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Abréviations en français :

EM = Estuaire maritime

GSL = Golfe du Saint-Laurent

NOGSL = Nord - Ouest du Golfe du Saint-Laurent

SMSL = Système marin du Saint-Laurent

TD = Temps de digestion

TQI = Taux quotidien d'ingestion

Abréviations en anglais:

ANCOVA= Analysis of covariance

BPA = Biomass per amphipod

DI = Digestion index

DIR = Daily ingestion rate

DT = Digestion time

FR = Feeding rate

LSLE = Lower St. Lawrence Estuary

NPA = Number of prey per amphipod

NWGSL = Northwest Gulf of St. Lawrence

SFI = Stomach fullness index

SLMS = St. Lawrence marine system

1. INTRODUCTION GÉNÉRALE

1.1. LE MACROZOOPLANCTON

Le macrozooplancton regroupe les organismes zooplanctoniques dont la taille est supérieure à 20 mm (Parsons & Takahashi 1973, Sieburth et al. 1978, Lenz 2000). Il est subdivisé en différents groupes d'organismes dont les principaux sont les cnidaires (ex. : hydroméduses, siphonophores, scyphoméduses), les cténophores, les mollusques (ex. : ptéropodes, hétéropodes), les crustacés (ex. : euphausiacés, amphipodes hypéridés, mysidacés, décapodes) et les chaetognathes (Pierrots-Bults 1997). Selon les régions, la dominance de certains de ces groupes a souvent été observée. En effet, les euphausiacés et les amphipodes hypéridés dominent la communauté macrozooplanctonique des mers du Nord (Norvège, Groënland, Islande et la portion Ouest de la mer de Barents) (Hirche et al. 1994, Dalpadado et al. 1998). Les régions arctiques Canadiennes sont, quant à elles, caractérisées par de fortes abondances d'amphipodes hypéridés et de chaetognathes (Longhurst et al. 1984, Sameoto 1984, Hudon et al. 1993). Les euphausiacés et les organismes gélatineux sont également très présents au large de la côte Ouest de la Colombie-Britannique et les euphausiacés semblent être le principal groupe dominant (Fulton & LeBrasseur 1984, Simard & Mackas 1989, Mackas 1992, 1995, Mackas et al. 1997, Mackas 1998).

De nombreux facteurs abiotiques et biotiques ainsi que les processus écologiques font varier la composition spécifique, l'abondance et la distribution des différents groupes macrozooplanctoniques (Angel 1997). Par exemple, Dalpadado et al. (2003) ont montré que les changements de la biomasse zooplanctonique de la mer de Barents étaient liés à la pression de prédation ainsi qu'à des facteurs environnementaux comme l'advection des masses d'eau. Selon Søreide et al. (2003), les masses d'eau déterminent également largement la composition macrozooplanctonique dans la mer de Barents, tout comme les saisons, l'aire géographique (latitude et longitude) et la profondeur. La distribution du macrozooplancton dans les mers nordiques et plus spécifiquement des euphausiacés et des amphipodes, semble également varier en fonction de la distribution des masses d'eau mais aussi en fonction des espèces prédatrices (Dalpadado et al. 1998). Ces dernières apparaissent donc être un facteur déterminant dans la composition spécifique, l'abondance et la distribution des espèces macrozooplanctoniques dans les écosystèmes marins.

1.2. LE MACROZOOPLANCTON DANS LE GOLFE DU SAINT-LAURENT

a) Généralités

Dans l'estuaire maritime et le golfe du Saint-Laurent, le macrozooplancton est très abondant puisqu'il représente environ 10 à 20% de la biomasse totale zooplanctonique observée dans cette région (123 kg km^{-2} de masse humide selon Harvey et al. (2002)). Malgré son abondance, le macrozooplancton du Saint-Laurent a très peu été étudié. Quelques listes taxonomiques rudimentaires sont disponibles (Runge & Simard 1990, de Lafontaine et al. 1989, Brunel et al. 1998) et quelques études ont été faites sur de riches agrégations de krill observées dans la partie nord du GSL (par ex. Berkes 1976, Sameoto 1976, Berkes 1977) et à la tête du chenal Laurentien (par ex. Simard et al. 1986, Simard & Lavoie 1999, Lavoie et al. 2000, Cotté & Simard 2005). Une étude sur la distribution et sur les variations interannuelles de l'abondance des principaux groupes macrozooplanctoniques (amphipodes hypéridés, chaetognathes, mysidacés, cténophores et cnidaires) dans l'estuaire maritime (EM) et le nord-ouest du golfe du Saint-Laurent (NOGSL) a récemment été effectuée par Descroix et al. (2005). Cette étude a montré que le mysidacé *Boreomysis arctica* représente l'espèce dominante dans chacune des deux régions et que son abondance varie peu entre les saisons et les années. La faible variabilité de cette espèce dans l'EM et le NOGSL, s'expliquerait par le fait qu'elle vit en permanence dans la couche profonde qui représente un environnement stable en terme de schéma de circulation, de température et de salinité (Descroix et al. 2005). Par contre, si on regarde les autres groupes macrozooplanctoniques, il semble que l'EM et le NOGSL soient caractérisés par deux groupes faunistiques distincts. Deux espèces d'euphausiacés (*Meganyctiphanes norvegica* et *Thysanoessa raschii*) semblent caractériser la communauté macrozooplanctonique de l'EM. Leurs abondances dans cette région sont respectivement 6 et 15 fois plus élevées que dans le NOGSL. D'un autre côté, la communauté macrozooplanctonique du NOGSL semble être dominée par les chaetognathes, les amphipodes hypéridés et les siphonophores. Ces groupes apparaissent deux fois plus abondants dans le NOGSL que dans l'EM. De telles variations inter-régionales semblent être liées aux différents schémas de circulation et aux différents réseaux trophiques trouvés dans les deux régions. La circulation estuarienne et l'arrivée tardive de la floraison phytoplanctonique printanière de l'EM favoriseraient l'accumulation d'espèces herbivores ou omnivores comme les euphausiacés alors que la circulation de la gyre d'Anticosti et la forte floraison phytoplanctonique observée au début du printemps permettant l'apparition de gros copépodes caractérisant le NOGSL, favoriseraient l'accumulation des espèces carnivores comme les chaetognathes, les amphipodes hypéridés et les siphonophores (Descroix 2004). De plus, d'importantes variations interannuelles de l'abondance des espèces macrozooplanctoniques, excepté pour les mysidacés, ont été observées entre 1998 et 2001 dans l'EM et le NOGSL. Dans le NOGSL, les espèces arctiques comme *Thysanoessa raschii*, *Themisto libellula* et *Aglantha digitale*, l'espèce boréo-arctique *Themisto abyssorum* et l'espèce *Sagitta elegans* ont été plus abondantes en 1998 qu'en 2000 et 2001. Par contre dans l'EM, elles semblent avoir été moins abondantes en 1998 qu'en 2000 et 2001 (Descroix et al. 2005). Cette variabilité semble coïncider avec la variabilité interannuelle des paramètres physiques, particulièrement des propriétés thermiques de la couche intermédiaire d'eau froide, surtout dans le NOGSL (Descroix 2004). Descroix et al. (2005) ont suggéré que l'augmentation de l'advection d'organismes macrozooplanctoniques dans l'EM, pourrait être liée aux fortes entrées d'eau froide, provenant du courant du Labrador *via* le détroit de Belle Isle dans le golfe du Saint-Laurent.

b) Invasion de l'amphipode hypéridé *Themisto libellula* dans le golfe du Saint-Laurent

Depuis le début des années 1990, la composition spécifique du macrozooplancton dans l'EM et le NOGSL a subi d'importantes modifications. L'apparition dans le golfe du Saint-Laurent (GSL) de l'amphipode hypéridé d'origine arctique *Themisto libellula* fait partie de celles-ci (Harvey et al. 2005). En effet, une recherche bibliographique remontant au début des années 1900 ainsi que l'analyse d'échantillons de zooplancton récoltés pendant les années 1980 dans différentes régions du GSL et dans l'EM, ont conduit à la conclusion que *T. libellula* était absent des eaux du système marin du Saint-Laurent avant les années 1990 (M. Harvey, données non publiées), excepté pour un certain nombre de juvéniles qui a été occasionnellement observé dans la partie nord-est du GSL, près du détroit de Belle Isle (Bousfield 1951, Huntsman et al. 1954, Hoffer 1971). Cette conclusion appuie l'observation faite par Bousfield (1951) selon laquelle le détroit de Belle-Isle représente la limite la plus au sud de la distribution de *T. libellula* le long de la côte est du Canada. À l'opposé, les différentes missions océanographiques effectuées annuellement par l'Institut Maurice-Lamontagne (Pêches et Océans Canada) ont montré que *T. libellula* est devenu un résident à temps plein et très abondant dans le SMSL depuis le début des années 1990 avec une abondance moyenne annuelle variant entre 0,17 et 16 ind. m^{-2} entre 1994 et 2005 (Harvey et al. 2005). De plus, ces études ont montré que *T. libellula* habite en permanence dans la couche intermédiaire d'eau froide (CIF) où les eaux ont une température inférieure à 3°C (M. Harvey, données non publiées).

Cette expansion géographique de *T. libellula* dans le SMSL pendant les années 1990 coïncide avec l'observation faite par Drinkwater et Gilbert (2004) selon laquelle, en moyenne, la température au cœur de la CIF dans les années 1990 était la plus froide des cinq dernières décennies. De plus, depuis 1996, les variations interannuelles de l'abondance moyenne de *T. libellula* observées dans le SMSL sont positivement corrélées avec le volume d'eau froide provenant du plateau du Labrador et entrant dans le GSL à travers le détroit de Belle-Isle pendant l'hiver (Starr et al. 2002, Harvey et al. 2004). Ces deux observations renforcent l'hypothèse selon laquelle *T. libellula* a été introduit dans le GSL par le détroit de Belle Isle pendant l'hiver et que sa survie a été facilitée par le fait que les années 1990 ont connu la CIF la plus froide des cinq dernières décennies. Un autre facteur pourrait avoir contribué à l'expansion géographique de cette espèce dans le SMSL. L'espèce *T. libellula* était apparemment plus abondante sur le plateau du Labrador durant les années 1990 que durant les années 1980. En effet, une récente étude comparant les contenus stomacaux de l'omble chevalier du plateau du Labrador sur une période de 18 ans, de 1982 à 1999, montre que *T. libellula* était quatre fois plus abondant pendant les années

1990 que pendant les années 1980 (Dempson et al. 2002, J. B. Dempson, Pêches et Océans Canada, St. John's, Terre-Neuve, comm. personnelle).

L'arrivée de cette espèce dans le SMSL peut avoir des conséquences importantes. De nombreuses études ont montré que les amphipodes hypéridés du genre *Themisto*, qui sont principalement des individus carnivores sur le mésozooplancton (Kane 1967, Falk-Petersen et al. 1987), représentent un maillon trophique important entre la production secondaire, les poissons (Lambert 1960, LeBrasseur 1966, Lønne & Gulliksen 1989, Dalpadado et al. 2001, Gislason & Astthorsson 2002, Dalpadado & Bogstad 2004), les oiseaux de mer (Ogi & Hamanaka 1982, Ogi et al. 1985, Bocher et al. 2000, Pedersen & Smidt 2000, Pedersen & Falk 2001) ainsi que les mammifères marins (Kawamura 1970, Nemoto & Yoo 1970, Lowry & Frost 1984, Nielssen et al. 1995, Wathne et al. 2000). De part sa position trophique au sein de l'écosystème marin, *T. libellula* pourrait donc exercer un contrôle sur ces organismes, sur l'abondance et la structure des communautés de mésozooplancton ainsi que sur la survie et le recrutement des larves de plusieurs espèces de poissons, par prédation directe ou par compétition avec les larves de poissons pour l'obtention de proies communes (copépodes).

