working hypothesis is that the structure of the zooplankton communities is influenced by the water depth and local hydrodynamic conditions which through their actions on the water masses properties (i.e. temperature, salinity and

stratification intensity) will lead to spatial differentiation in zooplankton communities in the HBS (from 2003 to 2006).

## MATERIALS AND METHODS

### *Study area*

Situated between 50 - 70°N and 95 - 65°W (Fig. 1), the HBS is a large subarctic/arctic estuarine basin with a seasonally complete cryogenic cycle (Straneo and Saucier, 2008). Eastward, this region is connected to waters of the Atlantic Ocean by the Labrador Sea (through HS), and in the north to the waters of the Canadian Arctic by Fury and Hecla Strait (through FB) (Fig. 1) (Prinsenber, 1986b). The HBS is mainly influenced by three water types: river runoff, seawater from the Arctic Ocean and seawater from the Baffin Island Current. Sea-ice melt water is the most significant source of freshwater in the seasonal cycle of the area, notably FB (Straneo and Saucier, 2008). Together, HB and FB covers an area of about  $10^6$  km<sup>2</sup>. FB is no more than 100 m deep with the shallowest regions in the east, and the deepest (200 m) in the south at Foxe Channel; the latter, along with southwestern FB, are considered to be an extension of HS (Prinsenber, 1986c). HB has a mean depth of 125 m with variable bottom topography, more gentle in the south and deeper trenches in the north; it has a rectangular shape of 925 by 700 km, ignoring the southeastern shallow area (Jones and Anderson, 1994; Prinsenber, 1986b). Both FB and HB are connected to the deeper HS, which is a narrow (70-150 km) and long (~750 km) channel with mean depths between 300 and 400 m (Drinkwater, 1986). Normally, ice-free

conditions are found in September and freeze-up begins by mid-October in northern FB, whereas HB is ice covered in winter and ice-free in August and September (Prinsenber, 1986c; Wang et al., 1994). HS is ice-covered  $\sim 3/4$  of the year, and normally being ice free from early August until late October (Percy, 1990).

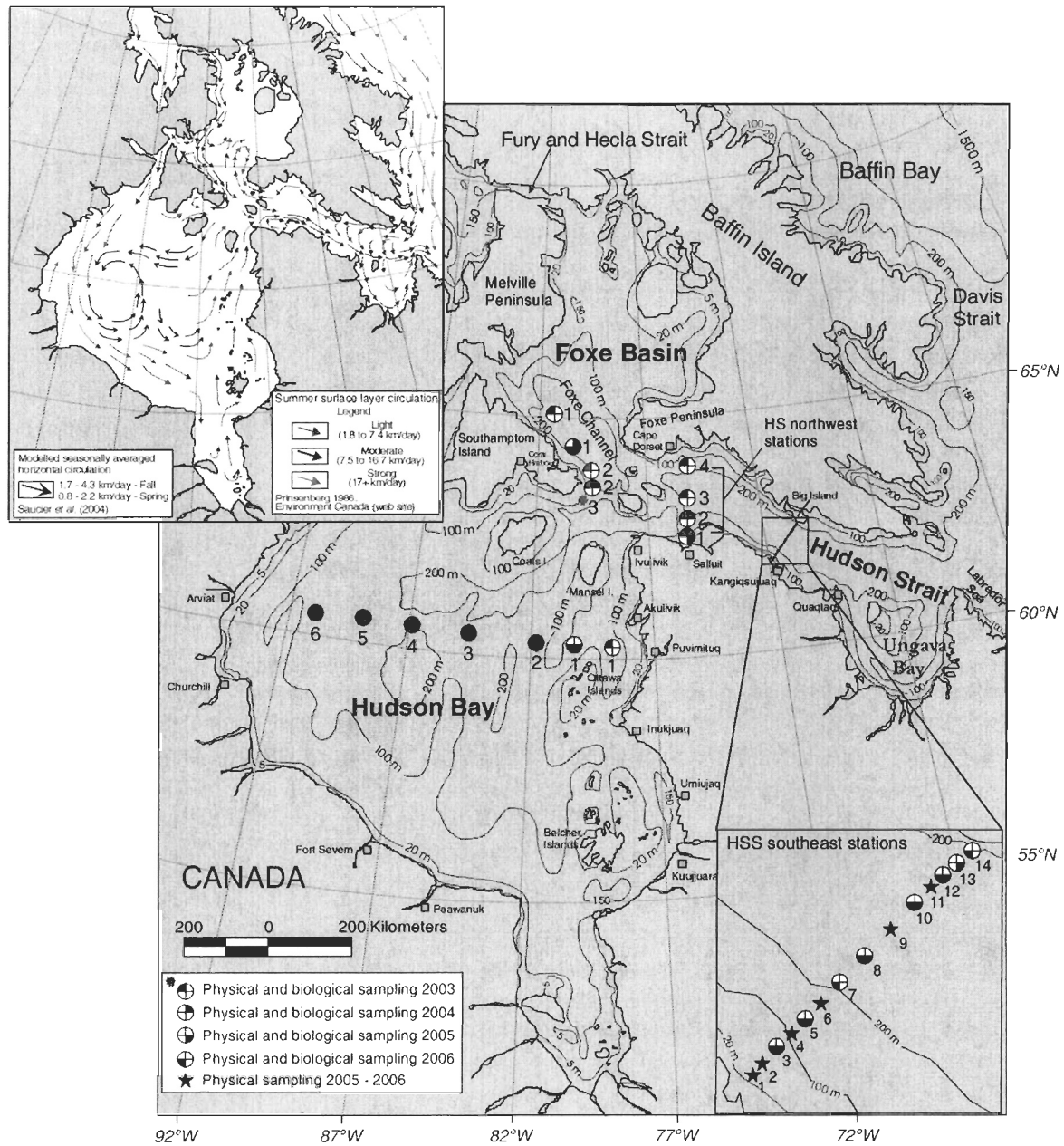


Figure 1. Location of the sampling stations in the HBS during 2003-2006. The summer surface layer circulation is shown in the inset (adapted from Prinsenberg, 1986; Saucier et al., 2004; Environnement Canada). \* Station (FB3) sampled only in 2003.



According to the summer salinity distribution and ice breakup patterns in FB, there is a cyclonic circulation in northern region of the basin with a strong southerly current ( $0.6 \text{ m s}^{-1}$ ) along the Melville Peninsula (which is a southward continuation of the Arctic water through Fury and Hecla Strait) (Prinsenber, 1986c). Additionally, in the southern part of the FB there is an inflow of waters from HS along Foxe Peninsula, and an outflow along Southampton Island (Prinsenber, 1986c) (Fig. 1, upper left corner). Particularly, FB has higher salinity bottom water (because of the brine released during sea-ice production and aging of) than waters entering from the Arctic Ocean and those from the bottom water at eastern HS; the freshwater layer ( $S = 33.1$ ) is around 2.5 m (Jones and Anderson, 1994). Summer surface water temperatures are  $\sim 3 \text{ }^\circ\text{C}$ , being warmer in the Foxe Channel area (Prinsenber, 1986c).

In HB, bottle drift data and salinity and temperature distributions indicate a cyclonic surface layer circulation ( $0.05 \text{ m s}^{-1}$ ) without north westward inflow, and an eastward surface outflow that moves along the eastern shore, leaving the bay as a warm and fresher water mass (Prinsenber, 1983; Prinsenber, 1986a). Furthermore, recent data models show that during the ice-free periods the waters of the bay experiment stronger surface eddy activity associated with the synoptic wind forcing and the presence of a large scale cyclonic gyre in the western half of the HB, with strongest currents in the fall ( $0.02\text{-}0.05 \text{ m s}^{-1}$ ) and half lower in spring (Saucier et al., 2004). The mean circulation in the bay is a combination of wind and density-driven currents resulting from dilution by river runoff; the latter comes from a large drainage area ( $3.1 \times 10^6 \text{ km}^2$ ) with a yearly mean discharge of  $2.1 \times 10^4 \text{ m}^3 \cdot \text{s}^{-1}$

(equals to an annual addition of a 0.78m layer of freshwater if spread out over the entire surface of the bay) (Fig. 1, upper left corner) (Prinsenbergh, 1986b; 1988). Remarkably, during the summer HB is vertically stratified with a strong pycnocline ranging 15-25 m; surface salinity ranges 10 to 30 from near major river systems to central and northeastern HB, respectively; summer surface water temperatures reach 12 °C, and the deep waters -1.7 °C, close to the freezing point. The resident time of deep HB waters lies between 4-14 years, increasing towards the centre of the bay (Pett and Roff, 1982; Roff and Legendre, 1986). HB deep waters, which are also considered to circulate cyclonically, are the product of: cold surface Arctic Ocean waters entering HS from the west (via Fury and Hecla Strait – FB); from the east (via a westward flowing extension of the Baffin current); and warmer, more saline Atlantic waters entering HS at depth (Barber, 1967).

In HS, the surface circulation has three main patterns: 1) a current flowing northwestward along southern Baffin Island (inflow); 2) a southeastward current flowing along the Quebec shore (outflow), which join that from Davis Strait and West Greenland recirculation current to form Labrador Current; and 3) a southward cross-channel flow in the eastern half of the strait (Drinkwater, 1986; LeBlond et al., 1981) (Fig. 1, upper left corner). According to Straneo and Saucier (2008), the HS inflow supplies ~44 mSv (milli Sverdrup) of freshwater ( $S = 33$ ) to the HBS; this water flows out of Davis Strait and thus is of Arctic influence. These waters are weakly stratified due to high vertical mixing at the eastern entrance of the HS. On the other hand, the HS outflow carries fresh, cold waters from the HBS, along the coast of Québec, towards the Labrador Sea; this flow extends 45-

50 km off the coast, with velocities ( $1 \text{ m s}^{-1}$ ) dominated by strong tides (mostly semidiurnal) exceeding 8 m. The outflow carries two classes of water masses: fresher ( $S = < 33$ ) and highly stratified waters exported between June and March, and more saline ( $> 33$ ) and less stratified waters exported beneath the freshwaters, during the fresh outflow period between March and June (Straneo and Saucier, 2008). It is estimated that 15 % of the volume and 50 % of the fresh water carried by the Labrador Current is due to the HS outflow, reflecting a large impact on the properties and ecosystem along the Labrador Shelf (Straneo and Saucier, 2008). Overall, high tidal elevations in HS (increasing from 2 m at the eastern entrance to over 3.4 m near Big Island, and then decreasing at the western entrance), and strong tidal currents (up to  $2\text{-}3 \text{ m s}^{-1}$ ) that produce intense vertical mixing, through bottom-generated turbulence, have strong local influence on the vertical stratification of the water column, temperature and salinity properties, and local biological production in different areas of the strait (Drinkwater, 1986; Drinkwater and Jones, 1987).

### *Sampling program*

Sampling was carried out in the Hudson Bay system from 1 to 14 August in 2003 and 2004 and from 31 August to 10 September in 2005 and 2006, on board of the CCGS Des Groseilliers in 2003 and Pierre Radisson during 2004-2006 (Fig. 1). A total of 56 stations were visited over the four years. Physical and biological data were collected at 5-6 stations along a longitudinal transect in the HB from 2003 to 2006, at 4 stations along a latitudinal transect in the northwestern HS in 2003 and at 13-14 stations along a cross-

channel transect in the southeastern HSS in 2005 and 2006 (see Fig. 1 and Table 1). The position of the HSS transect during 2005-2006 corresponds to the transect conducted by Drinkwater (1986). The FB was sampled at 3 stations in 2003, at 2 stations in 2004 and at 1 station in 2005 and 2006. The position of the station FB1 in Foxe Channel was relocated ca. 50 km southeast during 2004-2006 because of the presence of a thick sea ice cover north of the channel during summer 2004.

At each station, vertical profiles of water temperature, salinity, density ( $\sigma_t$ ,  $\sigma_t$ ) and *in vivo* fluorescence down to about 10 m above the bottom were measured with a Sea-Bird Electronics SBE 911+CTD and a Wetstar mini fluorometer (model 9512008) attached to a rosette sampler. Subsamples for chlorophyll *a* (chl *a*) determination were collected at 48 stations (from 56 visited over the four years) at 0, 5, 15, 25, 50, 75, 100, and 250 m (when depth permitting) with 10-l Niskin bottles mounted on the rosette system.

Table 1. Physical and biological characteristics of the sampling stations in the HBS from 2003 to 2006: bottom depth (Depth), upper mean temperature (UMT), lower mean temperature (LMT), upper mean salinity (UMS), lower mean salinity (LMS), stratification index (Strat) and integrated chlorophyll fluorescence from 0 to 100 m (Flu0-100).

Station/Year	Date (mm/dd/yy)	Latitude (°N)	Longitude (°W)	Depth (m)	UMT (°C)	LMT (°C)	UMS	LMS	Strat (kg m <sup>-3</sup> )	Flu0-100 (mg m <sup>-2</sup> )
FB1-3	08/09/2003	65°08'	81°20'	436	2.44	-1.71	29.42	33.39	3.02	66.8
FB2-3	08/14/2003	63°56'	79°39'	317	3.54	-1.65	30.49	33.25	2.27	72.0
FB3-3	08/10/2003	63°39'	79°34'	156	4.26	-1.27	31.11	32.78	1.35	85.0
HB1-3	08/01/2003	60°10'	78°55'	125	3.73	-1.20	10.79	31.72	4.55	83.0
HB2-3	08/02/2003	60°20'	81°59'	151	3.98	-1.37	26.23	32.35	5.46	211.1
HB3-3	08/03/2003	60°30'	85°00'	185	8.01	-1.35	28.14	32.89	4.54	73.0
HB4-3	08/04/2003	60°39'	87°26'	197	10.51	-1.34	30.70	32.86	2.91	79.0
HB5-3	08/05/2003	60°50'	90°00'	128	10.59	-1.44	31.33	32.80	2.44	99.8
HB6-3	08/06/2003	60°55'	91°46'	109	10.05	-1.53	30.77	32.85	2.91	111.2
HS1-3	08/12/2003	62°26'	75°29'	208	3.79	-1.05	29.15	32.41	2.65	152.5
HS2-3	08/11/2003	62°39'	75°29'	233	4.60	-1.00	28.79	32.49	2.97	265.7
HS3-3	08/11/2003	63°15'	75°30'	437	4.39	-0.93	31.97	33.21	1.10	29.9
HS4-3	08/13/2003	63°49'	75°30'	240	1.96	-0.91	32.55	32.87	0.33	38.0
FB1-4	08/14/2004	64°22'	80°32'	369	2.78	-1.68	29.59	33.34	2.96	116.5
FB2-4	08/09/2004	63°40'	79°33'	150	1.28	-1.35	30.54	32.88	2.02	144.4
HB2-4	08/06/2004	60°19'	81°59'	142	6.20	-1.29	28.70	32.36	3.75	143.9
HB3-4	08/05/2004	60°30'	84°59'	182	2.63	-1.43	27.45	32.80	4.62	164.5
HB4-4	08/04/2004	60°40'	87°27'	196	6.21	-1.29	28.78	32.83	4.12	26.5
HB5-4	08/03/2004	60°50'	90°00'	128	7.45	-1.21	30.82	32.70	2.38	42.6
HB6-4	08/02/2004	60°54'	91°46'	107	7.46	-1.50	31.10	33.00	2.55	33.0
HS1-4	08/10/2004	62°26'	75°29'	212	4.61	-0.69	30.30	32.62	2.05	144.9
HS2-4	08/10/2004	62°40'	75°30'	232	3.71	-0.97	30.44	32.75	2.12	169.6
FB1-5	09/01/2005	64°22'	80°31'	364	2.27	-1.65	30.97	33.36	1.80	91.8
HB1-5	09/07/2005	60°15'	80°29'	136	8.18	-1.02	27.55	32.52	4.20	20.5
HB2-5	09/06/2005	60°20'	82°00'	148	8.25	-1.22	27.44	32.54	5.14	26.9
HB3-5	09/05/2005	60°30'	84°58'	178	8.99	-1.37	28.12	32.80	4.73	21.6
HB4-5	09/04/2005	60°39'	87°28'	190	10.13	-1.50	30.04	33.11	3.45	24.0
HB5-5	09/03/2005	60°50'	90°00'	120	10.22	-1.51	29.80	32.98	3.78	29.5
HB6-5	09/03/2005	60°55'	91°46'	110	11.01	-1.70	26.74	33.21	6.47	46.7
HS1-5	08/31/2005	62°24'	75°29'	194	5.69	-0.97	29.26	32.99	3.03	48.9
HSS3-5	09/09/2005	61°54'	71°51'	101	2.77	0.26	31.01	32.38	1.39	84.8
HSS5-5	09/09/2005	61°58'	71°38'	187	3.23	-1.04	31.75	33.09	1.28	49.9
HSS8-5	09/10/2005	62°12'	71°15'	322	2.92	-0.25	32.40	33.38	0.73	70.0
HSS10-5	09/08/2005	62°22'	70°54'	334	2.81	-0.25	32.48	33.33	0.69	37.6
HSS12-5	09/08/2005	62°26'	70°45'	352	2.06	-0.26	32.80	33.24	0.29	72.8
HSS13-5	09/08/2005	62°29'	70°40'	324	1.88	-0.14	32.80	33.16	0.21	138.0
FB1-6	09/05/2006	64°22'	80°32'	355	3.04	-1.53	32.43	33.30	0.62	77.8
HB1-6	09/10/2006	60°15'	80°29'	134	8.64	-1.03	29.42	32.34	3.39	37.8
HB2-6	09/10/2006	60°20'	82°01'	152	8.58	-1.16	29.47	32.46	3.15	52.4
HB3-6	09/09/2006	60°30'	84°59'	200	8.57	-1.37	29.46	32.94	3.62	31.1
HB4-6	09/08/2006	60°39'	87°29'	195	7.70	-1.39	30.35	32.95	2.90	19.6
HB5-6	09/08/2006	60°50'	90°00'	121	8.23	-1.41	30.12	32.89	3.13	38.0
HB6-6	09/08/2006	60°55'	91°46'	102	8.41	-1.61	30.17	32.92	2.97	71.1
HSS3-6	08/30/2006	61°54'	71°51'	108	3.67	0.43	31.27	32.38	1.05	86.7
HSS5-6	08/30/2006	61°59'	71°38'	200	3.53	-0.75	31.52	32.91	0.81	150.7
HSS7-6	09/02/2006	62°07'	71°25'	337	3.85	-0.87	32.30	33.25	0.91	5.4
HSS8-6	09/02/2006	62°11'	71°15'	342	5.52	-0.85	32.26	33.28	1.10	22.6
HSS10-6	09/03/2006	62°22'	70°55'	334	5.59	-0.85	32.26	33.26	1.02	65.9
HSS12-6	09/01/2006	62°26'	70°45'	369	4.22	-0.68	32.42	33.16	0.69	55.7
HSS14-6	09/01/2006	62°30'	70°33'	311	1.87	-0.92	32.65	33.24	0.16	71.5

Two 500-ml subsamples were filtered through 25 mm Whatman GF/F fiber glass filters (nominal pore size of 0.7  $\mu\text{m}$ ). Concentrations of chl *a* were measured on board the ship with a Turner Designs TD-700 fluorometer, after 18 h of pigment extraction in 90% acetone at 4°C in the dark (Parsons et al., 1984). The extracted chl *a* concentration was used to calibrate the output of the Rosette fluorometer at each station, using Model I linear regression (Sokal and Rohlf, 1995).

Immediately following the rosette cast, zooplankton samples were collected at a total of 50 stations from *ca.* 10 m above the bottom to the surface with vertical tows at speed of 1 m s<sup>-1</sup>, using a 0.75 m diameter ring net, equipped with a 202  $\mu\text{m}$ -mesh net. At each station, the amount of filtered seawater (m<sup>-3</sup>) by the net was estimated using a General Oceanics electronic flowmeter (model 2031H). Three vertical tows per station were carried out in 2003 and 2004 and only one in 2005 and 2006. All sampling was performed during daylight hours.

The zooplankton samples were preserved in 4% buffered formaldehyde, and analyzed in two steps in laboratory: 1) larger organisms, defined here as macrozooplankton (length >2 mm, e.g. euphausiids, amphipods, chaetognaths, cnidarians, pteropods), were sorted, identified to species level (when possible), counted, and weighed individually by taxa (wet mass: WM), using a Mettler PC4400 precision balance ( $\pm 0.01$  g); 2) after macrozooplankton removal, samples were split in two half (using a Folsom splitter) to determine wet mass (first half), taxonomic composition, and abundance of the smaller

zooplankton organisms (length <2 mm, e.g. copepods and macrozooplankton larvae) defined here as mesozooplankton (second half).

The first half of the samples containing mesozooplankton (including macrozooplankton larvae) was filtered through pre-weighed Whatman GF/A filters with a vacuum pump during 10 seconds and then weighed with a Mettler PC4400 precision balance ( $\pm 0.01$  g) to obtain by difference the WM. Since some samples contained phytoplankton cells, especially those collected in the HB, the contribution of phytoplankton to total plankton biomass was estimated for these samples. To do this, a 10 ml aliquot of the second half sample was taken with a Stempel pipette and sorted into two fractions (i.e. zooplankton organisms and phytoplankton cells) under a binocular dissecting microscope. Both fractions were then filtered through pre-weighed Whatman GF/A filters and weighed with a Mettler PC4400 precision balance ( $\pm 0.001$  mg). The contribution of phytoplankton to the total plankton (i.e. phytoplankton + zooplankton) wet mass ranged from 0 to 78% (mean  $\pm$  SD =  $34.9 \pm 21.7\%$ ) in the HB during 2003-2006. Similar results were obtained from zooplankton and phytoplankton dry masses measured on selected samples. Hence, our wet mass mesozooplankton data were corrected for the presence of phytoplankton cells.