1.3. LE TROPHODYNAMISME

L'étymologie du mot trophodynamisme vient du grec, «tropho» qui signifie nourriture et «dynamisme» qui implique la notion de mouvements, d'échanges dans un système. Étudier le trophodynamisme d'un organisme revient à étudier la périodicité de son activité alimentaire, à calculer son taux de consommation, et à identifier ses proies. C'est également quantifier l'impact de sa prédation pour déterminer les interactions trophiques entre les organismes à l'intérieur de l'écosystème dans lequel il évolue et c'est aussi évaluer le transfert d'énergie à travers les réseaux trophiques (Cartes & Maynou 2001, Madurell & Cartes 2005). L'estimation du taux d'ingestion des prédateurs constitue ainsi une bonne approche pour établir l'impact trophique des espèces numériquement abondantes et donc d'étendre les connaissances sur les structures trophiques et le fonctionnement des écosystèmes (Cartes & Maynou 2001).

Les études sur le trophodynamisme dans le système marin se sont souvent centrées sur les poissons, en particulier sur les espèces ayant un intérêt commercial (Amundsen et al. 1999, Williams et al. 2001, Cardinale et al. 2003, Darbyson et al. 2003, Rindorf 2003, Madurell & Cartes 2005). Des études similaires ont également été effectuées sur quelques espèces macrozooplanctoniques carnivores comme les chaetognathes (Kimmerer 1984, Øresland 1990, Froneman & Pakhomov 1998), certains euphausiacés (Båmstedt & Karlson 1998, Pakhomov et al. 1998), les mysidacés (Cartes & Maynou 2001, Winkler & Greve 2004), les cténophores (Båmstedt 1990, Båmstedt et al. 1994, Båmstedt 1998), les méduses (Båmstedt 1990, Båmstedt et al. 1994), ainsi que les amphipodes hypéridés (Pakhomov &

Perissinotto 1996, Auel & Werner 2003). Ces études ont été réalisées afin de connaître l'impact de prédation de ces organismes sur les communautés zooplanctoniques et sur la production secondaire. Froneman et Pakhomov (1998) ont ainsi mis en évidence que *Eukrohnia hamata* et *Sagitta gazellae*, deux espèces de chaetognathes vivant dans le système pélagique des îles du Prince-Édouard (sud de l'océan Indien), se nourrissaient principalement de copépodes et que leur impact quotidien de prédation dans cette région était équivalent à 3,2% et 5,2% de la biomasse de copépodes. Ces deux espèces ont alors été considérées comme d'importants prédateurs pélagiques de ce système marin. Dans certaines régions, les copépodes sont également les principales proies de certains euphausiacés. Båmstedt et Karlson (1998) ont estimé que l'impact de prédation de ces derniers, dans les eaux côtières du nord-est de l'océan Atlantique, correspondait à une réduction journalière de 6,4% de la biomasse de *C. finmarchicus*. La prédation de ces euphausiacés a été considérée comme pouvant fortement contribuer à la mortalité des copépodes.

Le trophodynamisme des amphipodes hypéridés a également été étudié. À travers ces études, ces amphipodes ont été reconnus comme étant de grands prédateurs de mésozooplancton, d'euphausiacés, de ptéropodes, de chaetognathes et de larves de poissons (Dunbar 1946, Kane 1967, Sheader & Evans 1975, Hopkins 1985, Falk-Petersen et al. 1987, Pakhomov & Perissinotto 1996, Scott et al. 1999, Auel et al. 2002, Auel & Werner 2003). Ces études ont suggéré que les populations d'amphipodes hypéridés, principalement *Themisto* spp., exercent une pression de prédation importante sur la production secondaire dans certaines régions océaniques comme les eaux proches de South Georgia dans l'océan

Atlantique Sud (Pakhomov & Perissinotto 1996), dans le sud de la mer du Japon (Yamashita et al. 1984, Ikeda & Shiga 1999) et également dans l'ouest de l'océan Pacifique (Yamada & Ikeda 2006). Dans les eaux de South Georgia dans l'océan Atlantique Sud, l'impact de prédation de *Themisto gaudichaudi* s'élève à 2,1% de la biomasse de mésozooplancton par jour. Cependant, son impact sur la production secondaire est beaucoup plus sévère et atteint plus de 70% de cette production par jour (Pakhomov & Perissinotto 1996). Cette espèce est donc capable de contrôler les populations de mésozooplancton dans ces régions. L'impact de prédation de *T. gaudichaudi* vivant à proximité de l'archipel du Prince-Édouard, dans le sud de l'océan Indien, est toutefois plus faible et n'excède jamais 0,2% de la biomasse mésozooplanctonique pour de faibles abondances d'amphipodes (< 0.2 ind. m^{-3}) (Froneman et al. 2000). Gibbons et al. (1992) ont estimé que cette même espèce vivant dans les eaux du système de remontées d'eaux froides du Benguela, montre des impacts de prédation pouvant réduire de 4 à 38,5% le stock de copépodes par jour. Quant aux impacts de prédation sur la biomasse zooplanctonique de *T. pacifica* et *T. japonica*, deux amphipodes hypéridés habitant la région d'Oyashio dans la zone subarctique ouest du Pacifique, ils n'excèdent jamais 0,11% et 0,06% respectivement pour chacune de ces deux espèces (Yamada & Ikeda 2006).

Les recherches sur le trophodynamisme de l'espèce *Themisto libellula* (Fig. 1) sont très rares contrairement à celles de ses congénères *T. gaudichaudi* (Pakhomov & Perissinotto 1996), *T. japonica* ou *T. pacifica* (Yamashita et al. 1984, Ikeda & Shiga 1999, Yamada & Ikeda 2006) et seules quelques caractéristiques de son trophodynamisme dans deux régions arctiques ont été étudiées alors que sa distribution géographique s'étend dans

Figure 1. Deux espèces appartenant au genre *Themisto* : *Themisto libellula* et *T. abyssorum*.

plusieurs mers arctiques et dans quelques mers européennes (Fig. 2). Fortier et al. (2001) ont examiné la variation journalière de l'intensité et de la composition de l'alimentation de *T. libellula* dans la couche de surface sous le couvert de glace, pendant le soleil de minuit, dans le détroit de Barrow, au printemps. Dans cette région, l'ingestion de nourriture de *T. libellula* est maximale le matin (entre 7 : 45 et 11 : 00) et pendant la soirée (18 : 55 et 21 : 45). Dans son étude, Fortier ne décrit pas l'intensité d'ingestion de *T. libellula* sur une période de 24 h et ne peut donc pas mettre en évidence le cycle circadien de l'alimentation de cet amphipode. De plus, aucun calcul n'a été entrepris dans ce travail pour évaluer le temps de digestion de cette espèce, son taux d'ingestion ainsi que son impact de prédation sur la communauté mésozooplanctonique du détroit de Barrow. Auel et Werner (2003) ont estimé les taux quotidiens d'ingestion de *T. libellula* dans la zone de glace marginale du détroit de Fram, par des expériences de nutrition, des mesures de respiration et à l'aide d'une approche allométrique fondée sur la masse corporelle, ainsi que son impact de prédation sur la communauté mésozooplanctonique. Les résultats expérimentaux s'accordent à estimer un taux d'ingestion égal à 1,9% de masse sèche corporelle d'amphipode par jour. Dans cette étude, le taux d'ingestion a seulement été calculé pour des copépodes du genre *Calanus*, et non sur l'ensemble du mésozooplancton. Auel et Werner (2003) ont également évalué que la prédation de *T. libellula* pouvait expliquer une perte quotidienne de biomasse mésozooplanctonique de 0,03% dans le détroit de Fram. Cependant, dans cette étude, les auteurs n'ont pas calculé le temps de digestion de *T. libellula* ni estimé son cycle circadien d'alimentation.

Figure 2. Distribution géographique de l'amphipode hypéridé *Themisto libellula* (étoile) dans l'hémisphère nord (Dunbar 1957, Percy & Fife 1993, Dalpadado et al. 2001, Auel & Werner 2003). (carte: www.geographicguide.com).

1.4. OBJECTIFS DE L'ÉTUDE

La présente étude a pour objectif de décrire quantitativement et qualitativement le trophodynamisme de l'amphipode hypéridé *Themisto libellula* dans l'écosystème marin du Saint-Laurent et principalement dans l'estuaire maritime (EM) et le nord-ouest du golfe du Saint-Laurent (NOGSL). Nous nous proposons ainsi d'identifier, de quantifier les proies mangées par cet amphipode hypéridé, de déterminer son cycle circadien d'alimentation ainsi que son impact de prédation sur les biomasses zooplanctoniques.

L'hypothèse principale de ce travail est que *Themisto libellula* est capable de contrôler la communauté mésozooplanctonique locale dans le système marin du Saint-Laurent. Les objectifs spécifiques de cette étude consistent par conséquent à :

1) Décrire les variations circadiennes de l'activité nutritive de *T. libellula*.

2) Estimer le temps de digestion de *T. libellula* sous des conditions naturelles dans le SMSL.

L'étude des variations circadiennes permet d'estimer le temps de digestion sous des conditions naturelles. Même si cette activité est continue, les données fourniront une estimation minimale du temps de digestion et des taux de prédation qui pourront être comparés avec ceux d'autres espèces.

3) Décrire le régime alimentaire de *T. libellula* pour déterminer le groupe zooplanctonique le plus sujet à sa prédation.

4) Estimer les taux d'ingestion journaliers de *T. libellula* dans l'EM et le NOGSL.

5) Estimer l'impact journalier de la prédation de *T. libellula* sur la communauté zooplanctonique dans chacune des régions du SMSL.

Les amphipodes hypéridés nécessaires à la réalisation de cette étude ont été échantillonnés lors de la mission océanographique annuelle sur l'évaluation de la biomasse de zooplancton qui est effectuée annuellement dans l'EM et le NOGSL depuis 1994 par l'Institut Maurice-Lamontagne (Pêches et Océans Canada). Cette mission a eu lieu au début du mois de septembre entre 1994 et 2003 et début novembre en 2004 et 2005. L'échantillonnage a été fait sur 44 stations (26 stations dans l'EM et 18 dans le NOGSL) distribuées le long de 8 transects, des Escoumins jusqu'à Sept-Îles (Fig. 3).

Le chapitre qui suit présente les résultats sous forme d'un article scientifique en anglais.

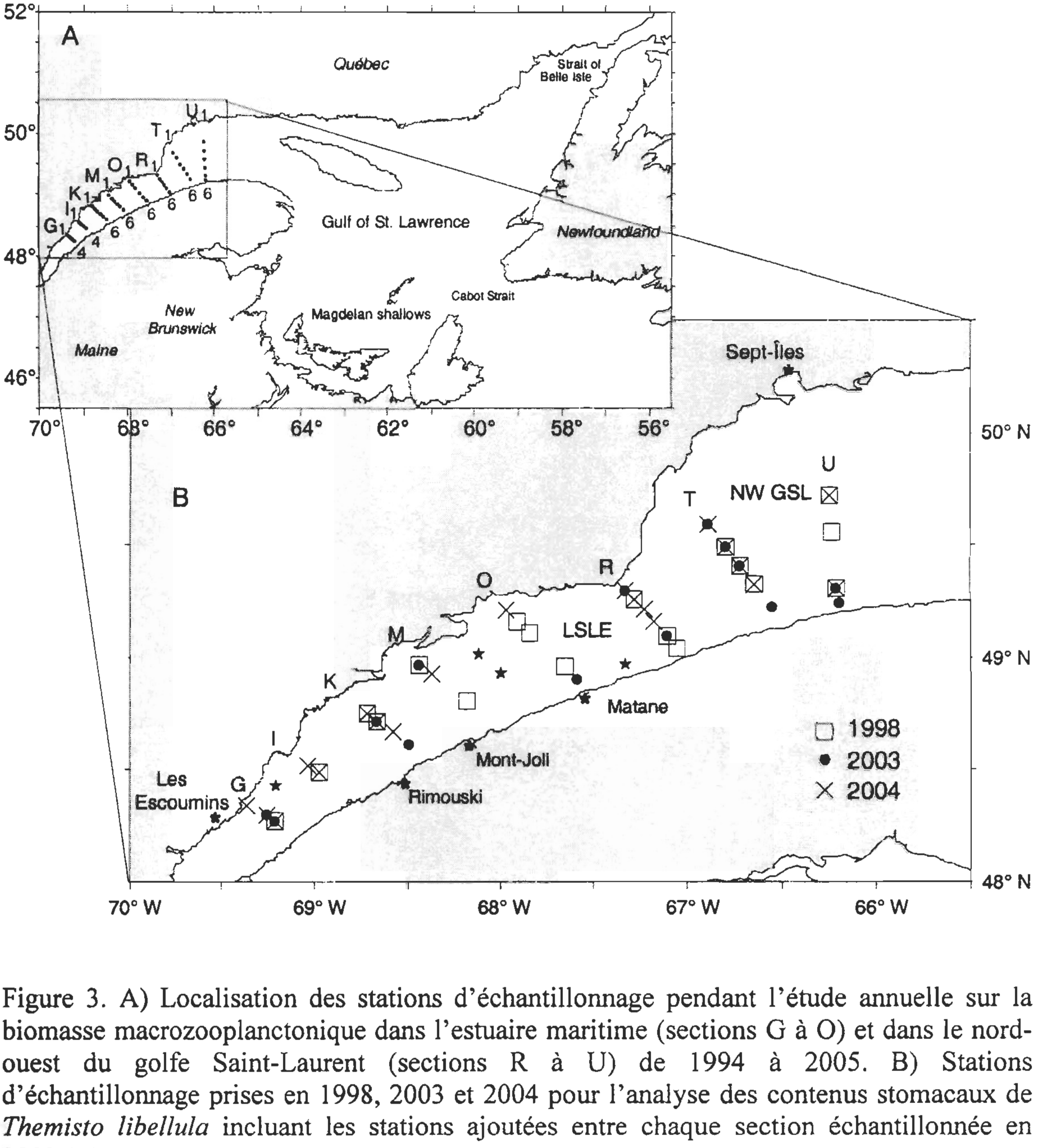

Figure 3. A) Localisation des stations d'échantillonnage pendant l'étude annuelle sur la biomasse macrozooplanctonique dans l'estuaire maritime (sections G à O) et dans le nord-ouest du golfe Saint-Laurent (sections R à U) de 1994 à 2005. B) Stations d'échantillonnage prises en 1998, 2003 et 2004 pour l'analyse des contenus stomacaux de *Themisto libellula* incluant les stations ajoutées entre chaque section échantillonnée en 2003 (⋆).

2. FEEDING ECOLOGY AND PREDATION IMPACT OF THE INVASIVE SPECIES *THEMISTO LIBELLULA* (AMPHIPODA, HYPERIIDEA) IN THE ST. LAWRENCE MARINE SYSTEM, CANADA.

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ABSTRACT

A literature review going back to the early 1900s and a reanalysis of several zooplankton samples collected during the 1980s in the St. Lawrence marine system (SLMS) have shown that *Themisto libellula* (Mandt) was virtually absent from this system before 1990. Since then, *T. libellula* has become an abundant, full-time resident of the SLMS. Hyperiid amphipods of the genus *Themisto* are principally carnivorous and they represent an essential link in the trophic pathway from secondary production to higher trophic levels. Sampling of the hyperiid amphipod *T. libellula* was carried out in the SLMS in fall 1998, 2003 and 2004 to study the feeding dynamics and the predation impact of this species on mesozooplankton and macrozooplankton communities in the SLMS. Our results illustrated that *T. libellula* was an opportunistic predator presenting a circadian cycle in its feeding activity with higher activity during the second part of the night and the sunrise period. Stomach content analyses showed that amphipods consumed chiefly copepods, which were the most abundant mesozooplanktonic group represented in the SLMS. Euphausiids, chaetognaths, amphipods and mysids constituted the other important preys of *T. libellula. Calanus finmarchicus* dominated the diet and stages CIV and CV were by far the main prey of *T. libellula*. Digestion time was estimated at 13 h. With the stomach fullness index (SFI) approach, the daily ingestion rates ranged from 7.19 to 9.54% and from 6.32 to 7.19% of body dry mass for the lower St. Lawrence Estuary (LSLE) and the northwest Gulf of St. Lawrence (NWGSL) respectively. Using feeding rates, we calculated consumption on zooplankton to be 17.02% of the body dry mass per day for the NWGSL and to 19.97% for the LSLE. Ingestion on *C. finmarchicus* ranged from 3.28 to 5.50% per day in the NWGSL and in the LSLE, respectively. Predation impact reached 2.18% of the combined mesozooplankton and macrozooplankton standing stock per day and 3.39% of *C. finmarchicus* standing stock. *T. libellula* may thus exert a significant control on the mesozooplankton population through direct predation in the SLMS.

KEY WORDS: Hyperiid amphipods, Feeding activity, Trophodynamics, Ingestion rate, Digestion time, Predation impact, Gulf of St. Lawrence

INTRODUCTION

The hyperiid amphipod *Themisto libellula* is widely distributed and abundant in the ice-covered central Arctic Ocean and most of the adjacent European and North American Arctic seas (see reviews in Dunbar 1957, Percy & Fife 1993, Dalpadado et al. 2001, Auel & Werner 2003). In that context, *T. libellula* was recognized as a typical arctic species that can be regarded as a good indicator of the presence of arctic waters in different subarctic regions (Dunbar 1957, Dalpadado et al. 2001).

Both a literature review, going back to the early 1900s, and a reanalysis of several zooplankton samples collected during the 1980s in different areas of the Gulf of St. Lawrence (GSL) and the lower St. Lawrence Estuary (LSLE) have shown that *Themisto libellula* was absent of the St. Lawrence marine system (SLMS) before the 1990s (M. Harvey, unpublished data), except for a few juvenile individuals occasionally observed in the northeast GSL, near of the Strait of Belle Isle (Bousfield 1951, Huntsman et al. 1954, Hoffer 1971). This supports the observation made by Bousfield (1951) that the Strait of Belle Isle represented the southernmost distribution limit of *T. libellula* along the Canadian east coast. On the other hand, different surveys carried out annually by the Maurice-Lamontagne Institute (Fisheries and Oceans Canada) since the beginning of the 1990s have showed that *T. libellula* has become an abundant, full-time resident of the SLMS, with an annual mean (±SD) abundance varying between 0.17 (±0.33) and 16.50 (±13.33) ind. · m^{-2}

in the LSLE and the northwest GSL (NWGSL) (1994 – 2005) respectively (Harvey et al. 2005).

Hyperiid amphipods of the genus *Themisto* are principally carnivorous (Kane 1967, Sheader & Evans 1975, Falk-Petersen et al. 1987) and mainly feed on a large variety of mesozooplankton such as calanoid copepods, euphausiids, and chaetognaths (Hopkins 1985, Pakhomov & Perissinotto 1996, Froneman et al. 2000, Auel et al. 2002). Reciprocally, they are an important source of food for fishes (Lønne & Gulliksen 1989, Dempson et al. 2002), seabirds (Pedersen & Falk 2001), seals (Nielssen et al. 1995), and whales (Lowry & Frost 1984) in arctic regions. Thus, they represent an essential component of the trophic pathways from the secondary production of mesozooplankton to higher trophic levels.

Contrary to its Antarctic congener *Themisto gaudichaudi*, which has been the subject of several studies on various ecological aspects (see review in Pakhomov & Perissinotto 1996), very few studies have been undertaken on *T. libellula*. Most of them have dealt with its distribution, reproductive behaviour, and life cycle in the Canadian Arctic (Dunbar 1957, Percy 1993a, Percy 1993b) and the Barents, Greenland, and Norwegian Seas (Koszteyn et al. 1995, Dalpadado et al. 2001, Dalpadado 2002). In addition, only two quantitative studies dealing with the feeding ecology of *T. libellula* have been published to date. Fortier et al. (2001) examined the daily variation in the intensity of feeding and the components of the diet of *T. libellula* in the under-ice surface layer during the midnight sun period in the arctic Barrow Strait, and Auel and Werner (2003) estimated the daily ingestion rates of *T. libellula* in the marginal ice zone of the arctic Fram Strait by feeding experiments, respiration measurements, and an allometric approach based on body mass.

Because of the importance of *T. libellula* in the SLMS and the lack of relevant data about the feeding ecology of this species, the purpose of the present study was to provide estimates of the diet composition, diel feeding behaviour, digestion time, daily ration, and predation impact on the zooplankton standing stock in the SLMS. Diet and feeding rate studies constitute a good approach for establishing the trophic impact of this invasive species, extending the knowledge on the St. Lawrence marine trophic ecosystem structure, and developing bioenergetic and ecosystem models.

MATERIELS AND METHODS

Field sampling

The present study is based on samples of hyperiid amphipods collected during the annual macrozooplankton biomass monitoring survey carried out in the LSLE and the NWGSL since 1994 by the Maurice-Lamontagne Institute (Fisheries and Oceans Canada) (Harvey et al. 2005). This survey was conducted in early September from 1994 to 2003 and in early November in 2004 and 2005. Zooplankton was sampled at 44 stations (26 stations in the LSLE and 18 in the NWGSL) distributed along eight transects from Les Escoumins to Sept-Îles (Fig. 4A) using a 1 m^2 BIONESS sampler (Sameoto et al. 1980) equipped with nine opening/closing nets having 333 µm mesh. Nineteen additional stations located between transects were sampled in 2003. The BIONESS was first deployed to 5 m off – bottom with the nets closed and then towed obliquely toward the surface with the ship traveling at *ca.* 2-3 knots. Depending on station depth, one or two depth strata were sampled: 0 – 150 m and 150 m – bottom for stations deeper than 150 m, and 0 m – bottom for shallower stations. At each station, the water column was sampled twice using four (> 150 m) or two (< 150 m) different nets. All surveys were carried out around the clock, so that approximately half the stations were sampled during daytime and half during nighttime. Total water volume filtered in each stratum was estimated using a General Oceanic electronic flowmeter (model 2031H) installed in the mouth of each net of the BIONESS. At the end of each BIONESS tow, nets were rinsed and the cod-end contents were preserved in 4% buffered formaldehyde within 10 minutes of the end of the tow.