The second half of the samples for mesozooplankton identification and enumeration was diluted in aliquots taken with a Folsom splitter or a Stempel pipette, depending on the sample size, in order to get >400 individuals per subsample. Aliquot sizes ranged from 1/10

to 1/200 of the total sample. Then, the diluted subsample containing zooplankton was placed into a slide counting chamber and examined under a binocular dissecting microscope. Copepods were identified taken into account their life stages (i.e. naupliar (N), copepodite (C), adult male (m) and adult female (f)). For *Calanus finmarchicus*, *Euchaeta norvegica*, *Metridia longa* and *Pseudocalanus* spp. only naupliar stages from N3-N6 were counted due to the mesh size ( $>202 \mu\text{m}$ ) of the net used during this study which excludes the smaller individuals. A minimum of 400 individuals was counted in each counting chamber. The following references were used for zooplankton identification: Rose (1970), Shi (1977), Smith (1977), amongst others. In total, 32 and 54 taxonomic categories were identified for the macrozooplankton and planktonic copepods, respectively. In the present study, biomass and abundance of zooplankton were expressed in  $\text{g WM m}^{-2}$  and in  $\text{ind. m}^{-2}$ , respectively.

### ***Data analysis***

The physical and biological variables collected at the 50 net tow stations over the 4 sampling years allowed us to establish 3 data matrices composed of: 1) environmental variables (including chl *a* and fluorescence), 2) zooplankton abundances, and 3) zooplankton biomasses. Figure 2 illustrates the environmental variables computed from the vertical profiles obtained by the Rosette CTD-fluorometer. At each station, the depth of maximum and minimum vertical gradients in water temperature ( $\Delta T/\Delta Z$ ) was used to determine the depth of the upper and lower limits of the thermocline, respectively. In



addition, the depth of the maximum vertical gradient in salinity ( $\Delta S/\Delta Z$ ) was used to determine the halocline depth. Within these zones, we calculated: 1) the upper (UMT) and lower (LMT) mean temperature above the upper and lower thermocline limit, respectively, 2) the upper mean salinity (UMS) above the halocline, 3) the lower mean salinity (LMS) below the lower thermocline limit, and 4) the integrated chl *a* fluorescence from 0-100 m (Flu0-100) (Fig. 2). The stratification index (Strat) was computed from the difference in  $\sigma_\tau$  between 80 m and 5 m ( $\Delta\sigma_\tau$ ). Hence, the environmental data matrix was composed of 7 variables (i.e. UMT, UMS, LMT, LMS, Strat, Flu0-100 and bottom depth). Contour plots of water temperature, salinity and chl *a* fluorescence were produced with the Ocean Data View (ODV) v3.4.0 software, using DIVA gridding integration (Schlitzer, 2008).

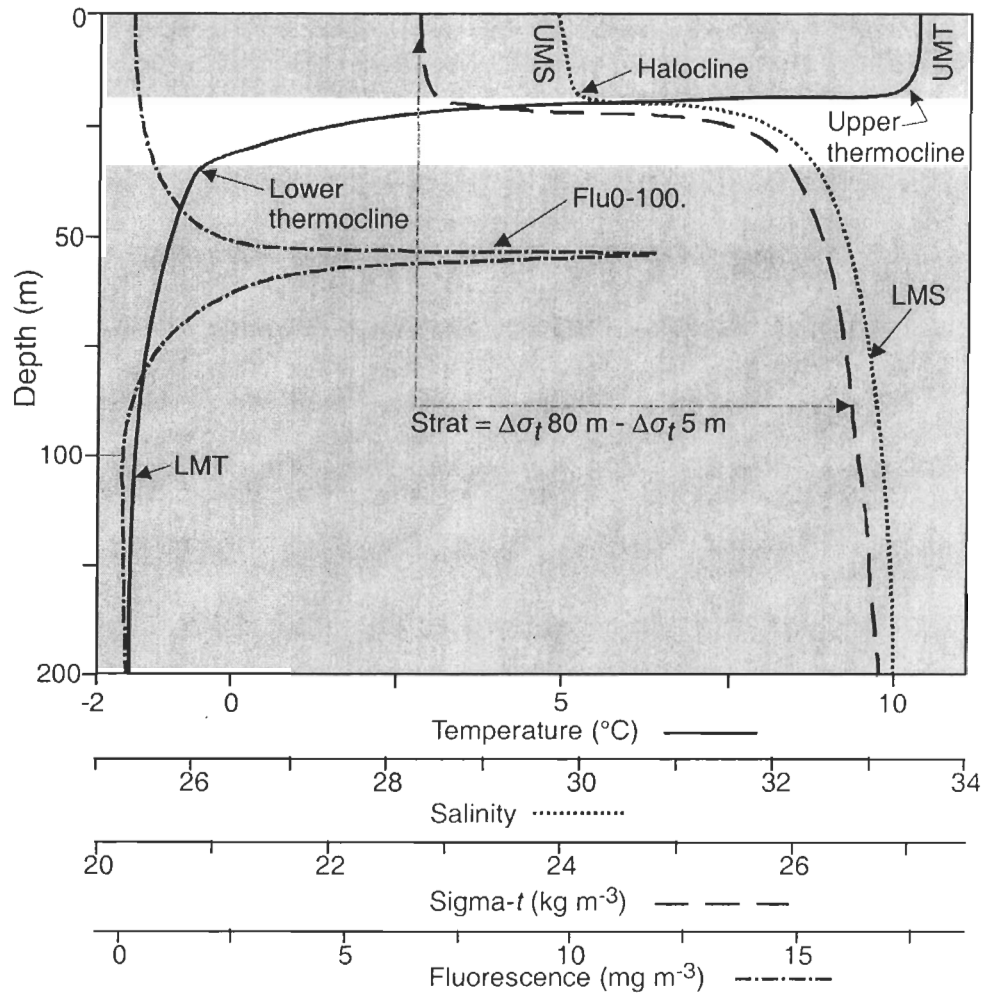


Figure 2. Sketch of typical vertical profiles of water temperature, salinity, sigma- $t$  ( $\sigma_t$ ) and chlorophyll fluorescence in the HBS. These data were used to calculate the upper mean temperature (UMT), lower mean temperature (LMT), upper mean salinity (UMS), lower mean salinity (LMS), stratification index (Strat) and integrated chlorophyll fluorescence from 0 to 100 m (Flu0-100).

To group stations with similar zooplankton composition, a cluster analysis using the Bray-Curtis similarity index followed by a non-metric multidimensional scaling (NMDS) ordination (Kruskal and Whish, 1978) were carried out on the data sets using the PRIMER v6 software (Clarke and Gorley, 2006). The similarity matrix was calculated on the relative abundance of zooplankton, which was previously  $\log_{10}(x+1)$  transformed. For this analysis, the less abundant taxa (e.g. Ctenophora, Gammaridae) and taxonomic categories present in less than 10 % of the stations were excluded from the input matrix.

A one-way analysis of similarities (ANOSIM) was conducted on the same similarity matrix to test differences in the taxonomic composition between the groups of stations (Clarke and Green, 1988). This test was used to seek differences in the faunal composition between “sampling years” (i.e. 2003, 2004, 2005 and 2006) and “sampling sites” (i.e. HB, FB, northwest HS and southeast HSS). The *R* statistic value generated by the ANOSIM ranges from 0 to 1; with 0 indicating no difference and 1 indicating large between-group differences (Clarke and Warwick, 2006).

The relationships between zooplankton taxonomic composition and environmental variables were evaluated with a canonical analysis, which combines the concepts of ordination and regression (Legendre and Legendre, 1998), using the CANOCO (CANONical Community Ordination) v4.5 software (ter Braak and Smilauer, 2002). The canonical analysis was run with the data sets from: 1) the entire HBS (50 samples), 2) the HB alone (23 samples), and 3) the FB - HS together (27 samples). First, detrended

correspondence analyses (DCA) were run to determine if a unimodal model (i.e. canonical correspondence analysis, CCA) or a linear model (i.e. redundancy analysis, RDA) best fit the data sets (ter Braak, 2002). The gradient lengths expressed in standard deviation units of the taxonomic turnover were 1.40, 0.96 and 0.98 for the HBS, the HB, and the FB-HS, respectively. Since the values were  $<3$ , this indicated a linear response of the zooplankton community along the environmental gradient and provided a statistical justification to run RDA instead of CCA. Then, RDAs were performed for the HBS and the FB-HS data sets. In addition, a partial RDA (pRDA) was carried out for the HB set alone with “sampling month” as covariable to remove seasonality in the data set which shows higher water column chl *a* fluorescence in early August 2003 and 2004 than in early September 2005 and 2006 (see Table 1). In this statistical method, the variability explained by the covariable was removed from the total variability and only the additional (partial) variability, which is not explained by the covariable, can be shown in the ordination results (ter Braak and Smilauer, 2002). As for the NMDS, the less abundant taxa and taxonomic categories present in less than 10 % of the stations were excluded from the input matrix. Hence, the input matrix was composed of 69 taxonomic categories x 50 net tow stations for the HBS, of 69 taxonomic categories x 27 net tow stations for the FB-HS and of 61 taxonomic categories x 23 net tow stations for the HB. Prior to the analyses, the relative abundances of the taxonomic categories were transformed logarithmically ( $\log_{10}(x + 1)$ ).

A total of 7 environmental variables (Depth, UMT, LMT, UMS, LMS, Strat and Flu0-100) were available for the RDA analyses (see Table 1). For the HBS and HB data sets, the variable UMS was excluded because it was strongly correlated with the stratification index ( $r^2 = 0.91$  and  $r^2 = 0.89$  for HBS and HB, respectively). Since salinity and sigma- $t$  profiles were almost perfectly correlated ( $r^2 = 0.99$ ), and the stratification index is a measure taken from the profiles, stratification appeared to be the best variable to use in the model. For the FB-HS data set, the variable Strat was excluded and we used UMS instead. According to tests made with all the variables while constructing the model, UMS was explaining a higher fraction of the taxonomic variability than Strat. The statistical significance of the relationship between zooplankton taxonomic composition and environmental variables (and covariables) was determined by Monte Carlo permutation tests (499 unrestricted permutations), and only those environmental variables that were significant ( $p < 0.05$ ) were taken into account in the data interpretation. The corresponding ordination RDA's diagrams display scores for samples (symbols), taxonomic categories (arrow tips) and quantitative environmental variables (full arrows). According to the "biplot rule" of ter Braak and Smilauer (2002), a close distance between a taxon arrow tip and an environmental variable arrow indicates a high correlation between the 2 variables. The angle between a taxon arrow tip and an environmental variable arrow points out their correlation, i.e. they are uncorrelated if they are perpendicular to each other and strongly correlated if the angle between each other is narrow. A longer environmental variable arrow means higher correlation with the taxon pattern than shorter ones. In addition, the collinear

factors were examined by checking the Variance Inflation Factor to evade multicollinearity problems (ter Braak and Smilauer, 2002).

Measures of diversity were computed by three different indices: 1) the Shannon' diversity index ( $H' = - \sum_i P_i \log(P_i)$ ), where  $P_i$  is the proportion of the total count arising from the  $i$ th taxonomic categories, and the logs are to the base e (Clarke and Warwick, 2001); 2) the Pielou's evenness, which expresses how evenly the individuals are distributed among the different taxonomic categories ( $J' = H'/\text{Log}(S)$ ); 3) and the taxonomic richness (total number of taxonomic categories present). These indices were obtained with the PRIMER v6 software package (Clarke and Gorley, 2006). These diversity indices were calculated with the zooplankton taxa (i.e. holoplankton and meroplankton; Tables 2 and 3) present in more than 10 % of the samples. For each copepod taxa, all the developmental stages were summed together (and not separately, as they appear in Table 3) in all diversity indices calculation.

Model I linear regressions were used to determine relationships between biological variables (i.e. total zooplankton biomass, Shannon' diversity index and taxonomic richness) and environmental variables (Sokal and Rohlf, 1995).

Table 2. Occurrence and abundance of the macrozooplankton taxa present in the HBS during 2003-2006. Abbr.: abbreviation.

Taxon	Abbr.	Occurrence (%)				Abundance (ind. m <sup>-3</sup> )							
						Mean (SE)				Min - Max			
		2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
<b>Amphipoda</b>													
Gammaridae unidentified	Gam U	31	56	21	50	1 (1)	5 (5)	2 (1)	4 (1)	0-9	0-41	0-9	0-14
Hyperia sp.	Hyp Sp	38	56	0	14	1 (0)	3 (2)	0 (0)	1 (0)	0-4	0-18	0-0	0-7
<i>Themisto abyssorum</i>	Taby	77	56	57	50	20 (12)	83 (82)	20 (11)	38 (29)	0-159	0-735	0-158	0-405
<i>T. compressa</i>	Tcom	77	44	14	14	36 (17)	2 (1)	2 (1)	1 (1)	0-201	0-7	0-14	0-9
<i>T. libellula</i>	Tlib	100	100	100	79	47 (21)	51 (19)	29 (8)	14 (6)	2-270	6-187	2-95	0-91
<b>Appendicularia</b>													
<i>Fritillaria</i> sp.	Fri Sp	92	100	100	100	11373 (4846)	13383 (4605)	14525 (4666)	23922 (9061)	0-53721	154-38528	453-57584	2535-135812
<i>Oikopleura</i> larvae	Oik L	38	22	71	50	1785 (1365)	58 (39)	14435 (4878)	1533 (845)	0-17957	0-287	0-63379	0-11951
<i>Oikopleura</i> sp.	Oik Sp	0	11	50	7	0 (0)	0 (0)	14 (5)	0 (0)	0-0	0-1	0-52	0-5
<b>Chaetognatha</b>													
Chaetognatha larvae	Cha L	92	67	86	86	2219 (657)	775 (245)	2134 (835)	2467 (693)	0-6640	0-2203	0-11770	0-10322
<i>Eukrohnia hamata</i>	Eha	46	44	71	36	21 (17)	2 (1)	42 (19)	29 (12)	0-223	0-10	0-197	0-129
<i>Sagitta elegans</i>	Sel	100	100	100	100	285 (31)	350 (71)	431 (47)	419 (53)	99-464	124-796	147-824	186-804
<b>Cirripedia</b>													
Cirripedia larvae	Cir L	38	33	36	14	3206 (2119)	95 (68)	1384 (992)	1649 (1608)	0-25563	0-617	0-14034	0-22545
<b>Cnidaria</b>													
<i>Aeginopsis laurenti</i>	Ala	85	100	86	86	34 (11)	44 (12)	47 (19)	47 (22)	0-124	1-120	0-274	0-290
<i>Aglantha digitale</i>	Adi	100	100	100	86	35 (7)	189 (107)	91 (24)	160 (49)	5-87	7-1024	7-358	0-525
Cnidaria larvae	Cni L	92	78	86	71	1869 (680)	303 (173)	4000 (2018)	2551 (1036)	0-8149	0-1643	0-28973	0-14849
<i>Sarsia</i> sp.	Sar Sp	62	44	36	14	2 (1)	1 (1)	1 (0)	0 (0)	0-12	0-7	0-5	0-2
<b>Ctenophora</b>													
Ctenophora unidentified	Cte U	62	67	43	29	1 (0)	1 (1)	1 (0)	1 (0)	0-6	0-6	0-2	0-5
<b>Decapoda</b>													
Decapoda unidentified	Dec U	15	44	14	21	0 (0)	1 (1)	0 (0)	0 (0)	0-2	0-4	0-5	0-2
<b>Echinodermata</b>													
Echinodermata larvae	Ech L	85	100	79	100	11859 (5083)	7506 (2972)	6755 (2172)	9513 (2369)	0-65492	149-27324	0-30784	1086-28249
<b>Euphausiacea</b>													
Euphausiacea larvae	Eup L	69	89	50	14	4820 (2227)	3092 (1442)	372 (189)	78 (53)	0-23028	0-13602	0-2716	0-543
<i>Thysanoessa raschii</i>	Trasc	23	33	21	14	1 (0)	1 (1)	2 (1)	1 (1)	0-4	0-8	0-14	0-11
Invertebrate egg	legg	15	100	79	14	46 (36)	962 (240)	1103 (272)	55 (39)	0-453	483-2581	0-3169	0-498
<b>Isopoda</b>													
Isopoda larvae	Iso L	0	56	0	14	0 (0)	89 (49)	0 (0)	91 (62)	0-0	0-450	0-0	0-634
<b>Mollusca</b>													
Bivalvia larvae	Biv L	46	44	64	71	228 (104)	149 (75)	1833 (578)	2645 (1543)	0-1207	0-602	0-6791	0-22183
<b>Mysidacea</b>													
<i>Meterythrops robusta</i>	Mrob	46	44	7	43	4 (3)	3 (2)	1 (1)	2 (1)	0-33	0-17	0-11	0-9
<i>Mysis mixta</i>	Mmix	23	22	21	43	1 (0)	3 (2)	1 (0)	4 (2)	0-5	0-16	0-5	0-27
<b>Ostracoda</b>													
Ostracoda larvae	Ost L	46	11	21	7	211 (128)	17 (17)	123 (80)	32 (32)	0-1690	0-152	0-1086	0-453
<b>Polychaeta</b>													
Polychaeta larvae	Pol L	92	89	93	100	3215 (1108)	587 (225)	2487 (499)	5630 (1337)	0-13430	0-1871	0-5885	498-17112
<i>Tomopteris</i> sp.	Tom Sp	8	11	29	7	0 (0)	0 (0)	3 (2)	1 (1)	0-2	0-1	0-32	0-9
<b>Pteropoda</b>													
<i>Clione limacina</i>	Clil	23	22	43	14	0 (0)	0 (0)	35 (32)	1 (1)	0-1	0-1	0-453	0-9
<i>Limacina helicina</i>	Lhe	62	56	36	29	10 (3)	2 (1)	2 (1)	5 (2)	0-32	0-10	0-7	0-25
<i>L. helicina</i> larvae	Lhe L	100	100	93	100	3292 (812)	2048 (413)	1323 (259)	3082 (576)	1207-10986	550-4180	0-3169	407-7334

Table 3. Occurrence and abundance of copepod taxa present in the HBS during 2003-2006. Abbr.: abbreviation.