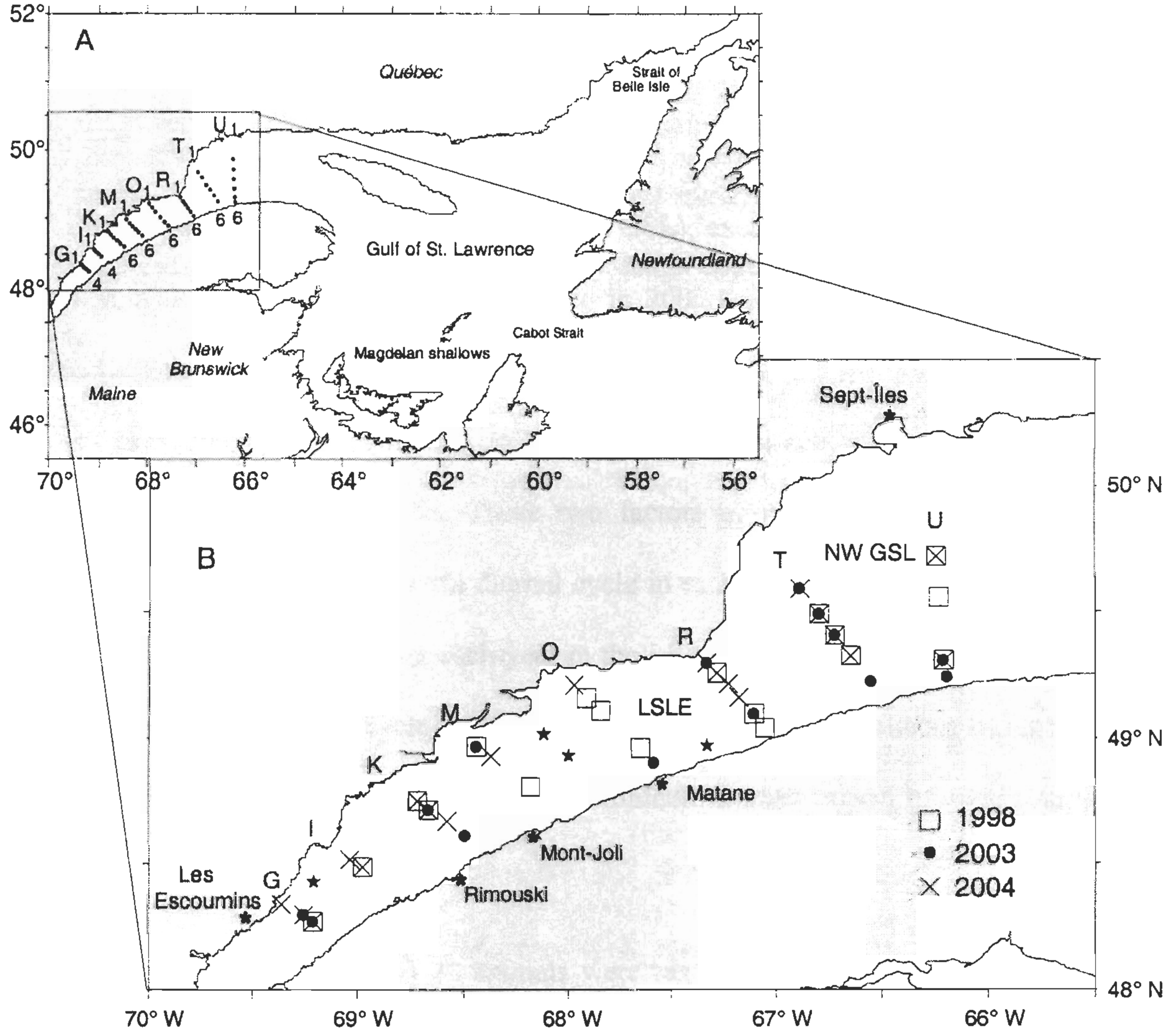

Figure 4. A) Location of sampling stations during the annual macrozooplankton biomass monitoring survey carried out in the LSLE (Lower St. Lawrence Estuary; transects G to O) and the NWGSL (Northwest Gulf of St. Lawrence; transects R to U) from 1994 to 2005. B) Stations sampled in 1998, 2003, and 2004 for the stomach content analysis of *Themisto libellula* including the additional stations located between transects sampled in 2003 (★).

Stomach content analysis

The stomach content analyses were made on *Themisto libellula* sampled in fall 1998, 2003 and 2004 in each region (LSLE and NWGSL), except that we did more extensive stomach content analyses in animals sampled in 2003 than in 1998 and 2004 (Fig. 4B). These surveys were chosen because of the high abundance of *T. libellula* (between 11 and 18 ind. m^{-2}) (Harvey et al. 2005). Also, nineteen additional stations were sampled in the LSLE and the NWGSL in 2003. These two factors improved our ability to describe variations in stomach content over a diurnal cycle in each region. In that context, nine and eight stations were chosen during each year in the LSLE and the NWGSL, respectively, in such a way to have a 24-h cycle with samples at intervals of *ca.* 3 hours in each region (Table 1). Three to five days of data were combined in each region to obtain sufficient coverage of the daily cycle.

For 2003, between 10 and 20 animals were randomly selected from each sampling interval and examined for stomach contents. A total of 110 and 96 animals were analyzed in the LSLE and the NWGSL respectively. First, total length was measured from the front of the head to the tip of the longest uropod (Dunbar 1957) using a stereomicroscope connected to the Pro Plus image analysis software. After measurements, each animal was blotted on filter paper and its wet mass determined to the nearest 0.1 mg. The digestive tract, excluding the mouth and the pharynx, was removed from each animal under a stereomicroscope, opened, and the content spread on a glass slide. After the stomach content was removed, each animal was placed in an oven-dried, pre-weighed aluminum

Table 1. *Themisto libellula.* Sampling dates, times (Eastern Daylight Time (EDT) in September and Eastern Standard Time (EST) in November), and stations sampled in the LSLE and in the NWGSL in fall 1998, 2003, and 2004. Scale bars represent daytime (in white), periods of sunset and sunrise (in grey), and nighttime (in black).

Sampling zone	Date, sampling times (stations)								
	1998			2003			2004		
LSLE	13-Sept	00:30 (M1)	■	14-Sept	01:29 (H1)	■	10-Nov	00:46 (G4)	■
	12-Sept	03:15 (I3)	■	13-Sept	03:52 (K4)	■	10-Nov	01:40 (G3)	■
	17-Sept	06:30 (O5)	▒	14-Sept	05:12 (G4)	▒	10-Nov	03:22 (G1)	■
	13-Sept	09:40 (M5)	□	14-Sept	07:14 (G3)	□	10-Nov	06:07 (I2,I3)	▒
	12-Sept	12:55 (K4)	□	11-Sept	11:50 (P6)	□	10-Nov	09:41 (K3)	□
	12-Sept	15:00 (K3)	□	12-Sept	14:36 (M1)	□	10-Nov	13:00 (K4)	□
	11-Sept	18:00 (G4)	▒	08-Sept	17:44 (O6)	□	10-Nov	15:00 (K5)	□
	13-Sept	22:00 (O3)	■	13-Sept	21:17 (K6)	▒	10-Nov	18:30 (M2)	▒
	13-Sept	23:40 (O2)	■	11-Sept	23:47 (N1)	■	11-Nov	22:38 (O1)	■
NWGSL	15-Sept	03:30 (T2)	■	09-Sept	0:04 (U6)	■	11-Nov	01:40 (U6)	■
	14-Sept	06:30 (R2)	▒	09-Sept	02:09 (U5)	■	11-Nov	No data	▒
	16-Sept	09:40 (U5)	□	11-Sept	05:12 (R1)	▒	11-Nov	09:51 (U2)	□
	15-Sept	11:25 (U2)	□	10-Sept	09:55 (T3)	□	11-Nov	12:49 (R4)	□
	14-Sept	14:00 (R5)	□	10-Sept	11:45 (T4)	□	11-Nov	14:53 (R3)	□
	14-Sept	15:55 (R6)	□	10-Sept	15:00 (T5)	□	11-Nov	15:43 (R2)	□
	15-Sept	19:00 (T3)	▒	10-Sept	21:30 (R5)	▒	11-Nov	16:40 (R1)	□
	15-Sept	22:50 (U3,T4)	■	09-Sept	23:46 (T1)	■	11-Nov	20:27 (T4,T5)	□
							11-Nov	22:30 (T2,T3)	■

cup, oven-dried at 60°C for 24 h, and weighed with a Mettler MT5 balance (± 0.001 mg).

The digestion index (DI) of the stomach content was estimated and assigned to one of the following categories. Stage I indicated no evidence of digestion. At this stage, prey identification was easy. At stage II, digestion had just started and prey were intact except for the most delicate parts. When prey were moderately digested and clearly affected by digestion, it was classified as stage III. Stage IV was when digestion was well advanced. Prey were highly fragmented and prey identification was difficult. Finally, at stage V, digestion was almost complete and prey were unidentifiable.

After estimating the stage of digestion, prey were counted and identified to the lowest possible taxonomic level. Prey items were divided into eight taxonomic categories: amphipods, chaetognaths, *Calanus* spp. (including the copepodid stages), other copepods, euphausiids, isopods, mysids, and other items. In the case where we found only fragments of copepods such as prosomes and/or urosomes, they were counted separately and only the higher number of the two was assumed to represent the number of prey. After prey identification, the stomach content of each amphipod was put in an oven-dried, pre-weighed aluminum cup, oven-dried at 60°C for 24 h, and weighed with a Mettler MT5 balance (± 0.001 mg). Finally, the stomach fullness index (SFI) was calculated by dividing the dry mass of the stomach contents by the dry mass of the amphipod body (Sameoto 1989, Pakhomov & Perissinotto 1996).

For 1998 and 2004, we only estimated total length, body wet mass, and stomach fullness index (SFI). Moreover, the spatial variation of the stomach fullness index (SFI) was estimated in two series of ten animals sampled at the same hour at two different stations, during three different periods of the day in each region (LSLE and NWGSL) in fall 2004. These periods of the day were selected according to the availability of stations sampled at the same hour.

Stomach content regurgitation and cod-end feeding were not regarded as important in this study since prey in the mouth and the pharynx were not taken into account in the data analysis. Concerning cod-end feeding, as for the lantern fish *Benthosema glaciale* sampled with the BIONESS at 2-3 knots by Sameoto (1988), most amphipods were dead or dying when captured even though their physical appearance was still very good. Sameoto (1988) suggested that the speed of the tow meant that the animals were forced against the mesh of the net and it is unlikely that they would be able to feed under these circumstances.

Data analysis

The number of *Themisto libellula* collected in the different depth strata were integrated over the entire water column to obtain the number of individuals per m^2. The length–frequency distributions of *T. libellula* sampled in the LSLE and the NWGSL in 1998, 2003, and 2004 were examined graphically and the relationships between the wet mass and the total length were compared between regions and years using an ANCOVA on log-transformed data.

The spatial variability of the SFI was analyzed by comparing the mean SFI estimated for two series of ten animals sampled at the same hour at two different stations during three different period of the day in each region (LSLE and NWGSL), with a Student's *t*-test on log-transformed data.

The diel variation of the SFI was first examined graphically in animals sampled every 3 hours during a 24-h period in each region (LSLE and NWGSL) in fall 1998, 2003, and 2004. Thereafter, the data were regrouped (regions and years) and the diel variation of the SFI was tested statistically using a generalized additive models (GAMs; Hastie & Tibshirani 1990) using the R software and MGCV package (Wood 2005). GAMs are an extension of generalized linear models in which relationships between the dependent and independent variables are not constrained to particular parametric forms. Instead, explanatory terms are modelled non-parametrically using a scatterplot smoother. The effect of time of day was modelled using a cubic spline function. Statistical significance was assessed using the Fisher test (see Darbyson et al. 2003). The same analyses were done using the DI estimated for animals sampled in the LSLE and the NWGSL in fall 2003.

Results from stomach content analyses after prey identification, were expressed as the mean number of prey items per *Themisto libellula* per time of the day in each region (the number of empty stomachs was included in the calculation of the mean number of prey) and as a percentage of each food item to the total number of food items counted. Results from stomach content analyses were also expressed in dry mass to estimate the SFI.

The daily ingestion rates of *Themisto libellula* (*DIR*) were estimated using two approaches, 1) the SFI and 2) the mean number of prey removed per unit of time and converted to prey biomass using the stage-species dry masses of each prey item. The SFI approach was made using a derived of Bajkov's relation, employed by Pakhomov & Perissinotto (1996) and Froneman et al. (2000):

$$DIR_I = G \times (24 / DT) \qquad [1]$$

where G is the average value of the 24 h-integrated (circadian cycle) SFI in % of body dry mass and DT is the digestion time in hour (Bajkov 1935, Eggers 1977). The digestion time was evaluated by calculating the difference between the time of the day when the highest values of the SFI and the DI, obtained by GAMs, were observed.

The second approach was based on the stomach content analyses from animals sampled in the LSLE and the NWGSL in fall 2003. In this approach, we first estimated the feeding rates (*FR*) using the following equation:

$$FR = (\text{mean } BPA \times 24) / DT) \qquad [2]$$

where mean *BPA* is the average biomass of the prey ingested · amphipod^{-1} during a 24-h period and *DT* the digestion time in hour (see Øresland 1995). Mean *BPA* was calculated as the mean biomass of the prey item found in the stomach content of each amphipod examined at every 3-h period over 24-h within each region (LSLE and NWGSL). This biomass was obtained from the copepod stage-species dry masses table produced by the Atlantic Zone Monitoring Program (AZMP) (Fisheries and Oceans Canada; unpublished data). This table includes the stage-species dry masses of several copepod species found at different times of the year along the Canadian Atlantic coast, including the Gulf of St. Lawrence. In addition, the dry masses of the other taxonomic categories found in the stomach content analysis (amphipods, chaetognaths, euphausiids, isopods, mysids) were obtained locally from different research projects (M. Harvey, unpublished data). Finally, the second daily ingestion rates (DIR_2), expressed as percentage of amphipod body dry mass, were calculated by dividing the feeding rates (*FR*) by the mean dry mass (47.2 mg) of all *Themisto libellula* individuals analyzed in the present study (16.5% of the wet mass).

To estimate the predation impact of *Themisto libellula* on the zooplankton standing stock, the daily ingestion rates, estimated using the two different approaches (DIR_1, DIR_2), were multiplied by the biomass of *T. libellula* at each station (see Froneman et al. 2000). This was then expressed 1) as a percentage of total zooplankton biomass, evaluated during the annual macrozooplankton biomass monitoring survey, and 2) as a percentage of total biomass of the most abundant copepod species found in the amphipod stomach contents, including the copepodid stages of *Calanus finmarchicus*. The mean abundance and biomass of the different copepod species were estimated from the AZMP zooplankton data collected in fall 2003 along two sections located in the LSLE and the NWGSL respectively (Harvey et al. 2004) and the AZMP copepod stage-species dry masses table.

RESULTS

Size distribution of *Themisto libellula*

Figure 5 shows the length-frequency distributions and the regressions between the total body wet mass and the total length of *Themisto libellula* sampled in the LSLE and the NWGSL in fall 1998, 2003, and 2004. The same two size classes were observed in each region in 1998 (22 to 38, 38 to 48 mm), 2003 (26 to 38, 38 to 48 mm), and 2004 (26 to 40, 40 to 50 mm) (Fig. 5). The relative occurrence of the small (22 to 40 mm) and the large (38 to 50 mm) size classes varied between 80 to 94% and 20 to 6% respectively during each year in both regions, except in the LSLE in 2003 and 2004, where the relative occurrence of the small and large size classes varied between *ca.* 40% and 60% respectively. Likewise, the median values of the smaller and the larger size classes did not vary between regions during each year but were lower in 1998 (30 and 42 mm respectively) than in 2003 (33 and 42 mm) and 2004 (36 and 45 mm) in both regions (Fig. 5). Interannual changes in the median values of both size classes, and the similarity between regions, were also observed with the interannual and inter-regional comparisons of the regressions between the total body wet mass and the total length using an ANCOVA. Results of the ANCOVA showed no significant effect of the sampling zone, a significant effect of the year, and no significant interaction between factors (Table 2).

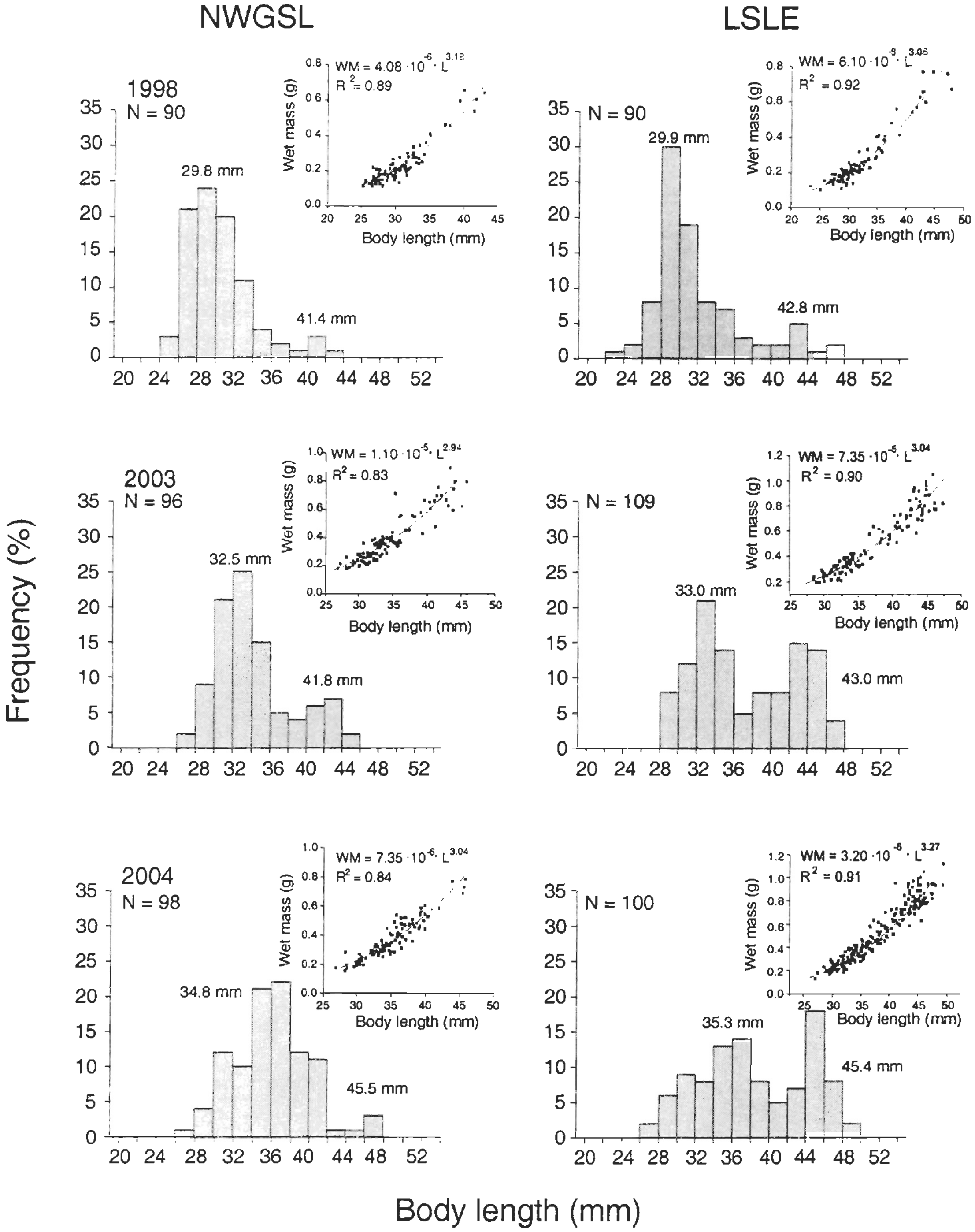

Figure 5. *Themisto libellula*. Length-frequency distributions and the wet mass – total length relationships of individuals used for the stomach content analysis in the LSLE and the NWGSL in 1998, 2003, and 2004. N = total number of individuals measured. The median is indicated as a number above each size class.

Table 2. *Themisto libellula*. Summary of 2-way ANCOVA on the individual wet masses with zone and year as factors and length as the covariate (SS: sum of squares; df: degrees of freedom; MS mean square).

Variable	Source of variation	SS	df	MS	F-ratio	P
Dry mass	Zone	0.002	1	0.002	0.389	0.53
	Year	0.413	2	0.207	50.002	0.00
	Zone*year	0.010	2	0.005	1.257	0.28
	Length	20.099	1	20.099	4864.238	0.00
	Error	2.392	579	0.004		

Spatial feeding pattern

Figure 6 illustrates the mean SFI estimated in two series of ten animals sampled at the same hour at two different stations, during three different periods of the day in each region (LSLE and NWGSL) in fall 2004. Based on the results of the Student's *t*-test there was no spatial variation of the mean SFI during the three periods of the day in both regions (Fig. 6). This result supports the hypothesis that there was no spatial variation of the circadian feeding cycle in each of the sampled regions.

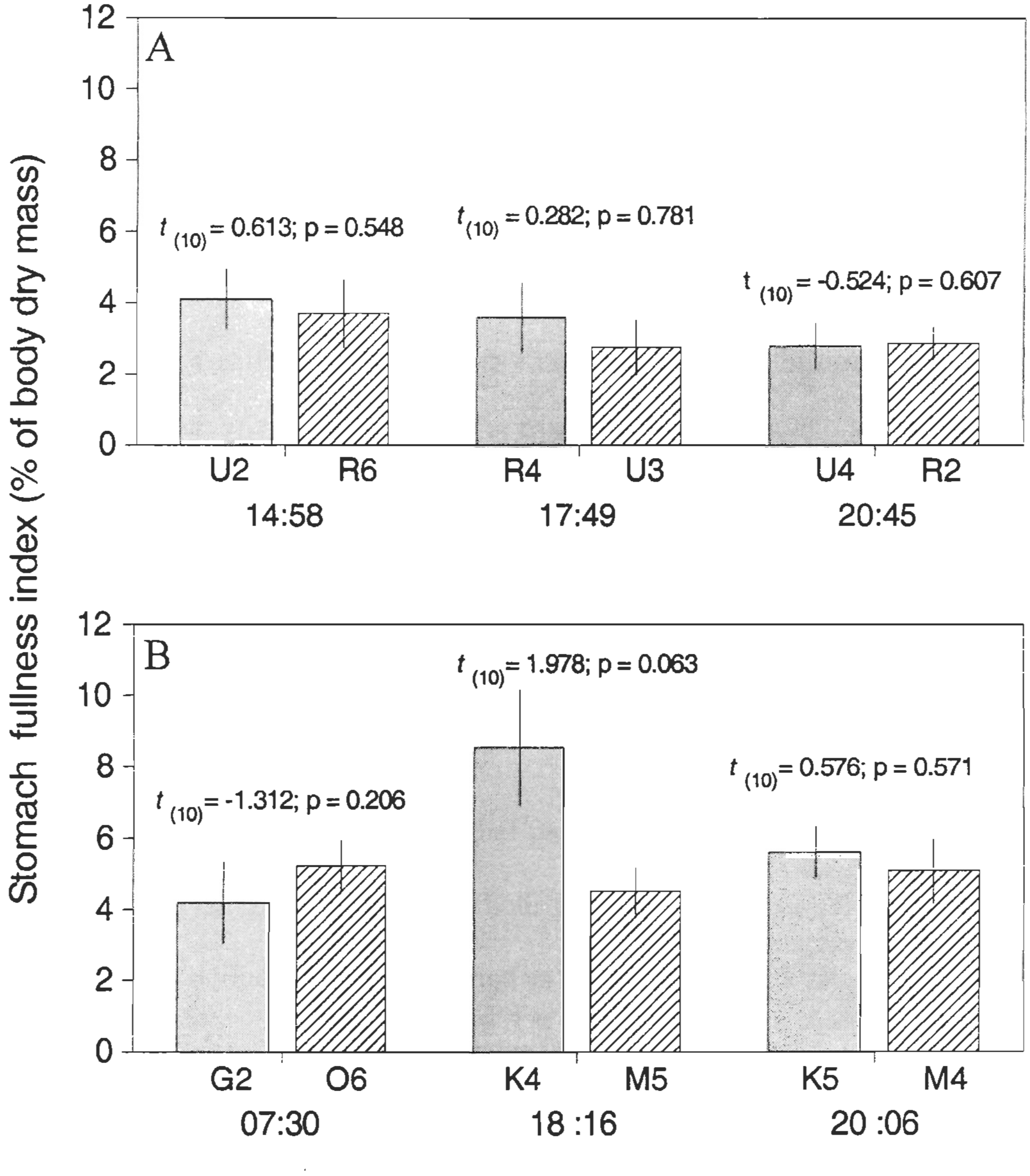

Figure 6. *Themisto libellula*. Spatial variation in stomach fullness index (SFI) (mean ± SE) in the NWGSL (A) and the LSLE (B) in fall 2004 at two stations sampled at the same time of the day. Results of the Student's *t*-test comparing the mean SFI ($\log_{10}$) between two stations chosen at the same hour are also shown.

Diel feeding pattern

Our estimation of daily pattern of variation of the SFI for fall 2003 showed a significant diel pattern in both regions (Fig. 7). Indeed, the mean values of the SFI ranged from 2.18 to 5.65% in the NWGSL and between 3.21 and 4.67% in the LSLE (Fig. 7). Mean SFI varied significantly between day and night periods in both regions (NWGSL: $t_{(5.9)} = -2.801$; $p = 0.032$; LSLE: $t_{(7)} = -3.918$; $p = 0.006$). The highest value was found during the sunrise period, between 5:00 and 7:00 in the morning, and was followed by a sharp diurnal decrease that led to the lowest value observed, around noon in both regions (Fig. 7). Thereafter, the SFI stayed at a low level during the afternoon and the evening periods and increased again during the night.