Taxon	Abbr.	Occurrence (%)				Abundance (ind. m <sup>-3</sup> )							
						Mean (SE)				Min - Max			
		2003	2004	2005	2006	2003	2004	2005	2006	2003	2004	2005	2006
<i>Acartia longiremis</i> CI-CV	AloCI-CV	54	56	57	43	1017 (458)	132 (63)	1581 (667)	1339 (717)	0-5282	0-580	0-8149	0-9778
<i>A. longiremis</i> CVI f	AloVIf	38	11	21	7	70 (26)	2 (2)	139 (79)	58 (58)	0-211	0-15	0-951	0-815
<i>A. longiremis</i> CVI m	AloVIm	23	33	14	14	121 (83)	25 (14)	94 (71)	171 (138)	0-1056	0-119	0-951	0-1901
Aetideidae sp.	Aet Sp	0	44	21	21	0 (0)	81 (39)	142 (85)	149 (80)	0-0	0-315	0-1086	0-815
<i>Calanus glacialis</i> CI	CgCI	8	100	29	21	35 (35)	571 (88)	265 (128)	246 (161)	0-453	149-994	0-1449	0-2173
<i>C. glacialis</i> CII	CgCII	69	89	86	50	1196 (314)	784 (194)	2603 (716)	1074 (506)	0-2867	0-1737	0-8601	0-6519
<i>C. glacialis</i> CIII	CgCIII	77	78	71	71	2635 (1242)	214 (71)	4728 (1716)	3010 (1662)	0-16267	0-577	0-18561	0-23631
<i>C. glacialis</i> CIV	CgCIV	69	44	57	57	1179 (747)	97 (70)	3337 (1480)	1190 (618)	0-9929	0-650	0-19919	0-8964
<i>C. glacialis</i> CV	CgCV	69	89	71	57	685 (343)	746 (343)	1145 (346)	1455 (491)	0-4648	0-3079	0-4074	0-4889
<i>C. glacialis</i> CVI f	CgVIf	38	56	21	36	114 (48)	90 (40)	116 (71)	304 (130)	0-483	0-350	0-905	0-1358
<i>C. glacialis</i> CVI m	CgVIm	15	22	0	0	35 (24)	12 (9)	0 (0)	0 (0)	0-241	0-80	0-0	0-0
<i>Calanus hyperboreus</i> CI	ChyCI	8	11	0	0	16 (16)	12 (12)	0 (0)	0 (0)	0-211	0-104	0-0	0-0
<i>C. hyperboreus</i> CII	ChyCII	23	22	0	0	135 (86)	50 (43)	0 (0)	0 (0)	0-1056	0-389	0-0	0-0
<i>C. hyperboreus</i> CIII	ChyCIII	46	44	0	0	116 (46)	49 (26)	0 (0)	0 (0)	0-453	0-209	0-0	0-0
<i>C. hyperboreus</i> CIV	ChyCIV	15	22	36	43	260 (243)	25 (20)	1138 (551)	2212 (1238)	0-3169	0-178	0-5432	0-16297
<i>C. hyperboreus</i> CV	ChyCV	46	56	29	36	214 (104)	163 (111)	388 (177)	485 (190)	0-1268	0-1035	0-1811	0-1901
<i>C. hyperboreus</i> CVI f	ChyVIf	15	33	36	21	65 (50)	52 (32)	246 (98)	285 (197)	0-634	0-281	0-905	0-2716
<i>Calanus finmarchicus</i> CI	CfinCI	100	100	93	64	8095 (2410)	2483 (511)	3127 (860)	3951 (1509)	151-31840	352-5631	0-11770	0-17384
<i>C. finmarchicus</i> CII	CfinCII	85	89	93	79	5646 (1456)	627 (145)	4482 (1281)	3162 (989)	0-15694	0-1189	0-15392	0-10865
<i>C. finmarchicus</i> CIII	CfinCIII	85	78	79	93	3327 (1498)	207 (60)	7512 (2427)	1646 (457)	0-20493	0-548	0-27615	0-5432
<i>C. finmarchicus</i> CIV	CfinCIV	54	44	71	50	1493 (1135)	42 (22)	4469 (1552)	369 (121)	0-15000	0-154	0-16750	0-1268
<i>C. finmarchicus</i> CV	CfinCV	46	56	57	43	353 (255)	228 (150)	2697 (1253)	407 (173)	0-3380	0-1397	0-16297	0-2264
<i>C. finmarchicus</i> CVI f	CfinVIf	46	33	29	7	246 (131)	28 (14)	259 (163)	65 (65)	0-1690	0-104	0-2264	0-905
<i>C. finmarchicus</i> CVI m	CfinVIm	0	0	0	7	0 (0)	0 (0)	0 (0)	39 (39)	0-0	0-0	0-0	0-543
Copepod egg	Cegg	85	89	14	50	7596 (4357)	1362 (439)	194 (162)	692 (247)	0-59154	0-3468	0-2264	0-2988
<i>Euchaeta norvegica</i>	Enorv	15	11	14	14	58 (40)	12 (12)	58 (40)	116 (84)	0-211	0-104	0-453	0-1086
Harpacticoid sp.	Har Sp	46	11	7	7	107 (35)	13 (13)	39 (39)	58 (58)	0-302	0-115	0-543	0-815
<i>Metridia longa</i> CI	MloCI	69	89	50	79	2665 (1318)	225 (105)	4003 (1564)	2774 (665)	0-16056	0-1013	0-18108	0-7605
<i>M. longa</i> CII	MloCII	38	44	50	57	761 (392)	62 (38)	1772 (686)	815 (270)	0-4648	0-335	0-7243	0-3169
<i>M. longa</i> CIII	MloCIII	54	56	21	36	149 (45)	266 (168)	291 (175)	352 (145)	0-423	0-1565	0-1811	0-1630
<i>M. longa</i> CIV	MloCIV	62	78	29	14	915 (366)	666 (200)	226 (132)	123 (85)	0-4376	0-1715	0-1811	0-996
<i>M. longa</i> CV	MloCV	85	89	64	71	3587 (1216)	1366 (517)	1158 (444)	1662 (916)	0-13732	0-3912	0-6338	0-13310
<i>M. longa</i> CVI f	MloVIf	85	89	64	64	1600 (514)	1612 (998)	2251 (982)	2787 (932)	0-5493	0-9241	0-12314	0-10774
<i>M. longa</i> CVI m	MloVIm	69	78	71	57	2289 (1035)	1002 (529)	1458 (501)	2225 (779)	0-11831	0-4726	0-6338	0-6972
<i>Microcalanus</i> spp. CI-CV	MicCI-CV	100	100	93	79	12344 (4537)	4458 (1721)	6875 (2175)	4689 (1188)	755-54295	462-12856	0-24446	0-15437
<i>Microcalanus</i> spp. CVI f	MicVIf	100	100	93	100	21512 (4700)	13393 (3005)	11922 (3649)	10128 (2203)	1660-51337	4806-26840	0-42102	1268-27298
<i>Microcalanus</i> spp. CVI m	MicVIm	92	100	43	64	3248 (1130)	915 (289)	459 (240)	601 (246)	0-12465	60-2913	0-3169	0-3486
Nauplii <i>Calanus finmarchicus</i>	CfinN3-N6	100	100	100	71	4666 (1225)	6990 (1075)	4883 (1013)	2525 (1036)	211-13521	1993-13017	453-12223	0-10865
Nauplii <i>Euchaeta norvegica</i>	EuN3-N6	8	11	7	14	65 (65)	17 (17)	26 (26)	116 (92)	0-845	0-149	0-362	0-1268
Nauplii <i>Metridia longa</i>	MeN3-N6	92	78	93	93	6619 (2483)	1572 (609)	10774 (2458)	12372 (3542)	0-31267	0-5562	0-28068	0-37484
Nauplii <i>Pseudocalanus</i> spp.	PsN3-N6	85	100	71	71	3478 (841)	5460 (2055)	1814 (734)	2532 (1138)	0-8451	298-20376	0-10412	0-15845
<i>Oithona similis</i> CI-CV	OsCI-CV	100	100	100	100	61408 (18622)	33829 (8576)	61875 (10533)	91932 (11903)	12555-251403	11130-72581	16750-173839	40744-176193
<i>O. similis</i> CVI f	OsVIf	100	100	100	100	39729 (8522)	38845 (11393)	32556 (7861)	33652 (4500)	6036-98871	12273-108479	11318-94525	8239-65552
<i>O. similis</i> CVI m	OsVIm	100	100	100	100	3710 (874)	5215 (2055)	2454 (492)	3939 (558)	724-10986	272-14078	905-7696	1086-8239
<i>Oncaea borealis</i> CI-CV	ObCI-CV	92	100	36	57	3352 (1259)	3211 (1519)	1080 (538)	831 (286)	0-16267	117-13973	0-5885	0-3667
<i>O. borealis</i> CVI f	ObVIf	100	100	100	100	32500 (12526)	27155 (8170)	36640 (8299)	46147 (8812)	5432-171546	6014-75334	4074-114625	2445-109555
<i>O. borealis</i> CVI m	ObVIm	77	100	64	57	1405 (580)	1619 (508)	938 (302)	899 (325)	0-6338	86-4335	0-3803	0-3803
<i>Pseudocalanus</i> spp. CI	PseCI	100	100	100	100	33533 (6816)	21742 (5682)	23007 (3218)	25753 (5849)	4014-96728	2862-55842	4346-47534	724-71618
<i>Pseudocalanus</i> spp. CII	PseCII	100	100	100	100	29301 (5347)	20512 (5856)	43709 (6167)	31444 (5386)	5191-66246	7922-56681	9778-97332	5704-62473
<i>Pseudocalanus</i> spp. CIII	PseCIII	100	100	100	100	22350 (3367)	14316 (3322)	52307 (7691)	32537 (3449)	6640-46478	4424-33095	12766-118609	14577-60300
<i>Pseudocalanus</i> spp. CIV	PseCIV	100	100	100	100	19062 (3097)	10554 (2526)	27392 (4649)	19877 (2417)	3712-46267	560-25533	1086-63017	8239-37484
<i>Pseudocalanus</i> spp. CV	PseCV	100	100	100	100	15801 (3511)	5615 (1331)	28627 (5857)	19816 (4250)	694-43520	117-14961	4753-78318	5704-62745
<i>Pseudocalanus</i> spp. CVI f	PseVIf	100	100	100	100	14296 (2489)	11825 (3907)	8673 (2014)	9749 (2031)	6036-30482	2953-33607	1086-24446	2716-32052
<i>Pseudocalanus</i> spp. CVI m	PseVIm	85	100	93	79	1490 (476)	1933 (619)	1575 (342)	973 (276)	0-6760	187-6495	0-4120	0-3803



## RESULTS

### *Hydrographic conditions*

In general, the hydrographic conditions in the HBS differed markedly along the sampled transects, allowing to differentiate distinct hydrographic regions within the system. The vertical distribution in the water column of temperature, salinity and fluorescence along the HB and HS sections, respectively, and single vertical profiles of the same parameters for the FB stations from 2003-2006 are shown in Figures 3, 4 and 5.

In early August 2003 and 2004, HB was generally free of sea-ice except at the two easternmost stations (HB1 and HB2), where pack ice was still present in 2003. During these years, the beginning of the stratification was clearly evident for HB. The east side of the bay was highly stratified, with a freshwater layer (salinity [S] 22-28) in the first 17 m, whereas the west side of the bay had more saline waters at the surface (S ~31) (Figs. 3 and 4). The presence of cold and less saline waters in the near-surface layer on the eastern side of the bay at Stns. 1 and 2 in 2003 (mean temperature [T] = 3.9°C and S = 22.0) as well as at Stn. 3 in 2004 (mean T = 3.9 °C and S 22.0) is probably due to recent input of sea-ice meltwater to the surface layer (Fig. 3). For the intermediate and the bottom layers, we observed a cold layer, with temperatures between -1 and -1.5°C along the HB transect; this was situated between 25 and 75 m on the eastern side and between 25 and 140 m on the western side (Fig. 3). This plume was likely a remnant of local winter mixing processes.

Below, warmer intermediate waters ( $> -1^{\circ}\text{C}$ ) were present between 75 and 140 m in the central part (Stns. HB3 and HB4) and on the eastern side (HB1) of the HB section. The water was mostly colder ( $< -1.4^{\circ}\text{C}$ ) close to the bottom on the western side and in the central part of HB.

The southern shore of HS (stations HS1 and HS2) was also strongly stratified in early August 2003 and 2004, with relatively fresh and warm waters ( $S \sim 29.0\text{--}30.0$ ,  $T = 4.2^{\circ}\text{C}$ ) in the top 20 m a result of outflow from HB. The HS was more weakly stratified towards the northern shore (stations HS3 and HS4), with warmer and saltier waters ( $S \sim 32.3$ ,  $T = 3.2^{\circ}\text{C}$ ) resulting from an inflow from the Labrador Sea. HS also showed evidence of colder waters around 100 m toward the southern coast. Similarly, the northernmost and deepest (436 m) station (FB1) in early August 2003 and 2004 was characterized by cold and less saline waters above the thermocline ( $S 29.4\text{--}29.6$ ,  $T 2.4\text{--}2.8^{\circ}\text{C}$ ) and by saltier and colder waters at depth ( $S = 33.4$  and  $T = -1.7^{\circ}\text{C}$ ). The other two stations, FB2 and FB3, are located further south are shallower than FB1 (317 and 156 m respectively). FB2 had colder and saltier ( $T = 1.3^{\circ}\text{C}$ ,  $S = 30.5$ ) waters above the thermocline than FB1 and warmer and fresher ( $T = -1.3^{\circ}\text{C}$ ,  $S = 32.8\text{--}33.0$ ) waters than FB1 at depth. Similarly, FB3 had warmer and saltier ( $4.3^{\circ}\text{C}$  and  $31.1$ ) waters above thermocline and warmer and fresher waters at depth ( $-1.3^{\circ}\text{C}$  and  $32.8$ ).

During the early September 2005 and 2006 samplings, the oceanographic conditions in HB varied to some extent compared to early August 2003 and 2004: the bay was

markedly stratified from east to west with warmer and fresher waters (mean  $T = 9.5^{\circ}\text{C}$ ,  $S = 28.3$ , and  $T = 8.36^{\circ}\text{C}$ ,  $S = 29.83$ , respectively) above the thermocline. During these two years, HB was completely free of sea-ice, and the thickness of the surface mixed layer (SML) varied from 12.6–15.6 m and 16.6–25.4 m from west to east in 2005 and 2006, respectively. In September 2005 and 2006, the cold water layer ( $< -1^{\circ}\text{C}$ ) extended from the surface (10 m) to about 50 m in the centre of HB. In 2005, there were warmer intermediate waters ( $> -1^{\circ}\text{C}$ ) between 75 and 135 m on the eastern side of HB that could have possibly come from Hudson Strait. Finally, the water was colder ( $< -1.5^{\circ}\text{C}$  near the bottom [central HB],  $< -1.6^{\circ}\text{C}$  on the western side of HB) at depth in 2005 and 2006 compared to 2004 and 2005, probably due to deep convection in the northwestern region of HB and in FB.

For the sections in southeastern HSS, the principal feature of the two-way circulation in the strait that is described in the literature was clearly evident in 2005 and 2006 (Figs. 3 and 4). In both years, the HSS sections revealed fresher waters (mean  $S = 31.3$  [2005] and  $31.4$  [2006]) in the top 25 m that spread from the coast of Québec (~40 km offshore). Another remarkable features found in the southeastern HSS during 2005 was a salty and cold (close to the freezing point) water mass (mean  $T = -1.2^{\circ}\text{C}$ ,  $S = 33.1$ ) situated between 100 and 150 m, right below the fresh water flowing out along the southern shore of the strait. A fairly thin (~20 m) warm (mean  $T = 2.6^{\circ}\text{C}$ ) layer due to summer heating was found at the surface over the entire transect. Also, there was a salty and cold water mass (mean  $T = -1.1^{\circ}\text{C}$ ,  $S = 33.1$ ) in 2006, but this time it was located at the centre of the strait between 100 and 225 m. In addition, a thick (~50 m) warm (mean =  $3.5^{\circ}\text{C}$ ) layer was

present from the surface to the middle of the water column at the southernmost outflow stations (HSS1 to HSS3), which then extended to the rest of the transect at the surface (~20 m) (mean  $T = 4.4^{\circ}\text{C}$ ). During 2005 and 2006, the waters of the outflow were generally much more stratified than those from inflow on the northern shore of the strait. The only station sampled in 2005 in northwestern HS (HS1) had oceanographic characteristics similar to those sampled in 2003 and 2004: overall, it was highly stratified, with warmer and fresher waters above the thermocline and warmer and saltier waters at depth (Table 1).

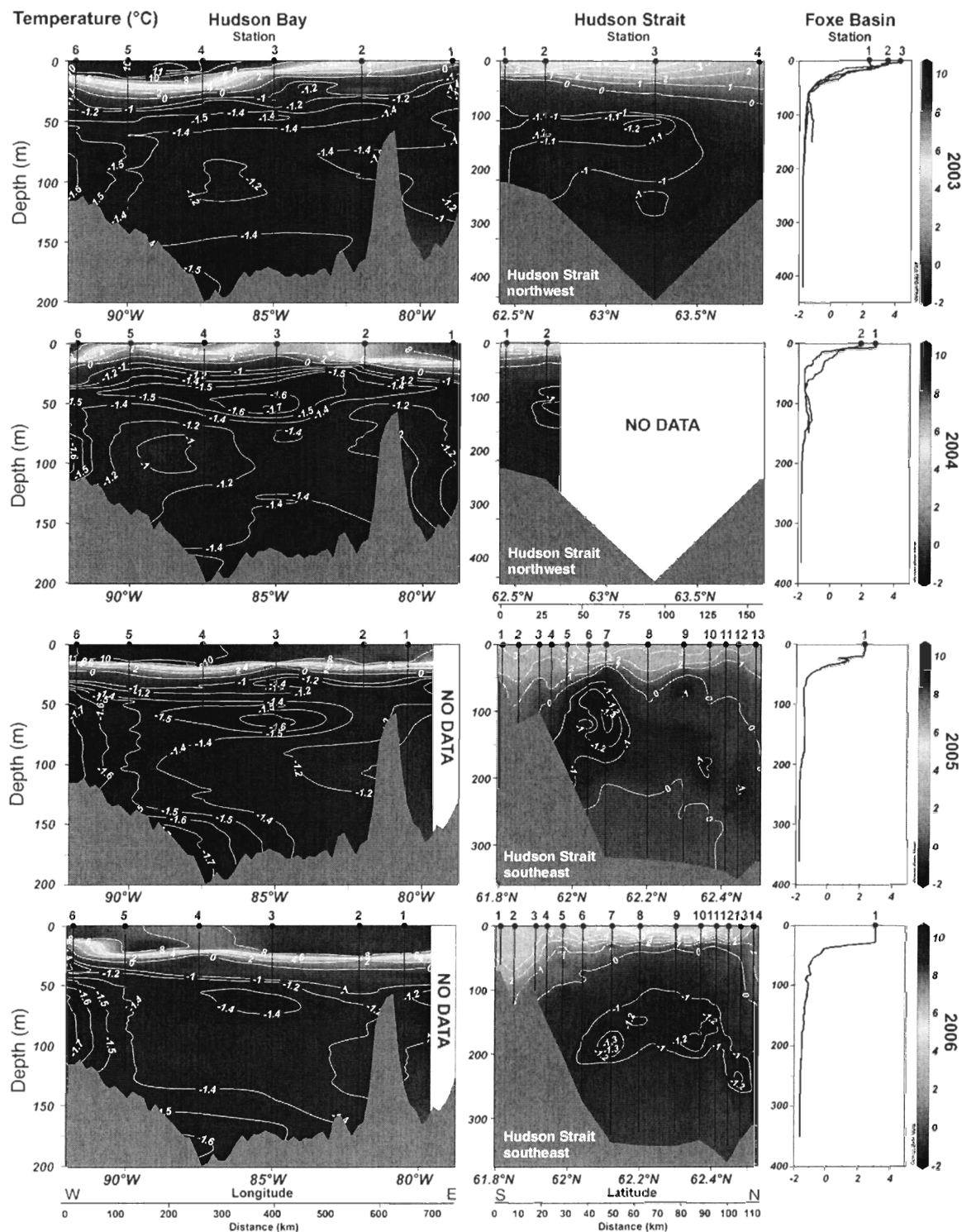


Figure 3. Water temperature distribution in Hudson Bay, Hudson Strait and Foxe Basin from 2003 to 2006.

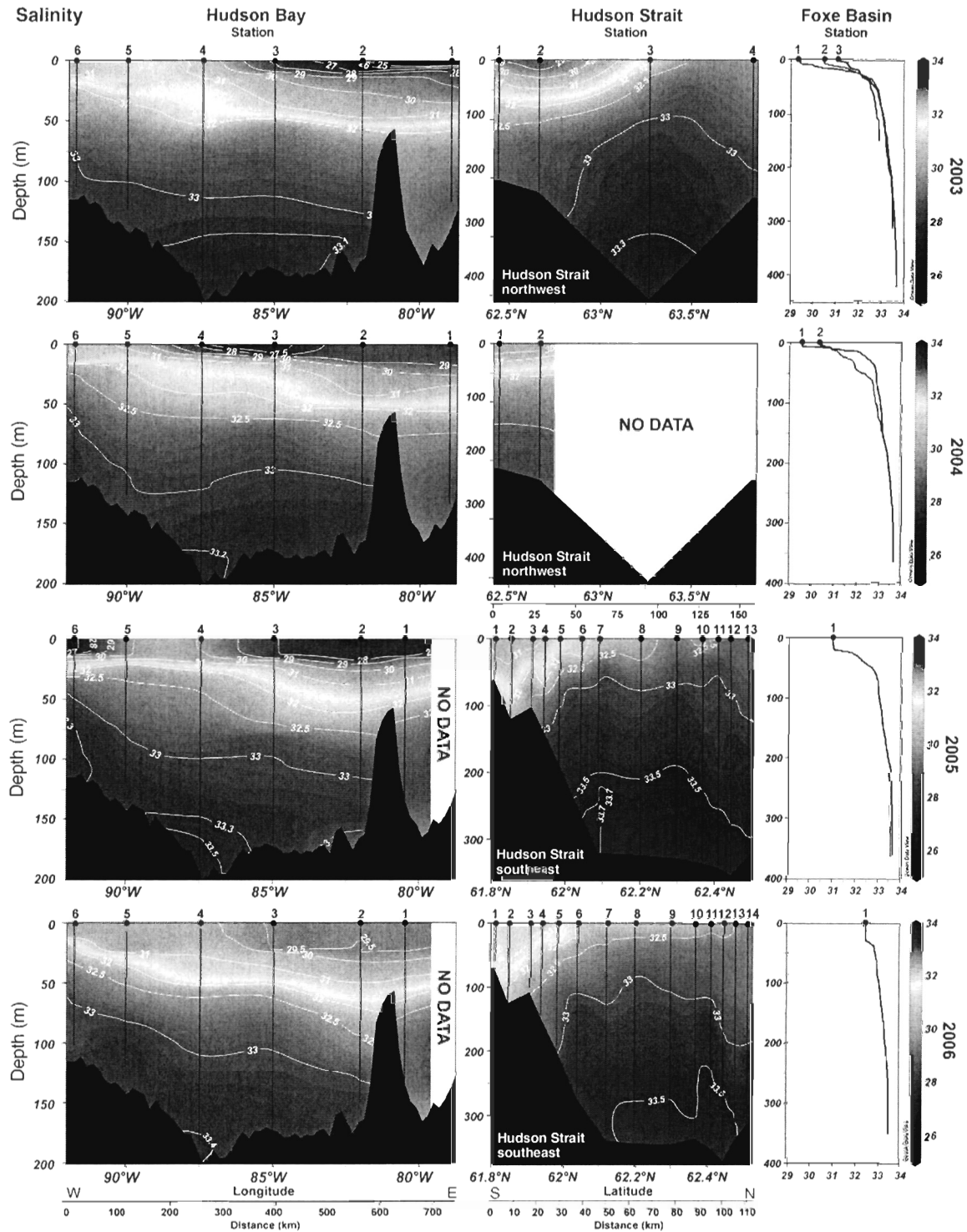


Figure 4. Salinity distribution in Hudson Bay, Hudson Strait and Foxe Basin from 2003 to 2006.

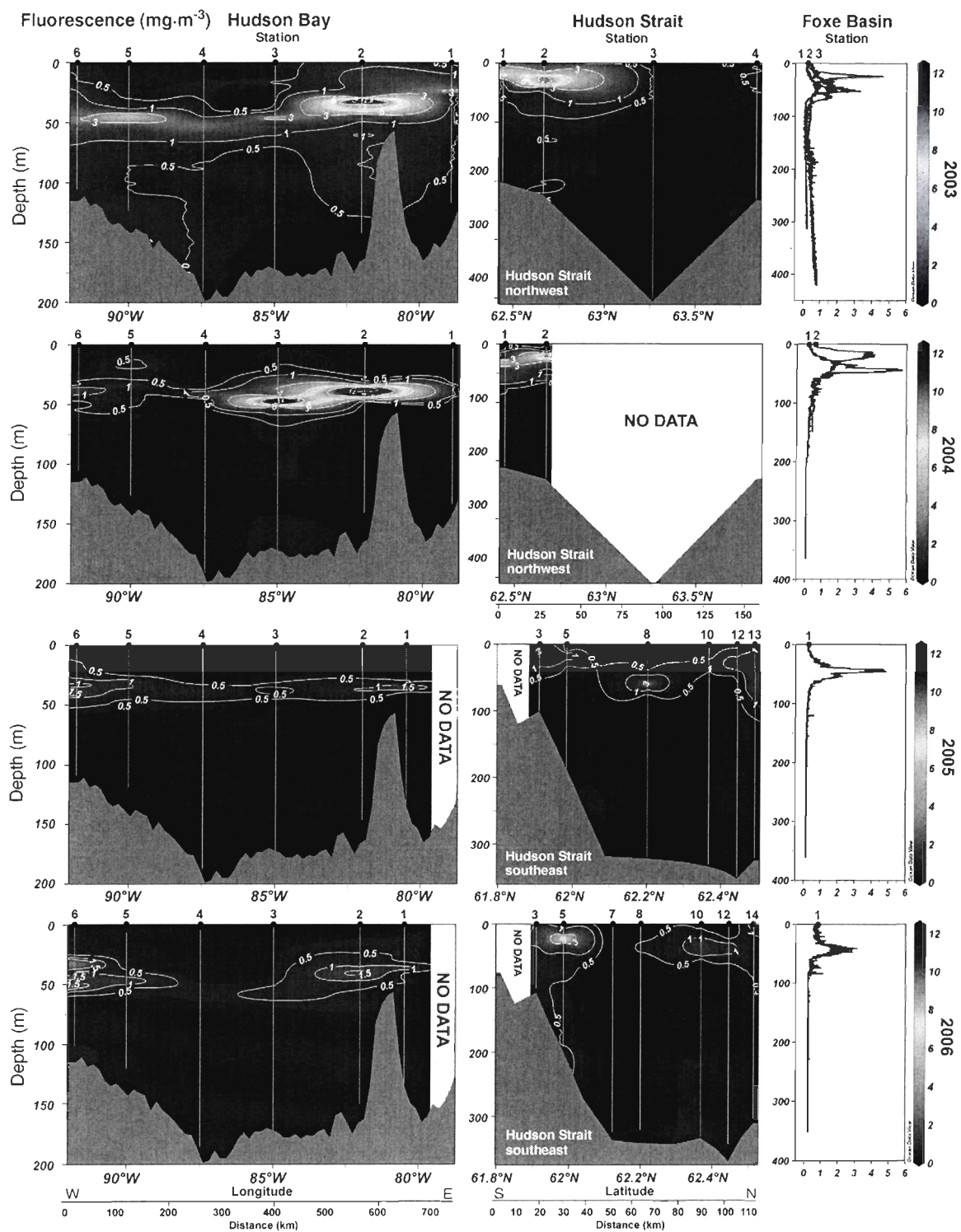


Figure 5. Chlorophyll fluorescence distribution in Hudson Bay, Hudson Strait and Foxe Basin from 2003 to 2006.

### *Phytoplankton standing stock*

During the four years of this study, maximum fluorescence values were registered between 25 and 50 m along HB transects (Fig. 5), and the average integrated (0-100 m) Chl *a* concentration was almost three times higher in August 2003 and 2004 compared to September 2005 and 2006 (means  $\pm$  SD =  $125.0 \pm 57.8$  vs  $30.3 \pm 10.0$  mg Chl *a* m<sup>-2</sup>, respectively) (Fig. 6). The spatial difference between 2003-2004 and 2005-2006 was particularly evident at the offshore stations HB2 to HB5 (Fig. 5). In early August 2003, the lowest Chl *a* concentration was recorded on the eastern side of the HB (HB1), where the water in the upper 50 m was fresher and colder and where some melting ice was still present. Much higher integrated Chl *a* concentrations were measured in the centre and western portions of HB. These sea-ice-free regions were distinguished by clear warmer and saltier surface waters. In 2004, the Chl *a* decreased from east to west in HB (from 130.4 to 41.3 mg m<sup>-2</sup>, but omitting the lowest value at station HB1 [37.1 mg m<sup>-2</sup>]). In 2005 and 2006, there were little interannual differences in the Chl *a* concentration in HB. In 2005, Chl *a* decreased gradually from west to east (45.7 to 22.8 mg m<sup>-2</sup>, respectively), and in 2006 the lowest average value (19.7 mg m<sup>-2</sup>) was recorded in the central part of the bay (Stns HB3 and HB4) (Fig. 6).

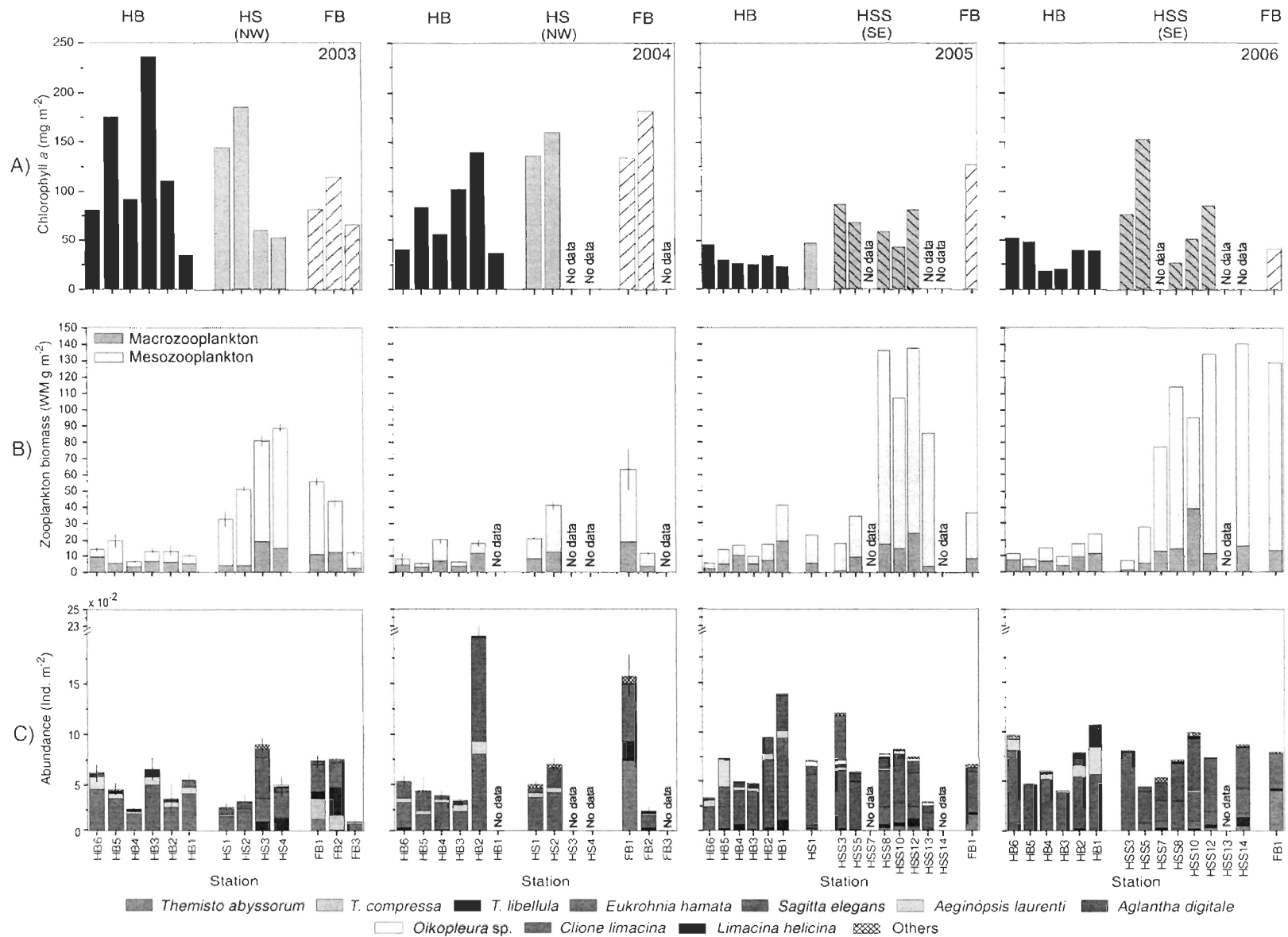
Along the northwestern HS section, maximum fluorescence values were measured within the upper 50 m of the water column, and the Chl *a* concentration (0–100 m) was, on average, almost three times higher in the outflow stations (HS1 and HS2), where the



surface waters were highly stratified, than in the inflow stations (HS3 and HS4) of the strait (average  $\pm 164.7$  vs  $\pm 56.9$  mg Chl  $m^{-2}$ , respectively) during 2003 (Figs. 5 and 6). Integrated values were nearly of the same magnitude in 2004 as those measured in 2003 at the outflow stations of the HS on the southern shore, while integrated values at the outflow stations (HS1) were almost three times lower in 2005 than in 2003 and 2004.

At stations sampled in FB from 2003 to 2006, the maximum Chl *a* fluorescence was found between 20 and 60 m (Fig. 5). Integrated values differed slightly between the northernmost station (FB1) (mean  $\pm$  SD =  $88.2 \pm 21.4$  mg  $m^{-2}$ ) and, the further south stations (FB2 and FB3) (mean  $\pm$  SD =  $100.5 \pm 38.6$  mg  $m^{-2}$ ), close to the HB and HS entrances (Fig. 6).

Finally, along the south-eastern HSS sections sampled only in 2005 and 2006, the maximum fluorescence values were located in the upper 60 m of the water column. In 2005 average integrated values (0-100 m) were, on average, only slightly higher in the south shore (outflow) (stations HSS3 and HSS5) than in the north shore (inflow) (Stns. HSS8 to HSS13) ( $86.8$  compared to  $43.2$  mg Chl *a*  $m^{-2}$ , respectively). This was not the case in 2006, where integrated values were more than two times higher in the southern shore (mean =  $118.7$  mg  $m^{-2}$ ) than in the northern shore (mean =  $53.9$  mg  $m^{-2}$ ) (Figs. 5 and 6).



**Figure 6.** Variations of (A) chlorophyll *a* (chl *a*) concentration (via *in vivo* fluorescence), (B) total zooplankton biomass and (C) total macrozooplankton abundance in the HBS from 2003 to 2006. HB: Hudson Bay; HS: northwestern Hudson Strait; HSS: southeastern Hudson Strait; FB: Foxye Basin. Chl *a* was integrated from surface to 100 m whereas zooplankton biomass and abundance were integrated from surface to bottom. In (B) and (C), mean and SD are shown for 2003 and 2004.

### *Zooplankton standing stock*

The mean total zooplankton biomass ( $\text{g WM m}^{-2}$ ) ( $\pm$  SD for 2003 and 2004) integrated from bottom to surface along the sampling transects in HB, HS, and FB from 2003 to 2006 is shown in Figure 6. In 2003 and 2004, the HB showed no variation pattern in total zooplankton biomass from one side to another, whereas the 2005 and 2006, HB transects showed a slightly decrease in zooplankton biomass from east to west (41.2 to 5.7, and 23.5 to 11.0  $\text{g WM m}^{-2}$  respectively) (Fig. 6).

In 2003, the total zooplankton biomass along the HS section, increased gradually from the southern shore (outflow) to the northern shore (inflow), from 32.6 to 88.9  $\text{g WM m}^{-2}$ , respectively. This pattern was also observed in 2004 at the outflow stations (HS1-HS2) (Fig. 6). In 2005 and 2006, the southeastern HS section showed a remarkably strong gradient in zooplankton biomass from the south towards the north side of transect. The lowest values were recorded at the outflow stations (HSS3-HSS5) in the southern shore, whereas higher values were found at the rest of the stations; here, zooplankton biomass ranged from 85.7 to 137.5 and from 77.5 to 140.7  $\text{g WM m}^{-2}$  in 2005 and 2006, respectively (Fig. 6).

In 2003 and 2004, the FB stations also showed a decrease in zooplankton biomass (from 55.9 to 12.5, and from 63.2 to 11.6  $\text{g WM m}^{-2}$ , respectively) from the northernmost station (FB1), that was also the deeper, to those situated near the entrance of HB (FB2-

FB3), East of Southampton Island (Fig. 1 and Fig. 6). Remarkably, zooplankton biomass at station FB1 was almost 4 times lower in 2005 than 2006 (36.3 vs 128.7 g WM m<sup>-2</sup>, respectively). Overall, much higher (from 3 to up to 6 times) integrated zooplankton biomasses were observed in FB and HS than in the HB from 2003 to 2006 (Fig. 6). From 2003 to 2006, the ratio of macrozooplankton (length > 2 mm) to mesozooplankton (mostly copepods) biomasses ranged fairly in the HB from 2:1 to ~1:3; strongly from 1:2 to ~1:11 and 1:3 to ~1:22 from the outflow towards the inflow at the northwestern HS and southeastern HSS, respectively; and moderately in the FB from 1:4 to ~1:9.

### ***Macrozooplankton***

A total of 25 macrozooplankton taxa, including 12 at species level, were recorded from 2003 to 2006 in the HBS (Table 2). The total integrated abundance (ind. m<sup>-2</sup>) of macrozooplankton did not show large variations among the three regions and among the study years in the HBS (Fig. 6). However, two peaks in abundance, mainly due to the cnidarian *Aglantha digitale* and the amphipod *Themisto abyssorum*, were found in 2004 at Stns. HB2 and FB1.

Remarkably, the chaetognath *Sagitta elegans* was the most abundant macrozooplankton species and it was found at each station of all the three regions of the HBS. *A. digitale* was the second most abundant macrozooplankton species in the HBS, but this species was nearly absent in the FB region. On the other hand, the cnidarian *Aeginopsis*

*laurentii* and the chaetognath *Eukrohnia hamata* were only found in the HB and HS regions (Fig. 6).

The hyperiid amphipods *T. libellula*, *T. abyssorum* and *T. compressa* were more abundant in FB and mainly on the northern shore stations of both northwest and southeasten HS sections (2003-2006) than at any other sampled stations, with some exceptions in 2005 where *T. libellula* was also recorded along the HB transect. The group labelled as others, comprises species that were not identified accurately or that were rarer and less abundant in the HBS (e.g. unidentified ctenophores, decapods and amphipods, the mysids *Meterythropus robusta* and *Mysis mixta*, the euphausiid *Thysanoessa raschii* and the polychaete *Tomopteris* sp.)

### ***Mesozooplankton***

A total of 22 mesozooplankton taxa, including 11 copepod taxa (from which 8 were identified to the species level and separated into developmental stages) and 11 macrozooplankton larvae were recorded from 2003 to 2006 in the HBS (Tables 2 and 3; Fig. 7). In contrast to the biomass values, the total mesozooplankton abundances (ind. m<sup>-2</sup>) integrated over the water-column depth were generally higher in the HB, with a peak of abundance on the western side of the HB (Stn. HB5) during 2003, and less pronounced in 2004 and 2005 (Fig. 7a). Overall, there was little variation in mesozooplankton abundances within the HBS areas, except during the 2003 peak at Stn. HB5, and during 2004 where the

westernmost station in HB and the southern HS stations showed the lowest values in mesozooplankton abundances compared to the other study years.

The mesozooplankton community was entirely dominated by copepods in the three regions during the four years. This community represented 92 and 88% of the total zooplankton abundance in the HB in 2003 and 2004, respectively, and this was slightly higher than in the HS (84 and 85%) and FB (83 and 86%) during the same two years. On the other hand, during 2005 and 2006, the only station sampled in the FB (FB1), had a slightly higher percentage in copepod dominance than the other two regions (HB/HSS: 90/87%, 2005; 88/87%, 2006), averaging 94 and 91%, respectively (data not presented).

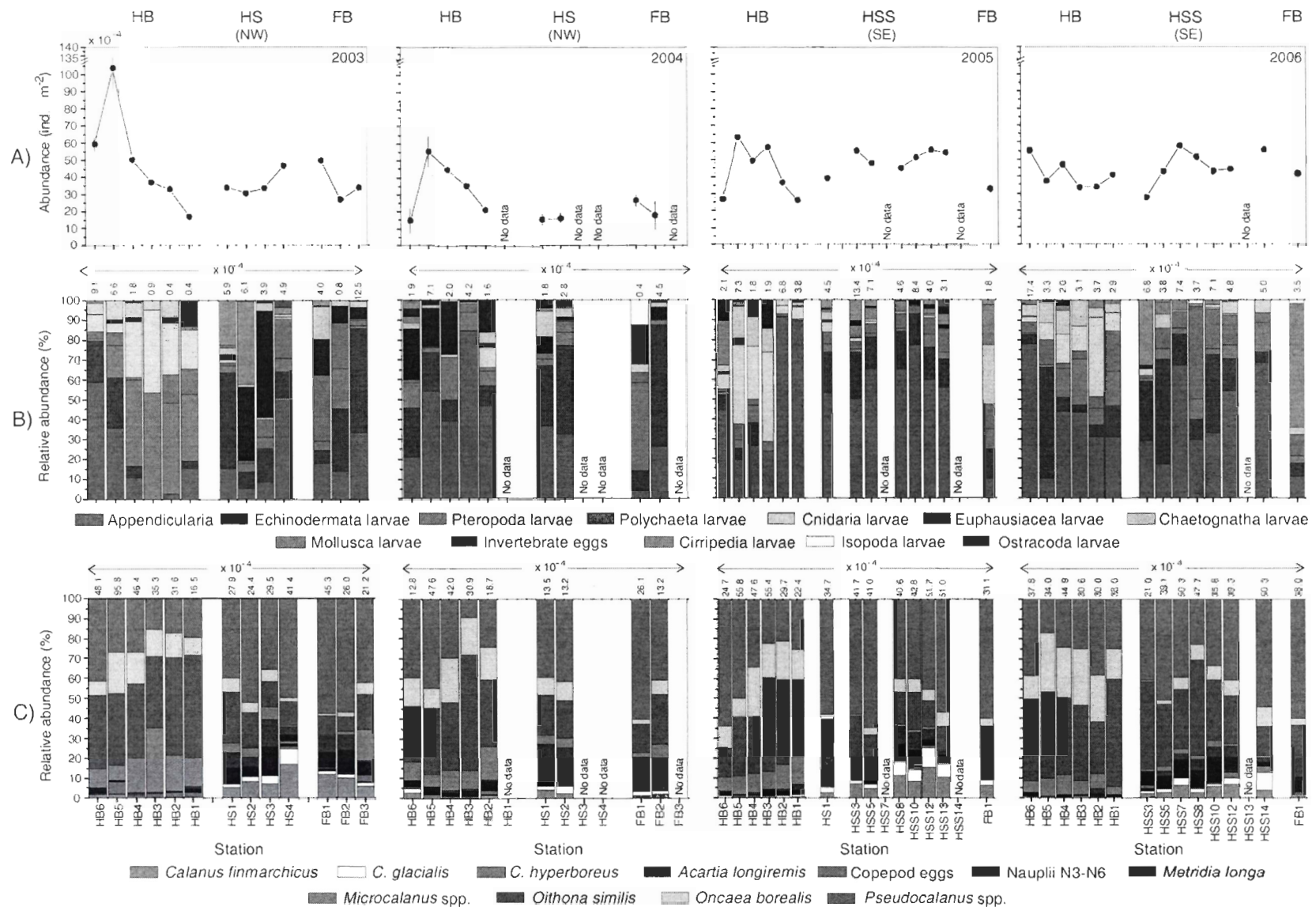


Figure 7. Variations of (A) total mesozooplankton abundance, (B) relative mero- and holoplankton abundance and (c) relative copepod abundance in the HBS from 2003 to 2006. HB: Hudson Bay; HS: northwestern Hudson Strait; HSS: southeastern Hudson Strait; FB: Foxe Basin. Zooplankton abundance was integrated from surface to bottom. In (A), mean and SD are shown for 2003 and 2004. In (B) and (C), numbers above bars indicate total abundance (ind. m<sup>-2</sup>).

The relative abundances of the community of mesozooplankton other than copepods that include the meroplankton (i.e. Echinodermata, Mollusca) and the holoplankton (i.e. Chaetognatha, Cnidaria) are shown on Fig. 7b. Although observed occasionally, the foraminiferans were excluded from our analyses because of size-related inadequate sampling (202  $\mu\text{m}$ ). The community of mesozooplankton (other than copepods) was dominated by the Appendicularia larvae (comprised by *Fritillaria* sp. and *Oikopleura* sp.), which were present in all stations and years in the three regions, except at HB3 in 2003. The second most abundant group were the larvae of Echinodermata, Pteropoda and Polychaeta, along with Cnidaria and Chaetognatha larvae; the former were found everywhere, whereas the latter were found mainly in HB (except the cnidarians in 2004) and at irregular intervals in the other two regions. The rest of the taxa (larvae of Euphausiacea, Mollusca, Isopoda and Ostracoda and invertebrate eggs) were found in lesser abundances and sporadically distributed in the HBS sampled regions from 2003 to 2006 (Fig. 7b).

In regards to the copepod communities from 2003 to 2006, they were dominated by small species such as *Oithona similis*, *Oncaea borealis* and *Microcalanus* spp. in HB and by *Pseudocalanus* spp. and larger species such as *Calanus finmarchicus*, *C. glacialis* and *Metridia longa* in the other two regions (FB/HS). The large copepod species were more present in HS/FB than HB with means = 65/68 vs 26%; 53/58 vs 32%; 69/75 vs 38%; and 60/70 vs 29% of the total copepod abundances, respectively (Fig. 7c).



The three replicates of both the biomass and abundance of macro- and mesozooplankton sampled in 2003 and 2004 in the HB, FB, and HS showed a very small variability in their respective coefficient of variation (CV). In 2003-2004, the CV for the total biomass ranged from 10 to 26% in the HB (except in 2003 at HB2 = 38%), 3 to 15% in the HS; and 7 to 26% in the FB (Fig. 6). For the macrozooplankton abundances, the CV ranged from 3 to 16% in the HB (except at HB2 in 2003 = 43% and HB5 in 2004 = 34%), 7 to 20% in the HS, and 4 to 21% in the FB (Fig. 6). In the case of mesozooplankton abundances (holoplankton and meroplankton), the CV ranged from 2 to 50% in the HB, 3 to 28% in the HS, and 4 to 46% in the FB (Fig. 7a).