Likewise, there was a significant diel pattern of variation of the DI in the NWGSL and the LSLE in fall 2003 (Fig. 7). In both regions, the lowest DI value was observed during the sunrise period, at the same period as the maximum SFI value. Thereafter, a sharp diurnal increase led to the highest DI value, observed around noon in the NWGSL and during the afternoon in the LSLE (Fig. 7). The maximum and the minimum values of the SFI and the DI observed during the sunrise period in both regions support the hypothesis that *Themisto libellula* consumes most of their prey during the second part of the night. The same daily pattern of SFI variation, showing higher values during the darkness period followed by a sharp diurnal decrease and the lowest value during the daylight period, was also observed in fall 1998 and in the LSLE (Fig. 8). However, this daily pattern of variation of the SFI was not apparent in the NWGSL in fall 1998 and in fall 2004 in both regions (Fig. 8).

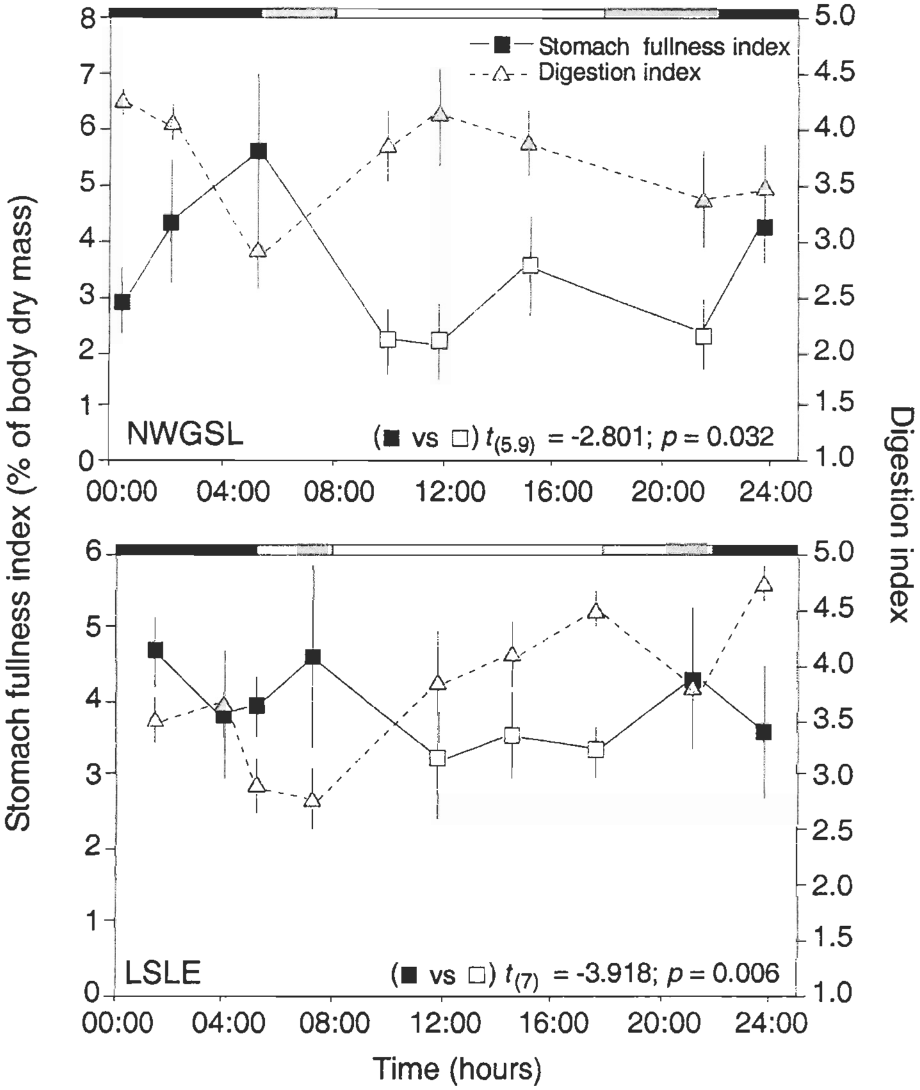

Figure 7. *Themisto libellula.* Diel variation of the stomach fullness index (SFI) and digestion index (DI) (means ± SE) in the NWGSL and the LSLE in fall 2003. Scale bars on the upper axis indicate daytime (in white), periods of sunset and sunrise (in grey), and nighttime (in black). Results of the Student's t-test comparing the mean SFI ($\log_{10}$) during the night (■) and the day (□) are also shown.

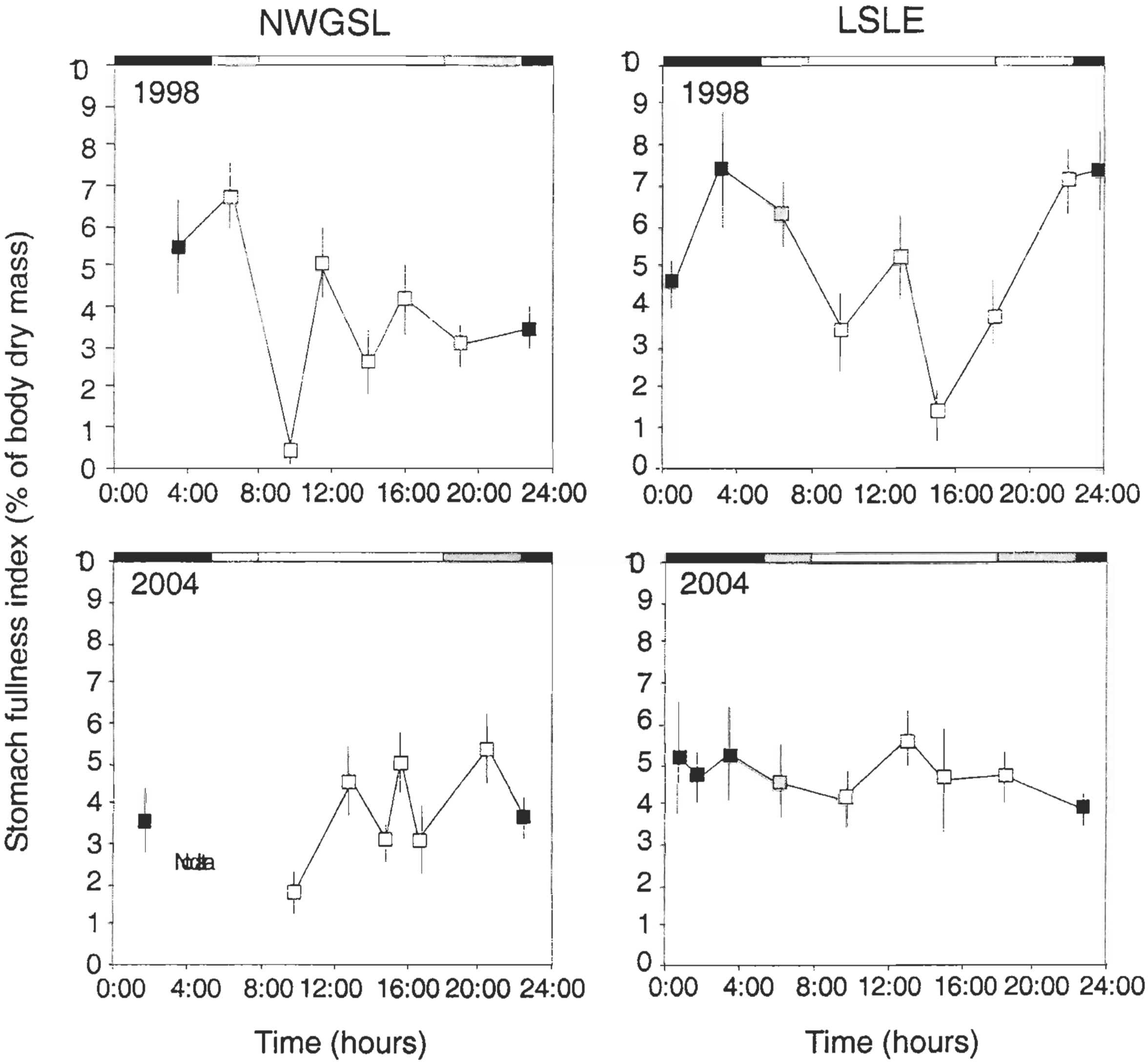

Figure 8. *Themisto libellula*. Diel variation of the stomach fullness index (SFI) (mean ± SE) in the NWGSL and the LSLE in fall 1998 and 2004. Scale bars on the upper axis indicate daytime (in white), periods of sunset and sunrise (in grey), and nighttime (in black).

The circadian cycle in feeding activity was tested statistically on the SFI and the DI with GAMs using all data combined (SFI: regions and years; DI: regions in 2003) (Fig. 9). There was a significant effect of the time of day on both SFI ($F_{(6.334)} = 2.504$, $p = 0.047$) and DI ($F_{(7.253)} = 5.299$, $p = 0.011$). These results confirm that *Themisto libellula* was a nocturnal feeder and that a large part of the stomach content was digested during the daylight period (Fig. 9). Nevertheless, the SFI slightly increases during the afternoon and the sunset periods. This suggests that *T. libellula* also acquires some food during this period (Fig. 9). Moreover, the curves of the SFI and DI versus time fitted by GAMs allowed the estimation of the digestion time (*DT*) of *T. libellula* by calculating the difference between the time of the day when the highest values of both variables (SFI and DI) were observed. In the present study, the highest values of SFI and DI were observed at 05:00 and 18:00, respectively, thus the *DT* was estimated to be *ca.* 13 hours in both regions (Fig. 9).