### *Multivariate analyses*

The 2-dimensional Non-metric Multidimensional Scaling (NMDS) that was carried out to examine the differences between the sampled stations according to their zooplankton composition is shown in Figure 8. In a first approach a one way ANOSIM analysis with factor "Year" (which included all sampled years from 2003-2006) was tested but the ANOSIM global statistic test scored an  $R$  value of 0.10,  $p > 0.05$  (data not presented), indicating no interannual variability in the zooplankton community. On the other hand, when factor Site (which included the FB, HB, and the northwest and southeast HS sections) was tested, the ANOSIM test scored an  $R$  value of 0.75,  $p \leq 0.001$ , which indicates large between-group differences. The one way ANOSIM analysis with factor "Site" confirmed the difference in zooplankton composition between the four regions mentioned, with a

stress value  $< 0.2$  that represents a potentially useful 2-dimensional ordination (Clarke and Warwick, 2001).

To examine the zooplankton distribution patterns in relation to the environmental variables found in the HBS from 2003 to 2006, three models were constructed with the relative abundances (%) from bottom to surface on 69 zooplankton taxa (copepods divided into developmental stages, macrozooplankton, meroplankton and holoplankton) and the best 6 fitted environmental variables. In the first model, all the sampled transects from all years were included (FB, HB, HS northwest and southeast) and 6 forward selected environmental variables in order of importance: Strat, Depth, UMT, LMT, LMS and Flu0-100 (Table 4), that explain together 47% of the total zooplankton variability in the HBS in early August 2003-2004 and early September 2005-2006 (Fig. 9a, b). These environmental variables (except fluorescence) were highly correlated to Axis I reflecting a clear and consistent pattern in the data set, i.e. a strong gradient along this axis (Table 4). In addition, Axis I was more important explaining 30.6% of the total taxonomic variation and 65.1% of taxon-environment relationship (Table 5).

Stratification index was the most important contributor variable to the model, explaining 25% of the overall zooplankton taxonomic variability (Table 4). This parameter along with UMT (explaining 5% of the zooplankton variability) distinguished the HB transect (which was characterized by increasing gradients on Stratification and UMT) from the other two regions (Fig. 9a). The taxa that showed a close relationship with these

variables, and that occurred more in the HB were *Microcalanus* spp. CI-CVIf, *O. borealis* CI-CVIf-m, *O. similis* CI-CVIf, *A. laurentii*, *Pseudocalanus* spp. CVIf-m, *S. elegans*, *Fritillaria* sp., and larvae of Cnidaria and Chaetognatha (Fig. 9b). Bottom depth, LMT and LMS explained 8, 4, and 3%, respectively, of the zooplankton variability (Table 4). These variables placed the southeastern and northwestern HSS as well as some FB stations, matching them positively with the increasing values on these environmental gradients (Fig. 9a).

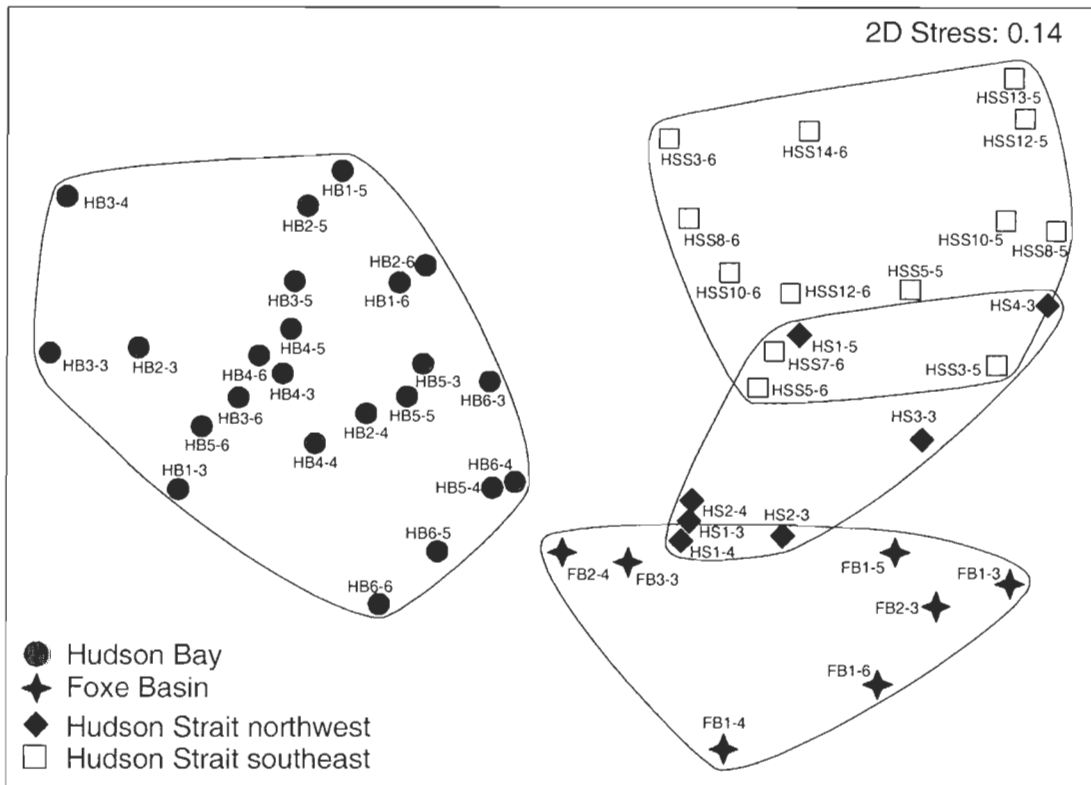


Figure 8. Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the zooplankton samples collected at 50 stations in the HBS during 2003-2006. The four groups of samples with similar taxonomic composition assessed with a cluster analysis using the Bray-Curtis similarity are superposed to the NMDS. Each group of samples belongs to a distinct region of the HBS (global one-way ANOSIM test,  $R = 0.75$ ,  $p \leq 0.001$ ). Stations names in the diagram labelled as: site/number-year.

Table 4. Forward selection of environmental variables influencing the horizontal distribution of the zooplankton community in the HBS during 2003-2006 (Monte Carlo permutation test in RDA with 499 unrestricted permutations,  $p < 0.05$ ). High correlations (i.e.  $r > 0.5$ ) between environmental variables and the first 2 RDA axes are in bold.

Environmental variable	F-value	p-value	Explained		Correlation	
			$\lambda$	%	Axis I	Axis II
Stratification index (Strat)	15.58	0.002	0.25	25	<b>-0.816</b>	-0.159
Bottom depth (Depth)	6.11	0.002	0.08	8	<b>0.712</b>	-0.425
Upper mean temperature (UMT)	3.57	0.002	0.05	5	<b>-0.734</b>	0.195
Lower mean temperature (LMT)	3.23	0.002	0.04	4	<b>0.575</b>	0.438
Lower mean salinity (LMS)	2.60	0.004	0.03	3	<b>0.512</b>	-0.072
Fluorescence 0-100 m (Flu0-100)	1.26	0.202	0.02	2	0.054	-0.306
Total			0.47	47		

The eigenvalue ( $\lambda$ ) for each variable indicates the portion of the total variance explained by the model.

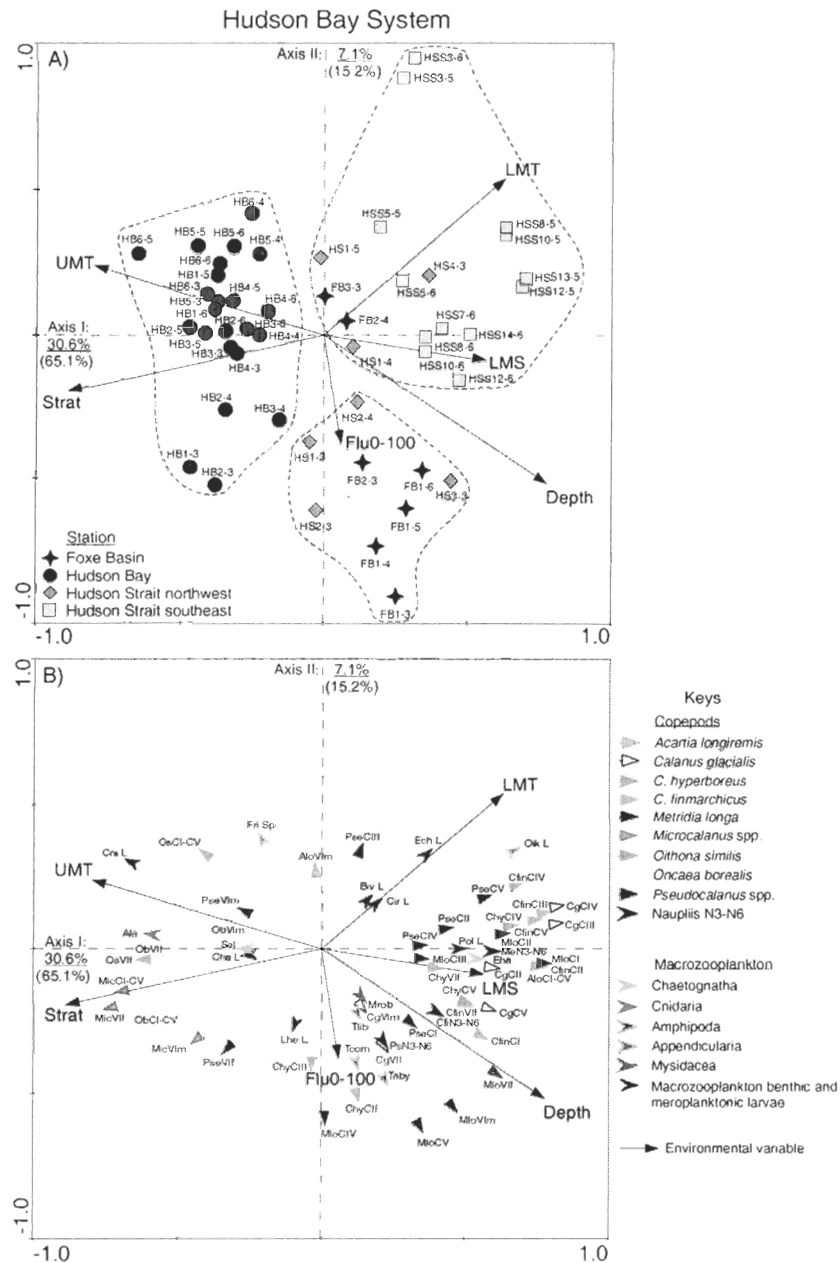


Figure 9. Redundancy analysis (RDA) ordination plots of axes I and II showing (A) sampling stations (symbols labelled: station-year) and (B) zooplankton taxonomic categories (coloured arrow tips) in relation to environmental variables (full black arrows) of data collected in the HBS during 2003-2006. Together axes I and II explain 37.7% of the total taxonomic variation (underlined values) and 80.3% of the taxonomic entry-environment relationship (values in parentheses). The model explains 47% of the total zooplankton variability within the HBS. For clarity, only taxonomic categories that fit 5% or more are shown in (B). Full names of environmental variables and of taxonomic categories are listed in Table 1 and in Tables 2 and 3, respectively.

The taxa that were more associated to these environmental variables were *Pseudocalanus* spp. CI-CV, *C. glacialis* CI-CVI, *C. finmarchicus* CI-CVI, *C. hyperboreus* CV-CVI, *A. longiremis* CI-CV, *M. longa* N3-N6, CI-CIII and CVIf, *E. hamata*, larvae of Echinodermata, Mollusca, and Cirripedia, Appendicularia, and Polychaeta. These taxa were also dominant at the regions mentioned previously, mainly at the southeastern HSS stations. The taxa that were more frequent in the FB (mostly the deepest stations FB1) and the HS northwest stations (mostly 2003-2004), as indicated by their close association with increasing depth, were *M. longa* CIV-CVIf-m, *C. hyperboreus* CIII, *C. glacialis* CVIf-m, *Pseudocalanus* spp. N3-N6 and CI, the hyperiid amphipods *T. abyssorum*, *T. compressa*, *T. libellula*, the mysid *Meterythrops robusta* and larvae of *L. helicina* (Fig. 9b).

Table 5. Summary of redundancy analysis (RDA) of 69 zooplankton taxonomic categories with six forward selected environmental variables (see Table 4) for the HBS during 2003-2006.

	Axis I	Axis II	Axis III	Axis IV	Total variance
Eigenvalues	0.306	0.071	0.044	0.024	1.000
Species-environment correlations	0.926	0.827	0.694	0.815	
Cumulative percentage variance					
of species data	30.6	37.7	42.1	44.5	
of species-environment relation	65.1	80.3	89.8	94.9	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.469



To further investigate how the environmental variables influence the zooplankton community patterns within the HBS, separate RDA's analyses were made by region. For HB, "sample period" was applied to remove the effects of the phytoplankton bloom linked to the season; so, when covariables are present, the arrow of an environmental variable becomes shorter, increase the relationship among this environmental variable and the covariables; and when the environmental variable is not correlated to the covariables, the arrow is unaffected, i.e. when it contributes to fully new information concerning the environment (ter Braak and Smilauer, 2002).

The pRDA model applied on the HB solely shows the relationship between the 6 selected environmental variables and the best 54 fitted zooplankton taxa (Fig. 10). The forward selection of environmental variables that significantly influenced the zooplankton distribution patterns in the bay were (in order of importance): Depth, LMS, Strat, LMT, UMT, and Fluorescence Fluo-100 (Table 6a). Together these environmental variables explained 46% of the total zooplankton variability in the HB, and allowed to distinguish three regions inside the bay (West, Central, and East side) with different environmental gradients and particular zooplankton assemblages (Fig. 10).

Depth was the stronger contributor explaining 16% of the overall zooplankton variability, and it grouped the deepest stations located at the center of the bay (HB4 and HB3); there, *O. similis* CVIf-m, *C. finmarchicus* CIV-CV, *M. longa* CIII-CV, *O. borealis* CVIf, *Microcalanus* spp. CI-CVIf-m and larvae of *L. helicina*, were the most frequent

species including Cnidaria larvae (not shown on pRDA diagram) (Fig. 10). Strat and LMT explained 7 and 5%, respectively, of the zooplankton variability. These parameters showed the highest correlation with the stations on the eastern side of the bay (HB1 and HB2), that usually were strongly stratified with higher temperatures below the thermocline, and less saline waters above it. A clear example of this was HB1-3 which was placed at the upper extreme of the diagram since it had fresher waters at the surface due to sea ice presence at sampling date (Fig. 10). *A. longiremis* CVIf-m, *C. glacialis* CIV-V-VIf, *C. hyperboreus* CIII-IV-VIf, *C. finmarchicus* N3-N6, *M. longa* CVIf-m, *A. digitale*, *A. laurentii*, *S. elegans*, *T. compressa*, and larvae of *Oikopleura* sp. (including *O. borealis* and *O. similis* CI-CV, not shown on the diagram) were positively correlated with increasing values of Strat and LMT, occurring more on the easternmost side of the bay section.

LMS and UMT contributed with 9 and 5%, respectively, to the zooplankton variability in the bay. These variables were positively correlated to the stations located at the west side of the bay (HB5 and HB6, but also with a few located at the center, mainly HB4), where the higher surface temperatures, coldest and saltier waters below the thermocline were persistent during the surveys (Fig. 10). *A. longiremis* CI-CV, *C. glacialis* CII-CIII, *C. finmarchicus* CI-CIII, *C. hyperboreus* CI, *O. borealis* CVIm, *Pseudocalanus* spp. N3-N6 and CI-CVI, *T. libellula*, *Fritillaria* sp., and larvae of Cirripedia, Chaetognatha, Echinodermata, Euphausiacea, Mollusca, and Polychaeta were the taxa being more frequent on the west side of the bay, and showing close relationship with increasing LMS and UMT and decreasing LMT and Strat, except *T. libellula*, *Pseudocalanus* spp. N3-N6,

CI-CII, *A. longiremis* CI-CV, and *C. glacialis* CI (which were negatively correlated to Depth).

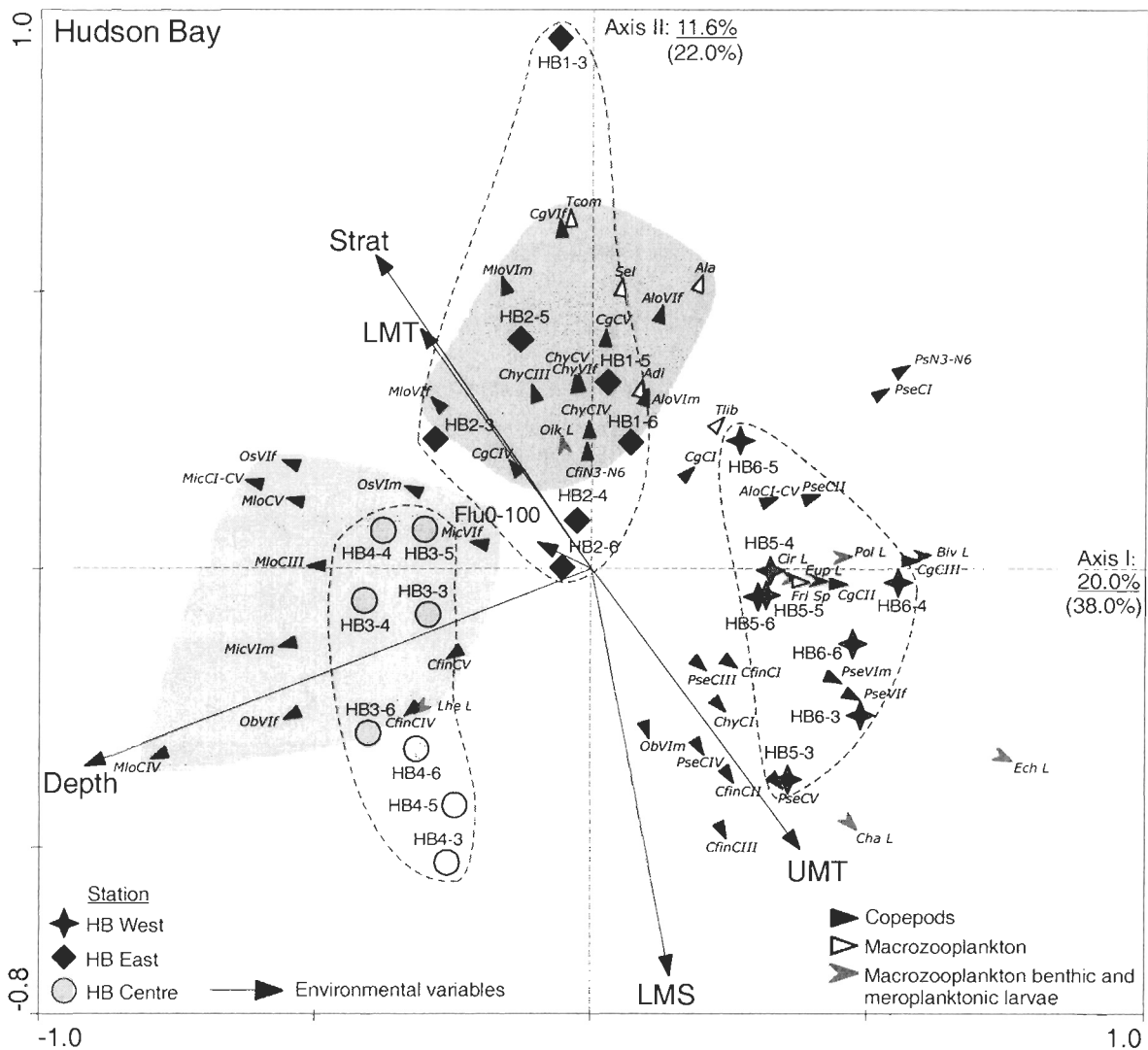


Figure 10. Partial redundancy analysis (partial RDA) ordination plot of axes I and II showing sampling stations (symbols labelled: station-year) and zooplankton taxonomic categories (coloured arrow tips) in relation to environmental variables (full black arrows) of data collected in Hudson Bay during 2003-2006. Together axes I and II explain 31.6% of the taxonomic variability (underlined) and 60.0% of the taxonomic entry-environment relationship (values in parentheses). The model explains 46.4% of the total zooplankton variability within this area. For clarity, only taxonomic categories that fit 5% or more are shown. Similar group samples are encircled (dashed line) and the taxonomic categories that occurred more on each group are shadowed. Full names of environmental variables and of taxonomic categories are listed in Table 1 and in Tables 2 and 3, respectively.

Table 6. Forward selection of environmental variables influencing the horizontal distribution of the zooplankton community in (A) the Hudson Bay (partial RDA) and the FB-HS) (RDA) during 2003-2006 (Monte Carlo permutation test in RDA with 499 unrestricted permutations,  $p < 0.05$ ). High correlations (i.e.  $r > 0.5$ ) between environmental variables and the first 2 RDA axes are in bold.

Environmental variable	F-value	p-value	Explained		Correlation		
			$\lambda$	%	Axis I	Axis II	
<b>A) Hudson Bay</b>							
Bottom depth (Depth)	4.49	0.002	0.16	16.00	<b>-0.880</b>	-0.322	
Lower mean salinity (LMS)	2.70	0.002	0.09	9.00	0.142	<b>-0.684</b>	
Stratification index (Strat)	2.04	0.008	0.07	7.00	-0.381	<b>0.517</b>	
Lower mean temperature (LMT)	1.79	0.024	0.05	5.00	-0.300	0.393	
Upper mean temperature (UMT)	1.72	0.040	0.05	5.00	0.405	<b>-0.511</b>	
Fluorescence 0-100 m (Flu0-100)	1.61	0.044	0.04	4.00	-0.118	0.055	
Total			0.46	46.00			
<b>B) FB, HS NW and HSS SE</b>							
Upper mean salinity (UMS)	5.51	0.002	0.18	18.00	<b>-0.779</b>	-0.129	
Bottom depth (Depth)	3.92	0.002	0.12	12.00	-0.227	<b>-0.859</b>	
Lower mean temperature (LMT)	2.29	0.002	0.06	6.00	<b>-0.594</b>	0.469	
Lower mean salinity (LMS)	2.11	0.014	0.05	5.00	-0.387	<b>-0.660</b>	
Upper mean temperature (UMT)	1.86	0.034	0.05	5.00	0.233	0.003	
Fluorescence 0-100 m (Flu0-100)	1.16	0.304	0.03	3.00	<b>0.525</b>	0.097	
Total			0.49	49.00			

In the third model, RDA was applied and it shows the relationship between the 6 selected environmental variables and the best 62 fitted zooplankton taxa among the FB and northwestern and southeastern HS from 2003-2006 (Fig. 11). The model explained 49.6% of all zooplankton variability. Axis I was more important explaining 23.3% of the total taxonomic variation and 47.1% of taxon-environment relationship (Table 7b). The forward selected environmental variables that significantly influenced the zooplankton distribution patterns in the northern region of the HBS were (in order of importance): UMS, Depth, LMT, LMS, UMT, and Flu0-100 (Table 6b). UMS and Depth were the strongest contributors explaining 18 and 12%, respectively, of the zooplankton variability, followed by LMT and LMS, explaining 6 and 5% respectively, of the overall zooplankton variability (Table 6b). These environmental variables separated well the outflow stations from those of the inflow shores of the strait, as well as those of the southern from the northernmost FB stations, showing occurrences of different faunal assemblages among the regions. UMT had little impact explaining 5% of the zooplankton variability, and integrated Flu0-100 had no significant impact on zooplankton distributional patterns ( $p = 0.30$ , Table 6b)

The inflow stations located on the north side of the HS and HSS transects showed slightly positive correlations with the increasing values of LMT (except HS3-3, HSS10-6, and HSS12-6), UMS, LMS, and Depth (except HS4-3) (Fig. 11). Interestingly, the HSS southeastern inflow stations (HSS7, 8, 10, 12, 13 and 14) showed a clear decrease in UMS (upper ~23 m) from 2005 to 2006 (mean = 32.6 vs 32.3, respectively) (Fig. 11). The taxa that occurred more at the HS and HSS inflow were *C. finmarchicus* CII-CVIf, *C. glacialis*

CII-CV, *C. hyperboreus* CII- IV -V -VIf, *M. longa* CI-CIII, *Pseudocalanus* spp. CIII-CV, *A. longiremis* CI-CV, *O. borealis* CVIf, *O. similis* CI-CVIm, *E. hamata*, *A. digitale*, and larvae of *Oikopleura* sp. and Polychaeta.

The stations at the HS-HSS outflow and FB south showed a more diffuse distribution than the rest on the third RDA model. Most of these stations (HS outflow and FB south) had decreasing gradients of Depth (except FB2-3 and HS2-3), LMS (except FB2-3), UMS and LMT (except HSS3-HSS5 2005-2006 and HS1-5) (Fig. 11). The taxa that occur more at these regions (mainly at the HS outflow and FB south) were *Microcalanus* spp. CVIf-m, *Pseudocalanus* spp. N3-N6, CI and CVIf-m, *O. borealis* CI-CV, *O. similis* CVIf, *C. finmarchicus* N3-N6, *C. hyperboreus* CI and CIII, *M. mixta*, *M. robusta*, *S. elegans*, *A. laurentii*, *Fritillaria* sp. and larvae of Cirripedia. Remarkably, Stns. HSS3-5 and HSS3-6 were located at the uppermost part of the RDA diagram (Fig. 11). These stations, situated at the southeastern HSS outflow, were the shallowest in the strait ( $\pm 105$  m) and featured the highest LMT ( $\pm 0.3$  °C) and lowest LMS ( $\pm 32.4$ ) compared to the other HSS stations in 2005 and 2006; there, *A. longiremis* VIm, *O. similis* CI-CV, *Fritillaria* sp, larvae of Cirripedia, Cnidaria and Echinodermata were more frequent. The other southeastern HSS outflow stations (HSS5-5 and HSS5-6) were just below the HSS3 stations in the RDA diagram, and featured similar zooplankton abundances and but different physical properties than the shallower outflow stations (HSS3): depth = 193 m; LMT =  $\pm -0.9$  °C; LMS =  $\pm 33.0$ .

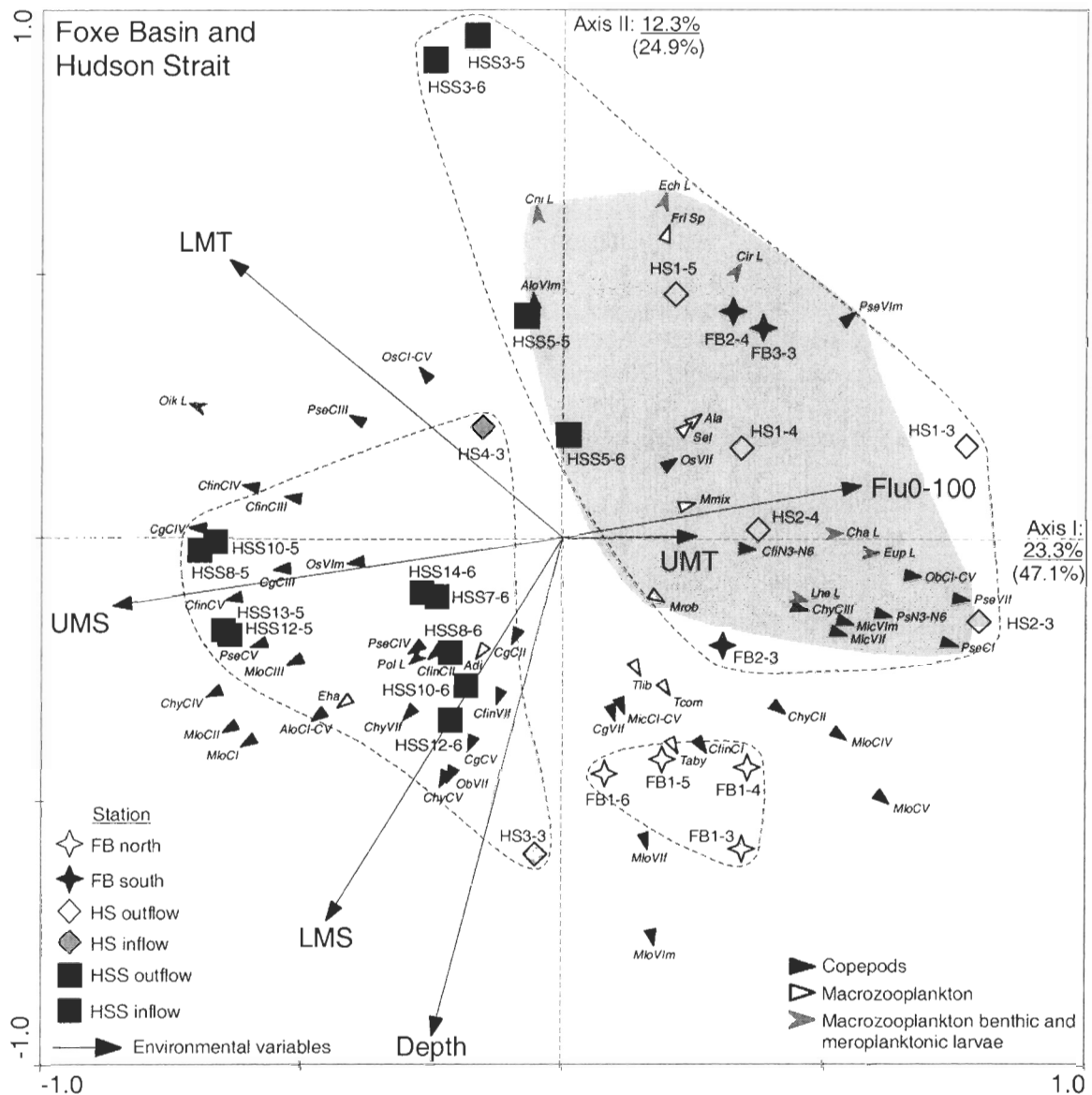


Figure 11. Redundancy analysis (RDA) ordination plot of axes I and II showing sampling stations (symbols labelled: station-year) and zooplankton taxonomic categories (coloured arrow tips) in relation to environmental variables (full black arrows) of data collected in Foxe Basin and Hudson Strait during 2003-2006. Together axes I and II explain 35.6% of the taxonomic variability (underlined) and 72% of the taxonomic entry-environment relationship (values in parentheses). The model explains almost 50% of the total zooplankton variability within this area. For clarity, only taxonomic categories that fit 5% or more are shown. Similar group samples are encircled (dashed line) and the taxonomic categories that occurred more on each group are shadowed. Full names of environmental variables and of taxonomic categories are listed in Table 1 and in Tables 2 and 3, respectively.



Table 7. Summary of partial redundancy analysis (partial RDA) of 61 zooplankton taxonomic categories with six forward environmental variables (see Table 6) and sampling month as covariable for the Hudson Bay, and of RDA of 69 zooplankton taxonomic categories with six forward selected variables (see Table 6) for the Foxe Basin – Hudson Strait during 2003-2006.

	Axis I	Axis II	Axis III	Axis IV	Total variance
<b>A) Hudson Bay</b>					
Eigenvalues	0.176	0.102	0.060	0.055	1.000
Species-environment correlations	0.962	0.911	0.917	0.841	
Cumulative percentage variance					
of species data	20.0	31.6	38.3	44.6	
of species-environment relation	38.0	60.0	72.9	84.7	
*Sum of all eigenvalues					0.882
*Sum of all canonical eigenvalues					0.464
<b>B) Foxe Basin – Hudson Strait</b>					
Eigenvalues	0.233	0.123	0.053	0.039	1.000
Species-environment correlations	0.912	0.906	0.811	0.792	
Cumulative percentage variance					
of species data	23.3	35.6	40.9	44.8	
of species-environment relation	47.1	72.0	82.6	90.6	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.495

The northernmost FB stations (named FB1 north, Fig. 11) were positively correlated to the increasing values of UMT, Depth and LMS and negatively correlated with LMT. The taxa that were more frequent at these stations were *T. abyssorum*, *T. compressa*, *T. libellula*, *C. glacialis* CVIf, *C. finmarchicus* CI, *C. hyperboreus* CII, *M. longa* CIV-CVIf-m, and *Microcalanus* spp. CI-CV. Stns. FB2-3 and HS3-3 had also similar zooplankton occurrences than the FB north stations.

### ***Interregional variability in zooplankton biomass and diversity indices.***

The interregional variability of total zooplankton biomass (see section 4.3 for description) and diversity indices ( $H'$ ,  $J'$ ,  $S$ ) from 2003-2006 are displayed in Figure 12. As occurred with biomass values (Fig. 12a), the taxa diversity indices were generally lower in the HB than in the HS, but almost equal compared to the FB (except at Stns. FB3-FB2 in 2003 and 2004, respectively). In 2003, 2004, 2005, and 2006, the values of the Shannon diversity ( $H'$ ) and the Pielou's evenness indices ( $J'$ ) varied between 1.23 and 2.01, and 0.38 and 0.64, respectively, at all stations (Fig. 12b). The  $J'$  index mirrored the  $H'$  diversity index at each one of the stations during the four years. Concerning the species richness index ( $S$ ), the values ranged from 15 to 30 taxa in 2003 in all regions, 18 to 29 in 2004, 14 to 25 in 2005, and 14 to 26 in 2006 (Fig. 12c).

The linear regressions of total zooplankton biomass ( $\log_{10}$  biomass g WM m<sup>-2</sup>) and diversity indices ( $H'$  and  $S$ ) against the environmental variables which they best correlated

within all the HBS (50 stations) from 2003 to 2006 are shown in Figure 13. Zooplankton biomass was positively correlated with bottom depth and UMS and negatively correlated with stratification index and UMT. These environmental variables explained between 31 and 68% of the zooplankton biomass variation (Fig. 13a). Likewise, the Shannon' diversity index ( $H'$ ) was correlated with the stratification index (negatively), as well as the LMT, and UMS (positively); these environmental variables explained between 24 and 33% of the  $H'$  in the HBS (Fig 12b). Finally, in regards with the species richness index ( $S$ ), like the zooplankton biomass, this variable was negatively correlated with the stratification index and the UMT and positively correlated with the bottom depth index. These environmental variables explained between 25 and 39% of the  $S$  variation (Fig. 13c).

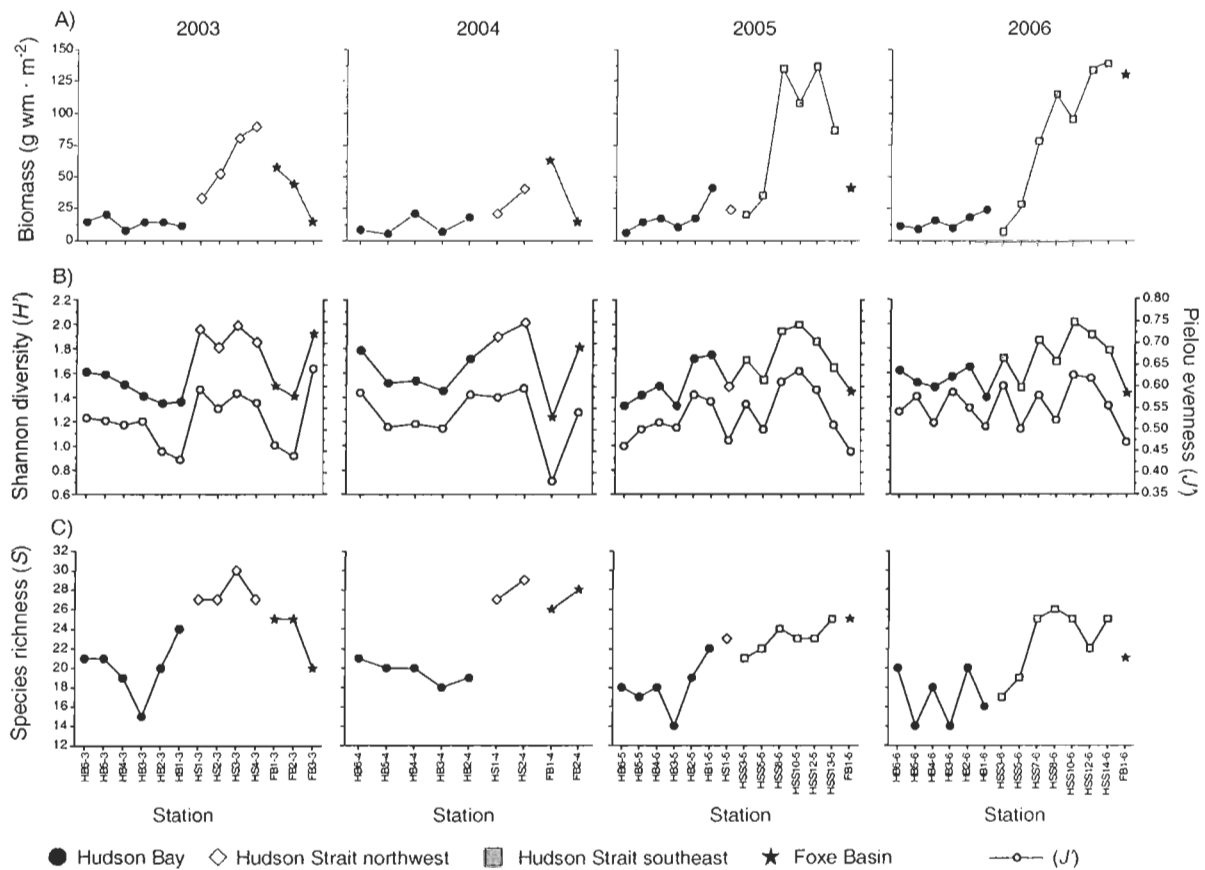


Figure 12. Variations of (A) total zooplankton biomass, and (B) Shannon's diversity index ( $H'$ ) and Pielou's evenness index ( $J'$ ) and (C) species richness ( $S$ ) of zooplankton in the HBS from 2003 to 2006. HB: Hudson Bay; HS: Hudson Strait; HS: northwestern Hudson Strait; HSS: southeastern Hudson Strait; FB: Foxe Basin. Zooplankton biomass was integrated from surface to bottom.

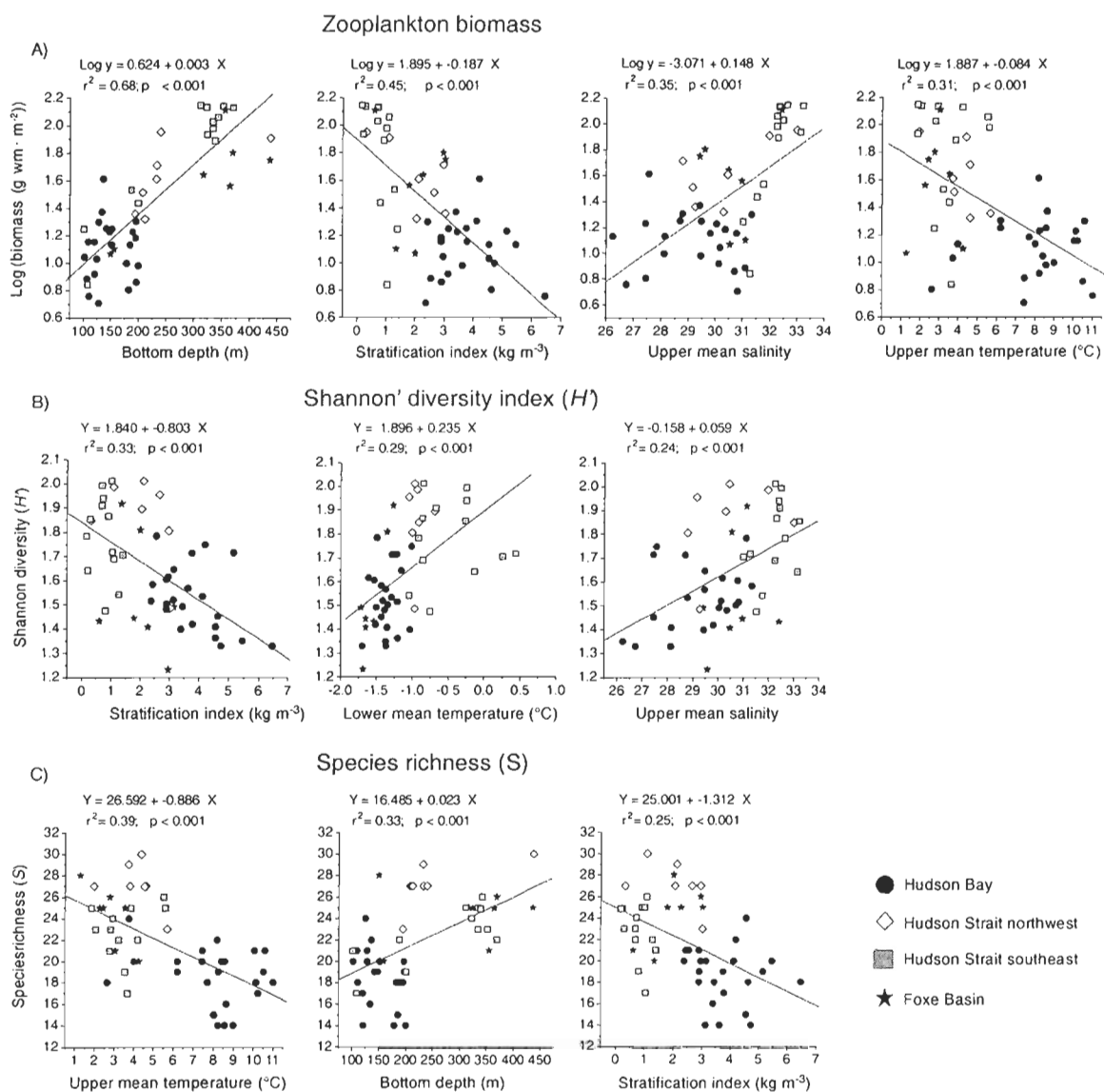


Figure 13. Relationships between (A) total zooplankton biomass and bottom depth, stratification index, upper mean salinity and upper mean temperature, (B) Shannon' diversity index ( $H'$ ) of zooplankton and stratification index, lower mean temperature and upper mean salinity and (C) species richness ( $S$ ) and upper mean temperature, bottom depth and stratification index in the HBS during 2003-2006.

## DISCUSSION

Studies on the relationships between hydrodynamics and zooplankton communities are scarce in the HBS. Up to now, studies have been made at particular locations (mostly at southeastern HB) of the HBS (cited in the introduction) and many of these focused on specific zooplankton groups and issues such as under-ice feeding, diel migrations and reproduction of copepods in relation to ice algal production cycles (Runge and Ingram, 1991; Tourangeau and Runge, 1991). There have been only two studies (Harvey et al., 1997, 2001) that have examined the phytoplankton and the zooplankton communities in relation to hydrography comparing two regions of the HBS (i.e., HB/HS). In the present study, we report for the first time the zooplankton communities in three different hydrographic regions of the HBS and their relationships with environmental variables during four consecutive years.