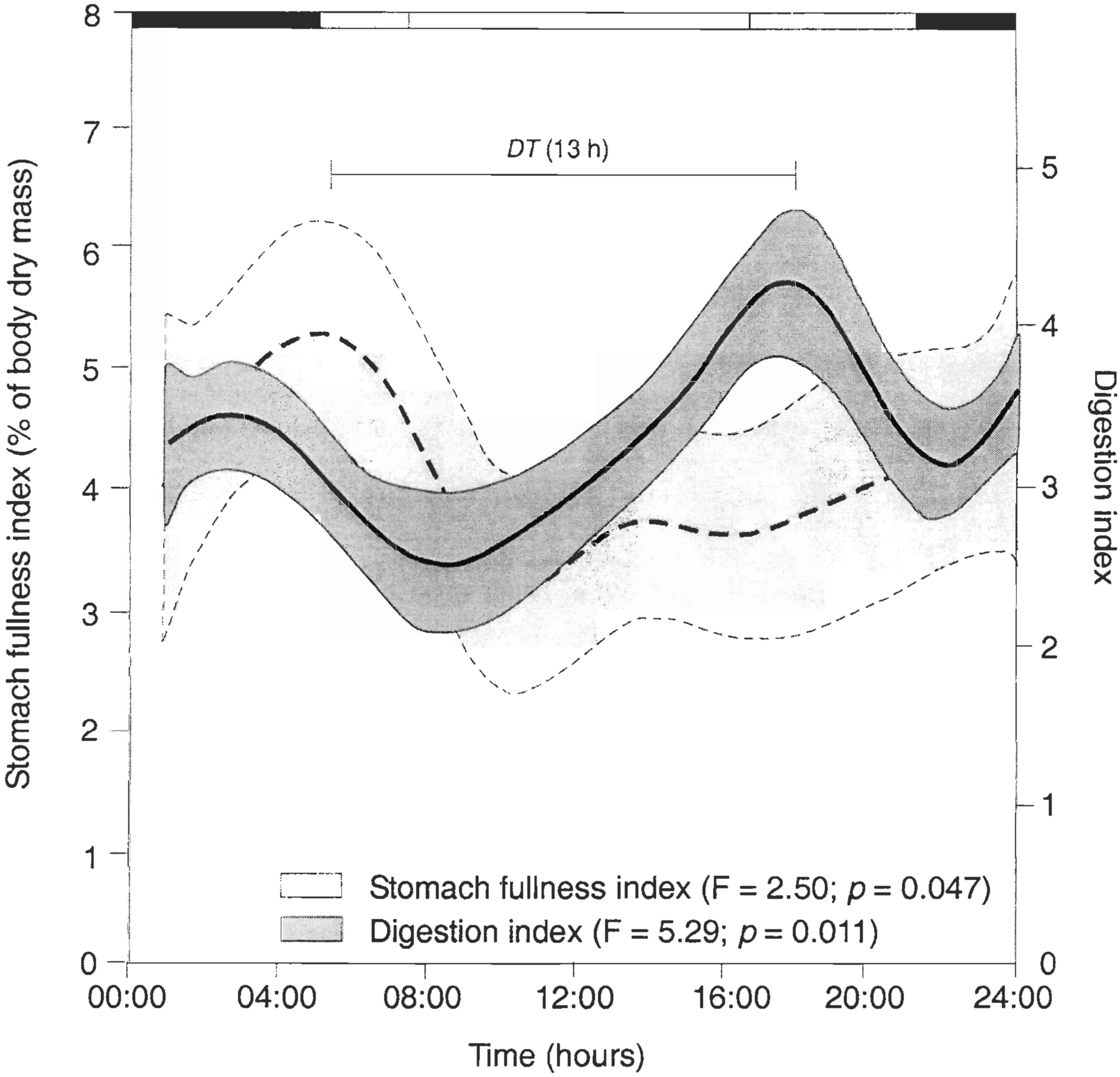

Figure 9. *Themisto libellula.* General Additive Models (GAMs) showing the diel variation in stomach fullness index (SFI) and digestion index (DI) using all data (SFI: regions and years; DI: regions in 2003). The thick lines show the fitted relationships based on GAMs; shaded bands are ± 2 SE. Scale bars on the upper axis indicate daytime (in white), periods of sunset and sunrise (in grey), and nighttime (in black). The digestion time (*DT*) was estimated by calculating the difference between the time of the day when the highest values of the SFI and the DI where observed.

Stomach content analysis

Table 3 and Figure 10 show the average numbers and percentages of different prey items found in the stomach contents of *Themisto libellula* sampled every *ca.* 3 hours over a 24-h period in each region (NWGSL and LSLE) in fall 2003. A total of 206 stomachs (96 individuals in the NWGSL and 110 in the LSLE) were examined, with prey items found in 188 individuals. Thus, 91.3% of the total number of amphipods examined contained food items in their stomachs (Table 3).

The mean number of food items found in the stomach contents varied between 2.9 and 13.1 prey $\cdot$ amphipod^{-1} in both regions. This diet was mostly composed of copepods, which made up between 83 and 97% of the food items (Fig. 10A). Amphipods, chaetognaths, euphausiids, isopods, and mysids accounted for the remainder of the prey. Euphausiids, mainly adults, were found to be the third most frequently identified prey within the stomach contents. The mean number of euphausiids eaten per amphipod at different times of the day varied between 0 and 0.5 ind. $\cdot$ amphipod^{-1} in both regions, and they were found in the stomach contents of at least one *Themisto libellula* in almost all periods of the day in both regions (Table 3). Chaetognaths followed euphausiids, with an average of 0.2 ind. $\cdot$ amphipod^{-1} $\cdot$ day^{-1} for the two zones, but they were present in the stomach contents during only half of the periods of the day analyzed in both regions. Isopods and mysids were only present in the NWGSL and only at one period of the day (Table 3). These two categories can thus be considered as occasional prey.

Table 3. *Themisto libellula*. Diet composition and mean number of prey items per amphipod sampled in the NWGSL and the LSLE in fall 2003.

Sampling zone	NWGSL								LSLE								
Sampling time (hours)	00:18	02:09	05:12	09:55	11:45	15:00	21:30	23:46	01:29	03:52	05:12	07:14	11:40	14:36	17:44	21:47	23:47
Prey identification																	
Amphipods																	
Unidentified amphipods	-	-	-	0.1	-	0.1	-	-	-	0.2	0.1	-	-	-	0.1	-	-
Chaetognaths																	
Unidentified chaetognaths	0.1	-	0.1	-	0.4	0.1	-	0.1	0.1	-	0.3	0.1	-	0.3	-	-	-
***Calanus* copepods**																	
Unidentified *Calanus*	2.2	0.7	2.0	0.5	1.3	0.4	0.2	0.6	0.7	1.0	0.6	1.2	0.2	0.9	-	0.5	0.1
C. finmarchicus	0.4	2.8	6.4	1.2	1.5	2.6	1.9	6.3	5.9	3.4	7.9	7.9	1.3	3.3	3.6	3.5	1.6
C. hyperboreus	-	0.1	0.7	-	0.1	0.1	0.1	-	-	0.1	0.3	0.5	-	-	-	-	-
Other copepods																	
Acartia longiremis	-	-	-	-	-	-	0.3	0.1	-	0.1	0.1	0.3	0.3	-	0.1	0.1	0.2
Euchaeta norvegica	-	0.1	0.3	0.3	0.2	-	0.2	0.3	0.4	0.3	0.6	0.6	0.2	0.6	-	0.5	0.1
Metridia longa	-	-	0.2	-	-	-	0.5	0.2	0.9	0.7	0.3	0.4	0.2	0.8	0.8	0.5	0.1
Microcalanus spp.	-	-	-	-	-	-	-	0.4	0.2	0.1	0.2	0.3	0.1	-	-	-	-
Oithona spp.	-	-	0.1	-	-	-	0.1	-	-	-	0.1	0.8	-	-	-	0.2	0.1
Pseudocalanus spp.	-	0.1	0.5	0.1	0.1	-	-	0.3	0.1	-	0.2	0.5	-	0.5	0.1	-	-
Unidentified copepods	0.1	0.4	1.2	1.1	0.6	0.2	0.2	1.1	0.7	0.6	0.5	0.2	0.2	1.1	0.8	0.8	0.3
Euphausiids																	
Unidentified adults euphausiids	0.1	0.5	0.3	0.1	-	0.2	0.7	0.4	0.4	0.6	0.3	0.1	0.4	-	0.5	-	0.4
Isopods																	
Unidentified isopods	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mysids																	
Unidentified adults mysids	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other items and debris																	
Unidentified	0.1	0.2	-	-	-	0.3	-	-	0.1	-	0.1	0.2	-	-	-	0.5	0.1
Number of stomachs	16	20	10	10	10	10	10	10	20	10	20	10	10	10	10	10	10
Number of empty stomachs	4	1	0	3	0	0	1	0	0	1	1	1	2	1	0	1	2
Mean number of prey / amphipod	3.1	4.8	11.9	3.4	4.2	4.0	4.2	9.8	9.3	7.1	11.2	13.1	2.9	7.5	6.0	6.6	3.0
Mean biomass of prey / amphipod (mg)	3.2	5.2	7.2	2.9	2.5	3.1	5.0	5.7	6.0	7.0	6.9	7.1	3.2	4.1	4.6	3.8	3.2

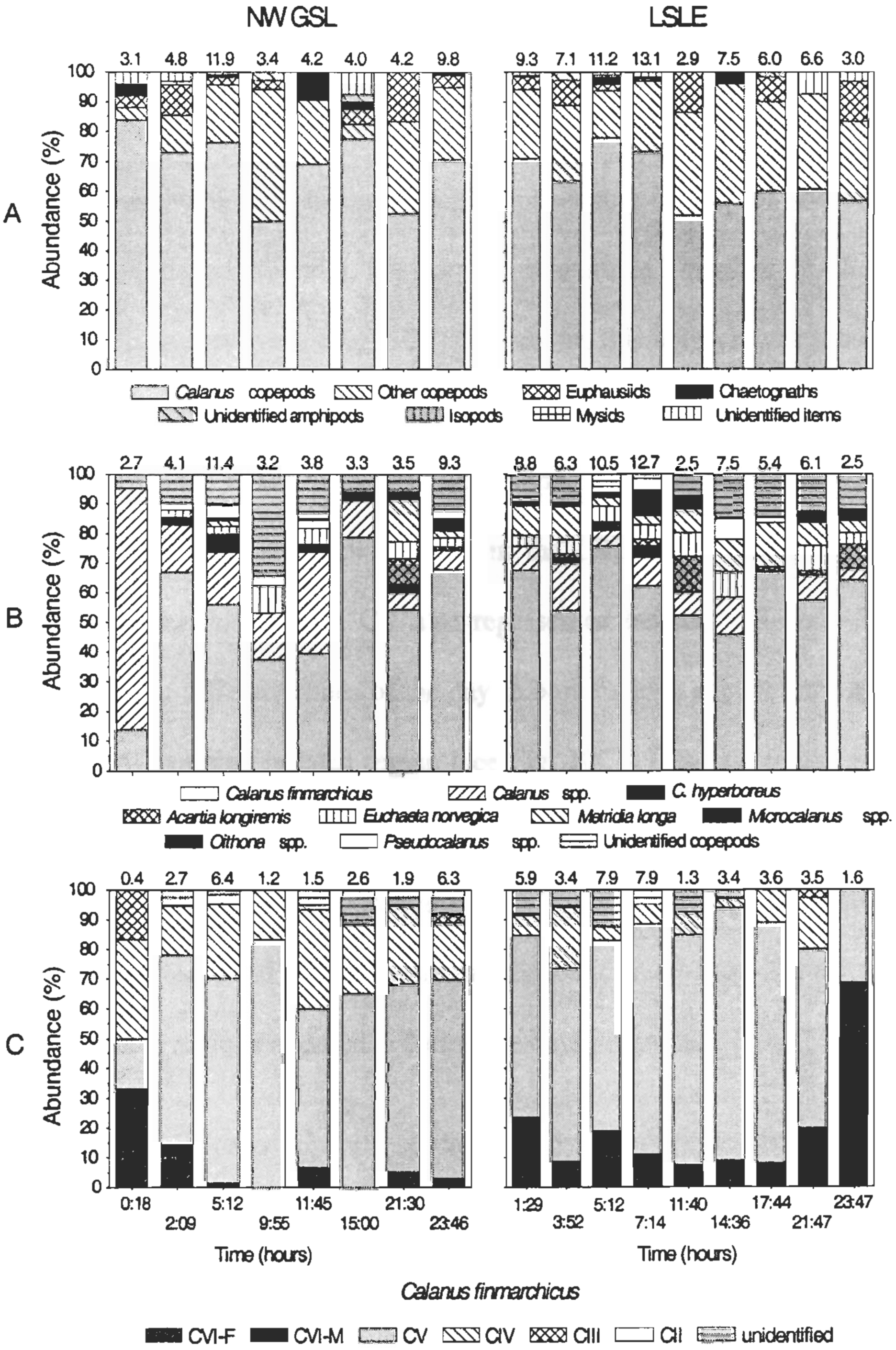

Figure 10. *Themisto libellula*. Diel variation in the prey composition in the NWGSL and LSLE in fall 2003 (A: general prey items; B: *Calanus* and other copepods; C: *Calanus finmarchicus* copepodids and adult developmental stages). Numbers above the figures represent the mean number of prey eaten per amphipod.

The mean number of copepods found in the stomach contents at different times of the day varied between 2.5 and 12.7 ind. · amphipod^{-1} in both regions (Fig 10b). *Calanus finmarchicus* was the most abundant species, representing 45 to 75% and 10 to 75% of the total number of copepods found in the stomach contents of *Themisto libellula* in the LSLE and the NWGSL, respectively (Fig. 10B). Moreover, this species was mostly represented by the copepodid and adult stages CIV, CV, CVI-F, and CVI-M (Fig. 10C). Of these stages, CV was the most abundant food item, representing 70 and 63% of the *C. finmarchicus* found in stomach contents in the LSLE and the NWGSL respectively. Moreover, *C. finmarchicus* stage CV also represented between 23 and 48% of the total food items found at different times of the day in both regions except during one of the two midnight periods sampled in each region (see Fig. 10C). Thus, *C. finmarchicus* stage CV was the most abundant food item found in this study. Three times more stage CIV copepodids were found in amphipods from the NWGSL (24.2%) than in the LSLE (8.6%) for all sampled periods, and females were mostly found in the stomach contents during the dark period in both regions and males during the daylight period in the LSLE (Fig. 10C).