The statement that marine zooplankton communities tend to form assemblages with close relationships to the specific physical properties of the water masses in the ocean has been well documented in the literature by means of ordination techniques such as Canonical Correspondence Analyses (CCA) (Cotrim et al., 2006; Søreide et al., 2003) and RDA analyses (Fossheim et al., 2006; Blachowiak-Samolyk et al., 2008b; Broms et al., 2008; Gislason et al., 2009). Nevertheless, when zooplankton is analyzed on a large scale (100 – 700 km), as presented here, it is important to interpret the data with caution and within their limits. This is because a great part of the studies on temporal and spatial

variability in plankton communities have been extended over large scales, with tendencies to over-average the data, hence masking the small scale variability found in the marine environment (see: Cowen et al., 1993; Albaina and Irigoien, 2007). It has been shown that mesozooplankton small-scale variability can be shaped by a series of biological events, such as growth, life cycle, diel vertical migration (DVM), and ontogenetic seasonal migration of zooplankton (Mackas and Tsuda, 1999; Blachowiak-Samolyk et al., 2008b and previous citations). Additionally, mortality (that has usually been ignored) has recently drawn the attention of researchers who have begun to recognize the potential of predation pressure in shaping the planktonic ecosystem (Irigoien and Harris, 2006; Verity, 1998). Furthermore, estimation of macrozooplankton abundance and biomass could be underestimated since this group of zooplankters includes highly mobile organisms such as krill and amphipods, and visual avoidance of the net can occur (Dalpadado and Skjoldal, 1991; Sameoto et al., 2000; Søreide et al., 2003). In spite of all these factors, the three replicates in our 2003-2004 samplings give us good confidence about the 2005-2006 data since there was little variability in the standard deviation (SD) of the zooplankton abundance and biomass except at a few stations, probably due to patchiness.

### *Zooplankton variability*

Although increasing evidence that zooplankton interannual variability is linked to changes in the physical and atmospheric environments as it has been shown in several studies in the Atlantic (see the previous citations), there was no interannual variability of

the zooplankton abundance and species composition in late summer in the HBS between 2003 and 2006 (NMDS technique). In this context, it has been shown that while inter-regional variation in plankton abundance and species composition are readily determined from data observations, interannual variations are near the detection limit. Therefore, we conclude that it is difficult to detect changes in a snapshot survey made at the time of year of our investigation, and even more since the environmental variables (i.e. temperature, salinity and fluorescence) recorded during the four surveys, did not vary considerably from one year to another except the state of the phytoplankton bloom in HB between 2003-2004 and 2005-2006 which could be more linked to sampling dates.

#### *Taxonomic entries and environmental variables relationships*

Redundancy analysis revealed that the major tendencies of the distribution of the absolute and relative abundances of the macro- and mesozooplankton taxa at a determined station, and/or group of stations (illustrated on the descriptive graphs), were well reflected on all the RDA diagrams. In all sampled stations and years, the copepods outnumbered by far all other zooplankton taxa including macrozooplankton, meroplankton, and holoplankton (larvae and adults).

The results of the first RDA analysis explained 47% of the total zooplankton variability in the HBS, revealing a clear evidence of a well-defined spatial differentiation of zooplankton distribution within the HBS. In this initial approach, three different



hydrographic zones (HB, FB, and HS) with different zooplankton communities were identified. The relatively high eigenvalue (0.3) obtained along the first axis suggested a good separation of samples, since eigenvalues between 0.3 and 0.5 point out a good separation in the biological data, i.e. that stations have a small number of taxa in common (ter Braak and Verdónschot, 1995). Thus, the best explanatory variables along Axis I justified these statements.

### ***Hudson Bay***

The first group corresponded to the HB section placed from east to west in the northern region of the bay with six stations. There, high stratification, reflected by the low salinities and high temperatures in surface waters, was the most important environmental variable distinguishing this region from the FB and HS. The physical oceanography of the HB during late summer was well in agreement with that in the literature at the same periods: strong stratification preventing vertical exchange between surface and deep waters (Prinsenber, 1977), high surface temperatures ( $\sim 12^{\circ}\text{C}$ , primarily due to summer heating and river input) and cold deep waters ( $\sim -1.7^{\circ}\text{C}$ ) (Roff and Legendre, 1986), as well as low salinity in surface waters (25-30) (Prinsenber, 1986a).

The zooplankton taxa that occurred more regularly in the waters of the HB section (from east to west) than any of the other sampled regions were the small copepods (*Microcalanus* spp. CI-CVI, *Oithona similis* CI-CVI, *Oncaea borealis* CI-CVI, and

*Pseudocalanus* spp. CVI) along with Cnidaria and Chaetognatha larvae, Appendicularia and Pteropoda. The presence of these taxa in HB is likely due to a good adaptation to the late summer oligotrophic and stratified water condition in HB (Ferland et al., in prep.). Confirming our mesozooplankton low biomass values obtained in the HB, these small copepod genera dominating the bay are well known to contribute weakly to the bulk copepod biomass, but may play an important role on pelagic secondary production as observed in Disko Bay (Western Greenland) (Thor et al., 2005). In Arctic regions (77° N), *Microcalanus* spp., *O. similis* and *O. borealis* are believed to reproduce continuously throughout the year, and to be opportunistic omnivores that feed on a variety of food sources (ex. marine snow, fecal pellets, detritus particles) commonly linked with the microbial food web (Pedersen et al., 2005; Ringuette et al., 2002). In the Arctic's Canada Basin, these small species are thought to remain active and continue with albeit reduced, growth and recruitment outside the summer phase (Hopcroft et al., 2005). Moreover, *Oithona* and *Oncaea* have also been reported to be quite successful in oligotrophic environments such as the eastern Mediterranean Sea (Siokou-Frangou et al., 1997).

*Microcalanus* spp. is likely to be Arctic in origin (Head et al., 2003), the occurrence of this genera in the HB could also be due to the incidence of cold bottom waters there, since these species seem to be in suitable conditions in colder and deeper environments as occurs in the Greenland/ Iceland Sea (Kwasniewski, 1994) and fjords of the Svalbard region (Walkusz et al., 2003). Buchanan and Sekerak (1982) suggested that *Microcalanus* spp. prefers deep waters (>250 m) during summer/fall months in the western Baffin Bay-

eastern Lancaster Sound areas. Furthermore, Kielhorn (1952) observed that *Microcalanus* undergoes a seasonal migration to deeper water in early summer, possibly as a response to warming. This was observed during the 2005 cruise in the HBS where three different ring net were sampled at different depth (bottom - surface, lower thermocline - surface, upper thermocline – surface) and *Microcalanus* spp. was mostly sampled in the deep coldest layer on the western side of the HB (M. Harvey; unpublished data).

*Oithona similis* is perhaps the most abundant and ubiquitous copepod in the world's oceans, but information on its seasonal depth distribution, feeding habits and life-cycle strategy is scarce (Gislason, 2003; and previous citations). *Oithona* spp. is widely distributed throughout the Atlantic Ocean and their occurrences reach as far as the Arctic Ocean (see review in Head et al., 2003). *Oithona* has also been described as a eurythermal, euryhaline species, and hence adapted to a wide range of habitats (Fransz and Gonzalez, 1995). In the central Baltic Sea (where a permanent halocline restricts the water exchange between the bottom water and the surface layer), *O. similis* have been observed to concentrate centrally in the permanent halocline (Hansen et al., 2004). More recently, all developmental stages of this species were found in high numbers throughout the year below the halocline in the same area (Schulz and Hirche, 2007). These findings coincide with our results on *O. similis* inhabiting the northern HB region, which in the summer/fall period displayed similar physical patterns than the central Baltic Sea (i.e. marked stratification, euryhaline conditions). According to the data on the vertical distribution of the zooplankton obtained in 2005 (M. Harvey; unpublished data), the adults *O. similis* (CVI) were

principally sampled in the surface layer (above the halocline/thermocline) on the west side of the HB whereas the copepodites (CI-CV) were sampled within the halocline/thermocline on the east side of the central part of the HB.

In the Greenland Sea (Richter, 1994), *Oncaea* spp. has been observed to keep high stocks in deep waters year-round with a long breeding season (more extended than *Oithona* spp.), which is not restricted to a particular season of the year, as reported for the Irminger Sea (Gislason, 2003). The occurrences of *Oncaea* spp. in deep waters was also observed by Thor et al. (2005) in Western Greenland (Aug. - Sep.) where they were found below 100 m, concluding that this genus is probably closely associated with sinking marine aggregates. The same observation was made on both sides of the HB in 2005 (M. Harvey; unpublished data). Diet is considered to be a key factor in the deeper distribution of *Oncaea* spp. (Gislason, 2003). On the matter, Alldredge (1972) revealed direct evidence that cyclopoid copepods of the genus *Oncaea* feed on abandoned larvaceans houses, which are present in the HB. The mucous feeding structures or 'houses' that Appendicularians produce are important components of marine snow (see review in Vargas et al., 2002).

Appendicularians, mainly *Fritillaria* sp., represented an important element of the mesozooplankton community in the late summer in HB, as observed by Nielsen and Hansen (1999) in the Gullmar fjord (Swede) and by Head et al. (2003) in different areas of the Labrador Sea. *Fritillaria* sp. is a cold water species tolerant to a wide range of salinities, but restricted to cool water (Ackefors, 1969). Moreover, in the Bornholm Basin *Fritillaria*

*borealis* has been observed in the upper layers in spring before the thermocline develops, then it is expelled from the surface layer in the warm period and uses the waters below the halocline as avoidance to survive unfavourable conditions (Schulz and Hirche, 2007). Thus, the oceanographic conditions in the HB during late summer seem to favour this appendicularians where they dominated numerically the non-copepod mesozooplankton component. It is interesting to point out that, if the small copepods found dominating the HB are to be associated to marine snow, as described previously, these affirmations could be seen as a possible scenario of small copepods feeding habits linked to appendicularian wastes in the stratified waters of HB, but direct observations are still needed.

The chaetognath *Sagitta elegans* tended to occur more in the HB (although it was present in the FB and HS). It was the principal constituent of the macrozooplankton community in the HBS as occurred in the Barents Sea in early summer (Falkenhaus, 1991). This is no surprise since *S. elegans* is an arctic species with a widespread distribution (Peijnenburg et al., 2005) and one of the two dominant chaetognaths in the North-East Atlantic.

*C. finmarchicus* is a true North Atlantic species that can be carried into the Arctic Ocean by Atlantic inflow east of Greenland and into Baffin Bay by the West Greenland Current (Buchanan and Sekerak, 1982). However, in our study this species was nearly absent in the bay (compared to the small copepods species) confirming that HB is not much influenced by Atlantic waters as proposed by Dunbar (1958) by examining T-S diagrams.

The fact that *C. finmarchicus* was yet found in very low abundances in northern HB is likely because the presence of this species in Arctic waters is limited by low temperatures (as those of HB deep waters) accordingly to previous observations (Hirche et al., 1997; Melle and Skjoldal, 1998). Moreover, it is believed that this Atlantic distribution species does not successfully breed in a pure arctic environment, but that is able to survive there for long periods of time (Buchanan and Sekerak, 1982). We conclude that this *Calanoid* is probably advected into HB waters in very low numbers to succeed, since it is known that expatriated populations of zooplankton can be depleted from a region, at least that new individuals can be supplied in great quantity by advection (Pedersen et al., 1995).

On the other hand, even if there was a very low abundance of *C. finmarchicus* into the HB in comparison with the two other regions (FB, HS), this group of organism played an important role in the second pRDA model which allow to separate three different zones (east, centre and west) inside the bay, that were related to different environmental conditions in the upper and deep layers as well as by the typical summer surface currents regime and local bathymetry features. The environmental variables assessed in the HB explained 46% of the total zooplankton variability. Nevertheless, there was a strong degree of faunal similarity among samples (mainly between the transition zones between west-center and center-east), accordingly to the low eigenvalues obtained ( $< 0.18$ ) along axis I.

The zooplankton taxa that distinguish the eastern HB area from the center and the western part of the HB were: *C. glacialis* CIV-CVI, *C. hyperboreus* CIII-CVI, *C.*

*finmarchicus* N3-N6, *M. longa* CVI, *A. longiremis* CVI, the hyperiid amphipod (*T. compressa*), the cnidarians (*A. digitale* and *A. laurentii*), appendicularia larvae (*Oikopleura* sp.), and the chaetognath (*S. elegans*). This list also includes *O. borealis* and *O. similis* CI-CV, which were not shown on the RDA diagram. The presence of these Arctic and Atlantic taxa, is in agreement with those previously reported for the eastern side of the HB (Rochet and Grainger, 1988; Harvey et al., 2001). Rochet and Grainger (1988) were able to determine their station groups according to the properties of surface layers, concluding that surface salinity and temperature data may be a good indicator of the composition and quantity of zooplankton in eastern HB. Likewise, *S. elegans* is sometimes referred to as 'distant neritic' since it normally has denser populations in nearshore areas (Tokioaka, 1979), along with *Oikopleura* sp. who is also typical of inshore and coastal waters (Acuña and Kiefer, 2000), but restricted to summer in accordance with its zoogeographic distribution (Schulz and Hirche, 2007). This could confirm the tendencies of these taxa to occur more near HB eastern shore. Runge and Ingram (1991) reported *C. glacialis* as one of the dominant components in the copepod biomass in spring under the ice in a coastal area of southeastern HB. In contrast to *C. finmarchicus*, *C. glacialis* is able to reproduce in waters close to freezing point, and to fuel reproduction by feeding on ice algae.

The center of the HB, which is the deepest region of the transect (~ 190 m), recorded the lowest number of taxa in comparison to the other two regions (West-East). The more frequent zooplankton taxa that were were: *C. finmarchicus* CIV-CV, *M. longa* CIII-CV, *Microcalanus* spp. CI-CVI, *O. similis* CVI, *O. borealis* CVI, and Pteropoda

larvae and adult (*L. helicina*). Roff and Legendre (1986) also found that the central waters of HB were very low in zooplankton populations with apparently very low secondary productivity. The presence of *C. finmarchicus* CIV-CV in the deep central waters of HB could be due to dormancy behaviour since this species has been observed to enter in diapause mainly as copepodite CV during mid-summer in the Faroe shelf (Debes and Eliassen, 2006). *M. longa* is known for inhabiting deep waters of Norwegian fjords (Balino and Aksens, 1993), and together with *Microcalanus* spp., were observed to attain high abundances in the deepest stations sampled in the Barents Sea by Blachowiak-Samolyk et al. (2008b). The one-year life cycle holoplanktonic pteropod *L. helicina* is the only pteropod found in the Arctic; with the largest known sizes in North-Atlantic waters (Gannefors et al., 2005). The presence of *L. helicina* larvae and some adults in the bay during late summer is well in agreement with Gannefors et al. (2005) observations showing that the reproduction peak of this species occurs in August in the waters of a Svalbard fjord.

The western portion of the HB, comprised the shallower stations in the bay transect (~ 116 m) where the highest surface temperatures (~ 9.2 °C), lowest temperatures and high salinities below thermocline (-1.5 °C and 32.3, respectively) were observed. The zooplankton taxa that allow to separate the western HB area from the center and the eastern part the bay were *C. finmarchicus* CI-CIII, *C. glacialis* CII-CIII, *C. hyperboreus* CI, *Pseudocalanus* spp. N3-N6 and CI-CVI, *A. longiremis* CI-CV, *O. borealis* CVI, hyperiid amphipod (*T. libellula*), Appendicularia (*Fritillaria* sp.), and several larvae taxa (Cirripedia, Chaetognatha, Echinodermata, Euphausiacea, Bivalvia, and Polychaeta). The



occurrences of Arctic and Atlantic young *Calanoid* species observed in the western portion of the HB (*C. glacialis* CII-CIII, *C. hyperboreus* CI and *C. finmarchicus* CI-CIII, respectively) is well confirmed by the cold Arctic waters entering HB via west of Southampton Island (northwestern HB) and Atlantic water entering the Bay through the middle and northern channels that communicate it to HS (Prinsenbergh, 1986a).

Interestingly all *Pseudocalanus* spp. nauplii, copepodite and adults occurred mostly in western HB. This species was reported as the dominant copepod in the outer Chesterfield Inlet (northwest HB) averaging 30 000 ind. m<sup>-2</sup> during August and September (Roff and Legendre, 1986). Hence, its occurrence in western HB stations could be associated to the circulation pattern and environmental conditions. The genus *Pseudocalanus* is considered to inhabit inshore waters and to be found mostly in upper waters layers (Buchanan and Sekerak, 1982; Roff and Legendre, 1986; Blachowiak-Samolyk et al., 2006a), and the same observation was made on the western sides of the HB in 2005 (M. Harvey; unpublished data).

A special remark between the summer surface circulation pattern and the distribution of the developmental stages of some meso- and macrozooplankton can be pointed out from the pRDA analysis in the HB. That is, if we compare the dominance of some copepodite and macrozooplankton benthic and meroplanktonic larvae from the west side of the bay, encircling the bay along the southern coasts, to finally reach the eastern regions on the way beyond southern HS coasts. For example, *C. glacialis* CII-CIII and *C.*

*hyperboreus* CI and Chaetognatha larvae (with juvenile Cnidaria and Pteropoda in the center of HB) were more frequent on the west side of the bay, and at the same time these taxa were found to dominate in the east at advanced developmental stages: *C. glacialis* CIV-CVI, *C. hyperboreus* CIII-CVI, and adult of *S. elegans*, *A. digitale* and *A. laurentii*. These observations could be attributed not only to the differences in peak and ontogenic timing typical of each species, in the case of copepods, but also to the effect of the physical and biological environment that each region display. For example, copepod stage durations vary with temperature (McLaren, 1978) and food availability, being longer and more variable when these two parameters are low (see Gentleman et al., 2008). Also development may be arrested in diapause without food abundance, so that stage durations can be longer than predicted (Runge et al., 1985). In the case of chaetognaths, food levels and temperatures are major factors influencing the growth of *S. elegans* according to Zo (1973) who found these species to pass from egg to full mature adults (after water temperature increases and food become abundant following spring zooplankton bloom in April) in 3 months from June to August in the Bedford Basin. The HB transect is ~700 km wide and different zooplankton cohorts may be present over this large area.

### ***Hudson Strait and Foxe Basin***

The first RDA analysis corresponded to a combination of two noticeable groups: 1) southeastern HSS and some southernmost FB and northwestern HS stations, and 2) a mixture of the northernmost FB and some northwestern HS stations. These similarities in

physical and faunal composition were probably due to the direction of the local surface currents that may be acting in carrying different zooplankton taxa from one area to the other. These regions were characterized by lower stratification (with exceptions), increasing gradients of depth, mean temperature and salinity below thermocline and, in lesser extent, fluorescence. The taxa that occurred more in the first group (but mainly at southeastern HSS) were different copepodite and adult stages of *Pseudocalanus* spp., *C. glacialis*, *C. finmarchicus*, *C. hyperboreus*, *A. longiremis*, *M. longa*, plus *E. hamata*, larvae of Echinodermata, Mollusca, Cirripedia, Appendicularia, and Polychaeta; in the second group: copepodite and adults of *M. longa*, *C. hyperboreus*, *Pseudocalanus* spp., the hyperiid amphipods *T. abyssorum*, *T. compressa*, *T. libellula*, the mysid *Meterythrops robusta* and larvae of *L. helicina*. However, a more clear distinction of the zooplankton assemblages within the FB and HS regions (as well as for the HB) was best represented when we applied a separated RDA analysis on these areas.

The third RDA model applied on the FB and northwest HS and southeastern HSS explained 49.6% of all zooplankton variability with a moderate degree (compared to the pRDA model in HB) of faunal similarity among samples accordingly to the relatively low eigenvalues ( $< 0.24$ ) along axis I, where the environmental gradients were more pronounced. The recorded environmental variables allowed a good distinction of the outflow stations from those of the inflow in both HS transects, as well as those of the southern from the northernmost FB stations. The general patterns of the physical oceanography of these regions found in our study are in agreement of those described in

past (Drinkwater, 1986; Prinsenberg, 1986c) and recent literature (Straneo and Saucier, 2008). The majority of the inflow stations in the strait were characterized by increasing LMT, UMS, LMS, and Depth at different degrees. The UMS and Depth were the most important variables explaining the variability of zooplankton within these regions. A clear evidence on faunal composition between the northern (inflow) and southern (outflow) in the strait was revealed on this analysis. The zooplankton taxa occurring the most in the inflow of the strait were *C. finmarchicus* CII-CVI, *C. glacialis* CII-CV, *C. hyperboreus* CII-CIV-CV-CVI, *M. longa* CI-CIII, *Pseudocalanus* spp. CIII-CV, *A. longiremis* CI-CV, *O. borealis* CVI, *O. similis* CI-CVI, *E. hamata*, *A. digitale*, and larvae of *Oikopleura* sp. and Polychaeta.

The presence of *C. finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Pseudocalanus* spp., *M. longa*, *E. hamata* and *A. digitale* in the inflow waters of the strait during our sampling dates is in agreement with Huntley et al. (1983). These authors studied the seasonal dynamics of zooplankton communities on the western side of Davis Strait and the Labrador Sea, and found these species to reach the mouth of the strait by August-September following the ice retreat which in turn, is followed by the “biological spring” (which is the time of the year where the annual phytoplankton increase brings the subsequent increase in zooplankton abundance) occurring in September and October in HS. The western Davis Strait sector features the Baffin Current which flows southward from Baffin Bay along the western side of the strait (Huntley et al., 1983). These currents reach the entrance of HS entering to the HBS as Arctic-North Atlantic modified inflow waters as far as the mid-HS

waters, but in the present, there is no clear estimation of how far this inflow penetrates into the HBS (Straneo and Saucier, 2008). Thus, the general pattern of these currents displays well the distribution of these Arctic and Atlantic species in the HS inflow waters as observed by Huntley et al. (1983).

Salinity is a marker which indicates the arrival of different water masses containing different populations (Raybaud et al., 2008). Interestingly, the slight interannual variability in the UMS (upper ~ 19 m) from 2005 (~ 32.6) to 2006 (~ 32.3) in the HSS southeastern inflow displayed in the third RDA, was also reflected in the *C. finmarchicus* copepodite abundances CIII-CV. They were generally higher in 2005 than in 2006 when apparently there was a strong inflow of Atlantic waters according to the relatively higher salinities in the surface water masses. It has been already observed that increased inflow of North Atlantic water into the Barents Sea during spring and summer is accompanied by 50-fold increase in *C. finmarchicus* in the near surface waters (Skjoldal et al., 1992). On the other hand, Fleminger and Hulsemann (1977) concluded that the North Atlantic species *C. finmarchicus* penetrated deeply into HS but that apparently it was not able to reproduce successfully there. *C. finmarchicus* can be used as a tracer of Atlantic water masses (Blachowiak-Samolyk et al., 2006a) and can co-occur with Arctic species (such as *C. glacialis* and *C. hyperboreus*) in areas of water mass convergence (Tande, 1991). Hence, the presence of this species, along with *C. glacialis* and *C. hyperboreus* (in lesser proportions) in the northwestern HS inflow stations (HS3-HS4) located ~ 288 km from southeastern HSS inflow stations is a clear signal that North Atlantic inflow waters,

combined with the Arctic current from Davis Strait, could penetrate farther than the mid-strait area, reinforcing Fleminger and Hulsemann's statements (1977).

The higher mesozooplankton biomass values found in the northwestern HS and southeastern HSS inflow stations could be attributed to the presence of the three species of *Calanus* (*C. finmarchicus*, *C. hyperboreus* and *C. glacialis*) in these areas. Together, these species dominated the biomass (expressed in mg dry weight  $m^{-2}$ ) of the mesozooplankton community in the Labrador Sea accounting for  $\geq 70\%$  during spring and early summer (Head et al., 2003), with *C. finmarchicus* comprising  $>60\%$  of the total biomass in the central part.

Contrary to the inflow stations, the HS-HSS outflow, along with the southern FB stations were sparsely distributed in the RDA diagram. These sites shared oceanographic features at different levels, but mostly higher UMT, UMS, LMS, Depth and LMT differing clearly from the inflow features. Even though, the physical and biological oceanography of these stations fitted well with the surface circulation patterns that characterize this area.

Remarkably, the northwestern HS outflow Stns. HS1 and HS2 (2003-2004) had generally higher values of chlorophyll *a*, zooplankton biomass and species diversity than the stations located farther southeast (~ 210 km) in the outflow current of the strait (Stns. HSS3 and HSS5, except HS1) during 2005-2006. The disparities in terms of chlorophyll *a* could be attributed to different sampling times since the 2003-2004 sampling differed of

about ~26 days from those of 2005-2006 in the outflow stations. Furthermore, Straneo and Saucier (2008) showed evidence of a net downwelling occurring at the coast of Quebec (southern HSS shore) that is consistent with the predominantly along-strait winds during early September; this is clearly reflected in the south-ward cross channel flow in the eastern half of the strait, that joins the outflowing current in the coast of Quebec (Drinkwater, 1986) (see Fig. 2 of the general introduction). We suggest that the latter along with the particular oceanographic features of the outflow (e.g. freshwater transport, high stratification, high velocities and strong tides; (Straneo and Saucier, 2008)), could be affected in turn by both relatively low primary and secondary production observed in this area.

The zooplankton taxa dominating mainly at the southern FB and northwestern HS outflow stations were *Microcalanus* spp. CVI, *Pseudocalanus* spp. N3-N6, CI and CVI, *O. borealis* CI-CV, *O. similis* CVI, *C. finmarchicus* N3-N6, *C. hyperboreus* CI and CIII, *M. mixta*, *M. robusta*, *S. elegans*, *A. laurentii*, *Fritillaria* sp. and larvae of Cirripedia and Echinodermata. The presence of these taxa in this area is in agreement with previous studies made in the zone by Grainger (1962) and more recent by Harvey et al. (2001). In agreement with Grainger (1962), we believe that the zooplankton fauna within this region is a mixture of surface Arctic waters coming from Fury and Hecla Strait (northern FB), eastern HB northward current entering southern HS waters, and in lesser degree, Arctic and subarctic fauna from HS inflow entering into FB (but confined to south FB) via Foxe Channel. The occurrence of *C. finmarchicus* in this area had been already noticed by

Grainger (1962) suggesting that it appeared to be the best indicator of subarctic and boreal waters.

In all years sampled, water mass properties at the northernmost FB stations (FB1), which also were the deepest ones (~381 m) (high UMT, Depth and LMS and low UMS and LMT) were in agreement with those in the literature. The salinity and temperature profiles in these stations confirmed the production of dense and cold waters at depth, probably associated with brine rejection during winter season which is in accordance with Prinsenbergh (1986c) and Jones and Anderson (1994). The species that occurred the most there (but also at Stns. FB2-3 and HS3-3) were the hyperiid amphipods *T. abyssorum*, *T. compressa*, *T. libellula*, and the copepods *C. glacialis* CVI, *C. finmarchicus* CI, *C. hyperboreus* CII, *M. longa* CIV-CVI, and *Microcalanus* spp. CI-CV. The presence of these species (except *T. compressa*) in this zone had already been observed by Grainger (1962) who carried out one of the earliest investigations in the FB during summertime covering a great portion of the basin, mostly the western portion, from north to south. For example, the occurrence of *M. longa* adult stages CVI in this area was also witnessed by Grainger (1962) in great numbers in southwest FB and most abundantly in Foxe Channel.

The presence of the three amphipods in this area agrees well with their geographic distributions and seasonal occurrences. For example, *T. compressa* and *T. abyssorum* are regarded as subarctic species, whereas *T. libellula* is considered as a good indicator of the presence of Arctic waters (Dunbar, 1964). In the Barents Sea, *T. abyssorum* and *T. libellula*



abundances were observed to peak in summer and early autumn, with their high abundances associated with Polar Front Waters (Dalpadado et al., 2001). Of the three *Themisto* spp., *T. compressa* was the rarest and least abundant amphipod in our study, which is in agreement with Dalpadado et al. (2001) who also reported this species as rare and restricted to Atlantic waters in the Barents Sea.

### ***Zooplankton diversity and environmental variables relationships***

The generally lower diversity indices found in HB compared to FB and HS can be attributed to the elevated numerical dominance of small copepods among the recorded taxa in the bay, primarily, *O. similis*. High numerical dominance of such small species tends to lower the diversity indices due to their high dominances, as observed in the Barents Sea during spring (Blachowiak-Samolyk et al., 2008b).

The diversity of zooplankton species is not great at high latitudes (Conover and Huntley, 1991). Moreover, it is well known that salinity gradients and freshwater discharge in estuarine systems are key factors controlling species richness overall (Witman et al., 2008). On this matter, the HBS seems to be no exception accordingly to our results and to the particular characteristics of this system: a large riverine input ( $\sim 900 \text{ km}^3 \text{ yr}^{-1}$ ) (Déry et al., 2005) combined with the inflow of Arctic (via Fury and Hecla Strait and HS) and North Atlantic waters (via HS) which make it an unusually fresh, large-scale arctic/sub-arctic estuarine system to completely freeze over in the winter and be ice-free in the late summer

(Straneo and Saucier, 2008). The decreasing gradient of diversity indices observed from the mid-strait inflow waters to the southernmost FB stations area reflected the presence of a more diverse mixed arctic-boreal fauna entering the HBS throughout HS that combine with less diverse arctic fauna entering Fury and Hecla Strait, passing thorough HB to finally join the outflow current in the southern coast of the strait.

The analysis of relationships between zooplankton biomass, diversity indices and environmental variables allowed us to identify the samples along the physical gradients that had more influence in the biological parameters within all the HBS sampled stations. In this case strong linear positive and negative relationships were registered, for example, the shallower, high stratified, lower surface salinities and higher surface temperatures stations corresponded to generally lower zooplankton biomasses, where the HB was mainly representing these features. The diversity index ( $H'$ ) was higher where sea surface waters were less stratified, warmer and saltier (mostly the HS and FB northernmost stations). Finally, the species richness index ( $S$ ) was higher when higher surface salinities, deeper strata and less stratification were present.

However, this generalized view of species diversity in the HBS and its relationships with the local environment must be taken carefully since there are some important aspects which could enhance or alter these indices. For example, Margalef (1967) found that diversity very often enhances through a seasonal succession, sometimes decreasing again toward the ending stage of succession. Our sampling was restricted to areas deeper than

100 m, thus ignoring the true coastal zones where fresh or brackish water zooplankton (e.g. *Acartia* and *Centropages* sp.; Harvey et al., 2001) can be flushed out of lakes and rivers during spring, and can be temporarily observed in the salt waters near the coasts (Roff and Legendre, 1986). Also, the species of the meroplankton (larval and adult) constitute temporary components of the plankton for the pelagic stages of their life and are linked to the more permanent habitats of the benthic phases of their lifecycle (Lindley and Batten, 2002). Additionally, the increase in species richness could be attributed to increase inflow, which can add species that are not permanent components of area region (ex. *C. finmarchicus*) but immigrants from surrounding waters with different physical characteristics (Lindley and Batten, 2002).

## CONCLUSION

We conclude from our study that the descriptive (graphics) and multivariate (NMDS and RDA) ordination methods, along with the linear relationships between physical and biological data, allowed identifying clearly three different regions into the HBS, with distinct zones inside every area (i.e., HB: west, center, east; FB: north and south; HS: inflow and outflow), displaying particular environmental variables and zooplankton communities. The differences observed between the HBS regions are characterized by different zooplankton assemblages and this could be not only because the local environmental conditions seem to be suitable for their survival, but also because of the local circulation patterns that must play a key role carrying and spreading the zooplankters, as occur in the St. Lawrence marine system (Descroix et al., 2005). Moreover, apart from environmental variables (i.e. temperature, salinity, depth) and current patterns, there are other important factors that could contribute to structuring zooplankton communities in marine ecosystems, such as competition for food, food preferences and a wide-spread interaction between species, particularly omnivores, called intraguild predation (IGP), defined as competitors that eat each other (Polis et al., 1987). In the context of climate change, recent modeling data suggest that the HB region will face significant environmental challenges in the near future with drastic scenarios, such as a longer ice-free season due to an earlier ice break-up and a later freeze-up date (Gagnon and Gough, 2005), with peaks in temperature and precipitations over surface waters. Therefore, it remains uncertain how the planktonic organisms will respond to the physical-chemical and

biological characteristics of a given water mass in such an expected scenario, since the habitat of the plankton is the water mass, which is dynamic (Lindley and Batten, 2002).

In the present study, the stratification index had the greatest influence in separating and distinguishing the hydrographic regions within the HBS. If a longer ice-free season along with an increase in precipitations and freshwater runoff is expected in arctic-subarctic regions (Gough et Wolfe, 2001; Gagnon and Gough, 2005), the duration of the stratification in the HB could be enhanced suppressing even more the essential nutrients for primary producers and influencing zooplankton composition and adaptations strategies to a warmer and more oligotrophic marine environment (excluding the pure coastal zones). This sort of scenarios have already been documented recently in the Bering Sea between August 1999 and August 2004, where the summer zooplankton community shifted from large (*Sagitta elegans*) to small (*Pseudocalanus spp*, *O. similis*) species accompanied by a 3-fold increase in water-column stability in 2004 relative to 1999 (Coyle et al., 2008). On this matter, our results in the zooplankton composition, at least, for HB suggest that these waters could be facing these events since small copepods (*Oithona*, *Oncaea*, *Microcalanus*, and in lesser degree *Pseudocalanus*) were found to dominate there during the late summer period. However, despite the events documented by Coyle et al. (2008), an early melting and a late freezing of the sea ice cover in arctic-subarctic regions, could alternatively support a longer period of primary production as proposed by Arrigo et al. (2008), thus influencing in an opposite (i.e. increase in nutrient supply for phytoplankton, proliferation of large size zooplankton) or an uncertain way the zooplankton communities in the HBS.

### 3. CONCLUSION GÉNÉRALE

Mon étude a permis pour la première fois d'identifier clairement trois différentes régions dans le SBH avec des zones distinctes à l'intérieur de chaque secteur (i.e., BH: ouest, centre, est; BF: nord et sud; DH: apport et sortie), affichant des communautés zooplanctoniques particulières, et des conditions environnementales typiques du système en été. Les variables environnementales testées (principalement celles représentant les couches d'eaux supérieures, i.e. Strat, UMS et UMT) s'avèrent être suffisamment représentatives pour révéler ces variations spatiales.

Brièvement, les taxons dans les assemblages de zooplancton qui caractérisent notamment chaque région à l'intérieur du SBH sont: pour la BH à l'ouest: *Pseudocalanus* spp. N3-N6 et CI-CVI, des larves des cirripèdes, échinodermes, bivalves, entre autres; au centre: *C. finmarchicus* CIV-CV, *M. longa* CIII-CV, *Microcalanus* spp. CI-CVI, adultes et larves de ptéropodes; à l'est: *C. glacialis* CIV-CVI, *C. hyperboreus* CIII-CVI, *A. longiremis* CVI, *Oncaea borealis* CI-CV, *Oithona similis* CI-CV, l'amphipode *T. compressa*, les cnidaires *A. digitale* et *A. laurentii*, le chaetognathe *S. elegans*; pour le BF, au nord: *Microcalanus* spp. CI-CV, *T. abyssorum*, *T. compressa*, *T. libellula*; au sud: *S. elegans*, *A. laurentii*, l'appendiculaire *Fritillaria* sp., des larves des cirripèdes et échinodermes; et pour le DH dans le courant entrant dans le SBH: *C. finmarchicus* CII-CVI, *C. glacialis* CII-CV, *C. hyperboreus* CII-CVI, *M. longa* CI-CIII, *Pseudocalanus* spp. CIII-CV, *A. digitale*, le chaetognathe *E. hamata*; dans le courant sortant du SBH: *O.*

*borealis* CI-CV, *A. longiremis* CVI, le mysidacé *M. robusta* et des larves de cnidaires, chaetognathes, euphausiacés et ptéropodes.

Aucune variabilité interannuelle dans la communauté zooplanctonique du SBH n'a été détectée, à l'exception de la présence d'une faune arctique et boréale dans le courant entrant dans le SBH en direction nord-ouest le long de la rive nord du DH. Ce courant se caractérise par une salinité de ses masses d'eau en surface plus élevée.

J'ai testé l'hypothèse selon laquelle la structure dans la communauté zooplanctonique est influencée par les conditions hydrodynamiques locales qui, à travers leurs actions sur la température, la salinité, la stratification, les conditions de mélange et la profondeur du milieu, conduisent fortement à la différenciation spatiale des communautés planctoniques. Les résultats de cette étude supportent cette hypothèse.

Je crois que les différences régionales observées dans le SBH, et le fait que les espèces de zooplancton qui dominaient dans une région donnée, pourraient ne pas être seulement attribuables aux conditions environnementales favorables à la survie de ces espèces, mais également aux patrons locaux de circulation, lesquels jouent un rôle clé dans le transport et la répartition du zooplancton.

Par conséquent, les organismes planctoniques doivent être capables de s'adapter ou non aux caractéristiques physico-chimiques et biologiques d'une masse d'eau particulière

dans laquelle ils vivent, puisque les masses d'eau sont dynamiques (Lindley et Batten, 2002). D'ailleurs, à part les variables environnementales (i.e. température, salinité, profondeur du milieu) et les patrons de courants, d'autres facteurs importants peuvent contribuer également à la structuration des communautés zooplanctoniques dans les écosystèmes marins, comme la compétition et les préférences alimentaire ainsi qu'une interaction répandue entre les espèces, particulièrement pour les omnivores, nommée la prédation intragilde (IGP) qui se définit comme étant des compétiteurs qui se mangent entre eux (Polis et al., 1987).

Des études récentes de modélisations dans le contexte des changements climatiques suggèrent que la région de la BH subira des changements environnementaux considérables dans un futur rapproché, telle qu'une prolongation de la saison libre de glace de mer causée par la fonte précoce de la couverture de glace et son gel plus tardif (Gagnon et Gough, 2005).

La présente étude démontre que l'indice de stratification avait la plus grande influence sur la séparation et la distinction des régions hydrographiques à l'intérieur du SBH. Aussi, les biomasses et les indices de diversité zooplanctoniques les plus bas se retrouvaient aux sites du SBH où la stratification était la plus marquée et où les couches de surfaces possédaient une faible salinité et une température élevée. L'augmentation anticipée de la saison libre de glace ainsi que l'augmentation des précipitations et le ruissellement d'eau douce (Gough et Wolfe, 2001) dans la BH, pourraient intensifier la



durée et l'intensité de la stratification dans cette région et diminuer d'avantage les apports des nutriments essentiels à la surface, lesquels sont nécessaires pour les producteurs primaires. Par ce fait, cela influencera la composition zooplanctonique et les stratégies d'adaptations à un environnement marin plus chaud et doux en surface et plus oligotrophique (en excluant les zones côtières pures). Ce genre de scénarios a été documenté récemment dans la mer de Béring entre le mois d'août 1999 et août 2004, où la communauté zooplanctonique estivale a changé en passant d'espèces de grande taille (*Sagitta elegans*) à des espèces de petite taille (*Pseudocalanus* spp., *O. similis*). Ce changement s'accompagnait d'une triple augmentation de la stabilité dans la colonne d'eau en 2004 en comparaison avec 1999 (Coyle et al., 2008). À ce sujet, nos résultats concernant la composition de zooplancton pour la BH suggèrent que ces eaux pourraient faire face à ce genre d'événements puisque de petits copépodes (e.g. *Oithona*, *Oncaea*, *Microcalanus*, et dans un moins grand nombre *Pseudocalanus*) ont été retrouvés en grande quantité durant la période de la fin de l'été. Par contre, malgré les évènements documentés par Coyle et al. (2008), la fonte précoce de la couverture de glace de mer et son gel tardif dans les régions arctiques pourrait alternativement favoriser une plus longue période de production primaire tel que proposé par Arrigo et al. (2008), influençant ainsi d'une façon opposée (e.g. augmentations des apports des nutriments essentiels pour le phytoplancton, prolifération zooplanctonique de grande taille), ou incertaine, les communautés zooplanctoniques dans le SBH.

Même si des espèces de grande taille (*C. hyperboreus*, *S. elegans*, *T. libellula*) provenant de l'Arctique et de moyenne taille (*C. finmarchicus*) provenant de l'Atlantique Nord ont été retrouvées dans les eaux de la BH, il est difficile d'estimer un possible changement dans l'ampleur des occurrences de ces espèces par le passé puisque le couvert de glace de mer avait déjà connu d'importantes réductions depuis les années 1990 dans la baie et dans le DH (voir Fig. 1 dans l'introduction générale). Généralement, le SBH est une région difficile d'accès pour la recherche en raison de son couvert de glace (Prinsenbergh, 1986c; Straneo et Saucier, 2008). Le manque de données lorsque la glace était plus abondante ne permet pas de confirmer s'il y a ou non un changement dans la communauté zooplanctonique dans l'une des régions du système de la baie d'Hudson tel qu'observé par Coyle et al. (2008) dans la mer de Béring.

L'importance de la glace de mer pour les communautés de copépodes dans le sud-est de la BH a déjà été soulignée par Runge et Ingram (1991) qui concluent que la croissance des algues ;à l'interface glace-eau, est une source de nutrition principale et régulière pour les copépodes pélagiques durant et immédiatement après le bloom algal glacial. Donc, il est clair que d'une façon ou d'une autre, la perte de la glace de mer pourrait avoir des effets importants sur les communautés zooplanctoniques dans le SBH.

D'un point de vue général concernant les impacts d'un changement de climat pour des écosystèmes arctiques marins et terrestres, une des utilités d'un programme de monitoring à grande échelle (comme celui présenté ici) pourrait être sagement appliqué si

on considère un des scénarios récents proposés en cette matière par Stempniewicz et al. (2007). Ces chercheurs proposent que le changement de climat influencera la circulation océanique et le régime hydrologique, ce qui amènera subséquemment a une restructuration des communautés zooplanctoniques entre les eaux froides arctiques, avec une dominance des espèces de zooplancton de grande taille (favorisant les oiseaux planctonophages (e.g., Mergule nain: *Alle alle*), et les eaux de l'Atlantique prédominées par des espèces de plus petite taille (ce qui réoriente la chaîne alimentaire vers les poissons planctonophages et vers les oiseaux piscivores (e.g., guillemots *Uria* sp.). Ainsi, dans les régions où les deux masses d'eaux rivalisent pour la dominance (e.g. la mer de Barents), les oiseaux planctonophages devraient dominer l'avifaune lors des périodes froides et diminuer lors des périodes plus chaudes, lorsque les piscivores prévalent. Cela à son tour pourrait avoir de sérieuses conséquences sur la structure et le fonctionnement de la partie terrestre des écosystèmes arctiques dû partiellement aux changements dans l'avifaune arctique marine, majoritairement le mergule nain qui promeut la prolongation du flux de nutriments (sous la forme de guano) de la mer à la terre, favorisant les communautés végétales et animales de la toundra (Stempniewicz et al., 2007).

Certains de ces changements pourraient déjà être en train de se dérouler dans le SBH. Une combinaison d'une vue d'ensemble générale de la présente étude sur le zooplancton, et les tendances dans la composition de la diète des oisillons de Guillemot de Brünnich (*Uria lomvia*) dans le nord de la BH (Gaston et al., 2003), et l'occurrence de Petit

pingouin (*Alca torda*) sur l'île de Coats dans le nord de la BH (Gaston et Woo, 2008) pourraient être de fortes preuves supportant ces hypothèses.

De part toutes ces observations réelles (mentionnées dans l'introduction générale) et ces faits, nous suggérons que les habitudes alimentaires et les occurrences des oiseaux marins et des différentes espèces de poissons liées aux changements climatiques dans le SBH mettent en évidence l'importance de renforcer les recherches concernant le zooplancton dans cette région pour une meilleure compréhension de la dynamique dans la chaîne alimentaire marine locale et leurs réponses à leur environnement, alors des modèles plus précis pourraient être développés couplant les données atmosphériques, physiques et biologiques marines afin de produire des scénarios concernant les changements climatiques et leurs impacts sur l'écologie dans l'ensemble du SBH.

Les résultats de ce travail représentent un avancé majeur dans les connaissances sur la répartition spatiale du zooplancton métazoaire des systèmes côtiers subarctiques en général et dans le système de la baie d'Hudson en particulier.

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