Of the other *Calanus* copepod species found in both regions, *Calanus hyperboreus* were present but did not make up a major component of the amphipod diet (Table 3 and Fig. 10B). *Acartia longiremis*, *Euchaeta norvegica*, *Metridia longa*, *Microcalanus* spp., *Oithona* spp., and *Pseudocalanus* spp. were found in the stomach content of *T. libellula* in both regions (Table 3). Four copepod species, *M. longa*, *E. norvegica*, *Pseudocalanus* sp., and *A. longiremis* were found in the stomach contents of *T. libellula* during almost all periods of the day in the LSLE. Among these species, the most abundant was *M. longa*, with an average abundance of 0.52 ind. · amphipod^{-1} · day^{-1}, followed by *E. norvegica* (0.37 ind. · amphipod^{-1} · day^{-1}), *Pseudocalanus* spp. (0.16 ind. · amphipod^{-1} · day^{-1}), and *A. longiremis* (0.13 ind. · amphipod^{-1} · day^{-1}). On the other hand, only two copepod species, *E. norvegica* and *Pseudocalanus* sp., were present in amphipod stomachs throughout the day in the NWGSL, with an average abundance of 0.18 and 0.14 ind. · amphipod^{-1} · day^{-1}, respectively. Finally, two very small copepods, *Oithona* spp. and *Microcalanus* spp., were found in the stomach contents of *T. libellula* at different periods of the day, principally in the LSLE (Table 3 and Fig. 10B).

Daily ingestion rate

Tables 4 and 5 show the results of the two approaches used to estimate the daily ingestion rates (*DIR*) of *Themisto libellula* in both regions (LSLE and NWGSL) in fall 1998 (approach 1), 2003 (approaches 1 and 2), and 2004 (approach 1). According to the approach based on SFI (DIR_1), the 24 h-integrated SFI (*G*) expressed in % of amphipod body dry mass, varied between 3.42 to 5.16% in both regions in fall 1998, 2003 and 2004 (Table 4). Using the estimated digestion time of 13 hours obtained from the GAMs (Fig. 6), the DIR_1 varied between 7.19 and 9.54% of the amphipod body dry mass per day in the LSLE and between 6.32 and 7.19% in the NWGSL during the three years (Table 4). In the second approach (DIR_2), which is based on the calculation of the mean biomass of prey removed per unit of time, the daily ingestion rate was estimated to be 19.97 and 17.02% of the amphipod body dry mass per day in the LSLE and the NWGSL, respectively in fall 2003 (Table 5). If we consider only *C. finmarchicus*, the DIR_2 was estimated at 5.50 and 3.28% of the amphipod body dry mass per day in the LSLE and the NWGSL, respectively (Table 5).

Table 4. *Themisto libellula*. Estimates of the daily ingestion rate (DIR_1) calculated according to the first approach in animals sampled in the NWGSL and LSLE in fall 1998, 2003 and 2004 (SFI: stomach fullness index).

Sampling zone	Year	SFI (% body dm)	DIR_1 (% body dm · d^{-1})
NWGSL	1998	3.89	7.19
	2003	3.42	6.32
	2004	3.75	6.92
LSLE	1998	5.16	9.54
	2003	3.89	7.19
	2004	4.73	8.74

Table 5. *Themisto libellula*. Estimates of the daily ingestion rate (DIR_2) calculated according to the second approach in animals sampled in the NWGSL and LSLE in fall 2003 (Mean *BPA*: average biomass of the prey ingested · amphipod^{-1} during a 24-h period, *FR*: feeding rate).

Organism	Sampling zone	Mean *BPA* (mg)	*FR* (mg · d^{-1})	DIR_2 (% body dm · d^{-1})
Mesozooplankton Macrozooplankton	NWGSL	4.40	8.03	17.02
	LSLE	5.10	9.43	19.97
C. finmarchicus	NWGSL	0.84	1.55	3.28
	LSLE	1.41	2.60	5.50

Predation impact

The daily predation impact was estimated in each region (LSLE and NWGSL) in fall 1998 (approach 1), 2003 (approaches 1 and 2), and 2004 (approach 1). The calculated daily predation impact using the SFI approach (approach 1) was generally low, accounting for < 0.8% of the zooplankton standing stock in both regions in fall 1998, 2003, and 2004 (Table 6). The average value of the daily predation impact estimated in 1998, 2003 and 2004 was 2 times higher in the LSLE than in the NWGSL (approach 1). On the other hand, the calculated daily predation impact using the feeding rate approach (approach 2) was 3 times higher than in the first approach, accounting for 2.18 and 0.49% of the zooplankton standing stock in the LSLE and the NWGSL respectively (Table 6).

Table 7 shows the calculated daily predation impact on the standing stocks of various copepod species found in the stomach contents of *Themisto libellula* in both regions in fall 2003, including the different copepodid stages of *Calanus finmarchicus*. The daily predation impact estimated using the second approach varied from 0.04 to 39.62% and < 0.01 to 2.40% in the LSLE and the NWGSL, respectively (Table 7). The standing stocks that were most affected by the daily predation impact of *T. libellula* in the LSLE were *Euchaeta norvegica* (39.6%), *C. finmarchicus* CVI-F (18.5%), CVI-M (10.3%), CV (2.8%), CIV (2.7%), *Metridia longa* (2.5%), and *Acartia longiremis* (1.8%). The standing stocks of these same species were also observed to be the most affected in the NWGSL, except for *M. longa* and *A. longiremis*. However, the daily predation impact was *ca.* one order of magnitude lower in the NWGSL than in the LSLE on the standing stocks of each copepod species (Table 7).

Table 6. *Themisto libellula.* Predation impact on mesozooplankton and macrozooplankton standing stock in fall 1998, 2003, and 2004 in the St. Lawrence marine system estimated using the two different approaches. The first approach is the stomach fullness index and the second approach is where the mean number of prey is converted to prey biomass. Zooplankton biomass data is from the Atlantic Zone Monitoring Program in 2003 (M. Harvey, unpublished data).

Approach	Organism	Sampling zone	Year	Zooplankton Biomass (g dm · m^{-2})	*Themisto libellula*		Daily predation impact (% biomass)
					Abundance (ind · m^{-2})	Biomass (g dm · m^{-2})	
1	Mesozooplankton Macrozooplankton	NWGSL	1998	20.49	10.64	0.41	0.14
			2003	20.05	13.65	0.58	0.18
			2004	23.58	11.86	0.59	0.70
		LSLE	1998	19.31	11.67	0.46	0.23
			2003	11.47	23.26	1.25	0.78
			2004	17.80	27.85	1.55	0.76
2	Mesozooplankton Macrozooplankton	NWGSL	2003	20.05	13.65	0.58	0.49
		LSLE		11.47	23.26	1.25	2.18
	C. finmarchicus	NWGSL	2003	4.61	13.65	0.58	0.41
		LSLE		2.03	23.26	1.25	3.39

Table 7. *Themisto libellula*. Predation impact on copepod population standing stocks in the St. Lawrence marine system in fall 2003. Copepod biomass was estimated from data of the Atlantic Zone Monitoring Program collected in 2003 (M. Harvey, unpublished data). Mean *BPA* is the average biomass of the prey ingested · amphipod^{-1} during a 24-h period, *FR* is the feeding rate calculated with the mean *BPA*, and *DIR* is the daily ingestion rate.

Sampling zone	Species	Average biomass ($mg \cdot m^{-2}$)	Mean *BPA* (mg)	*FR* ($mg \cdot d^{-1}$)	DIR_2 (% body dm $\cdot d^{-1}$)	Daily predation impact (% biomass)
LSLE	***Calanus* copepods**					
	C. finmarchicus					
	CVI-F	55.67	0.21	0.39	0.83	18.52
	CVI-M	21.46	0.05	0.08	0.18	10.31
	CV	1861.58	1.06	1.96	4.16	2.79
	CIV	73.74	0.04	0.08	0.16	2.68
	CIII	9.30	< 0.01	< 0.01	< 0.01	0.16
	C. hyperboreus	6396.18	0.18	0.34	0.71	0.14
	Other copepods					
	Acartia longiremis	2.10	< 0.01	< 0.01	< 0.01	1.78
	Euchaeta norvegica	97.85	0.79	1.46	3.10	39.62
	Metridia longa	162.78	0.08	0.15	0.33	2.50
	Microcalanus spp.	5.30	< 0.01	< 0.01	< 0.01	0.57
	Oithona spp.	19.11	< 0.01	< 0.01	< 0.01	0.04
	Pseudocalanus spp.	8.41	< 0.01	< 0.01	0.01	0.83
NWGSL	***Calanus* copepods**					
	C. finmarchicus					
	CVI-F	134.11	0.04	0.07	0.16	0.67
	CVI-M	17.31	0.01	0.01	0.02	0.81
	CV	3873.09	0.69	1.27	2.69	0.40
	CIV	526.92	0.08	0.14	0.29	0.32
	CIII	48.58	< 0.01	< 0.01	< 0.01	0.02
	CII	3.82	< 0.01	< 0.01	< 0.01	0.11
	C. hyperboreus	12315.61	0.13	0.24	0.51	0.02
	Other copepods					
	Acartia longiremis	1.40	< 0.01	< 0.01	< 0.01	0.49
	Euchaeta norvegica	369.16	0.39	0.72	1.53	2.40
	Metridia longa	260.08	0.02	0.03	0.07	0.16
	Microcalanus spp.	3.66	< 0.01	< 0.01	< 0.01	0.22
	Oithona spp.	21.89	< 0.01	< 0.01	< 0.01	< 0.01
	Pseudocalanus spp.	28.73	< 0.01	< 0.01	0.01	0.10

DISCUSSION

Population structure

The length-frequency distribution of *Themisto libellula* sampled in the LSLE and the NWGSL in September 1998 and 2003 and November 2004 revealed two size classes with median lengths of 30 and 42 mm in 1998, 33 and 42 mm in 2003, and 36 and 45 mm in 2004 in both regions. Observations made by Percy (Percy & Fife 1993) in the Hudson Strait, and by different authors in other Arctic seas (see review in Auel & Werner 2003) found that a cohort of juveniles measuring between 5 and 12 mm was usually present in August-September. However, this category of small individuals has never been observed during the annual macrozooplankton biomass monitoring survey, which has been carried out in early September in the LSLE and the NWGSL since 1994. In fact, May-June is the only period of the year that has revealed some small individuals (8-20 mm) in the SLMS (M. Harvey, unpublished data).

The larger size class of *Themisto libellula* sampled in September in the GSL (median length 43 mm) were *ca.* 1.5 times larger than individuals sampled in August-September in the Hudson Strait, the Hudson Bay, the Barents Sea, the central Fram Strait, and the East Greenland shelf (median *ca.* 28 mm) (Percy & Fife 1993, Dalpadado 2002, Auel & Werner 2003). Interestingly, the individuals sampled with BIONESS in the GSL were of the same size (between 43 and 50 mm) as those found in ringed seal and cod stomachs (47 and 50 mm) at Baffin Island and the Barents Sea (Dunbar 1957, Dalpadado et al. 2001). The ringed seal habitually feeds on the larger individuals of the *Themisto* population (Dunbar 1957). Based on the information provided by Auel & Werner (2003), our study would be the first net-based study to report the presence of *T. libellula* larger than 40 mm. This group represents between 4 and 40% of the total number of individuals sampled in each region in the fall of 1998, 2003, and 2004.

The difference in the median size of the larger *Themisto libellula* sampled in the SLMS and in some Arctic seas cannot be attributed to net avoidance since they were sampled with the same type of plankton net in both areas (1 m^2 BIONESS, 1 m^2 MOCNESS, 8 m^2 Rectangular Midwater Trawl). Also, this difference cannot be attributed to the sea water temperature during the summer season since *T. libellula* lives permanently in the cold intermediate layer (CIL) in the SLMS, at temperatures varying between -1 and +3°C (M. Harvey, unpublished data). This is comparable to the temperatures of the surface layer during the summer season in various Arctic seas where *T. libellula* was usually observed (see Auel & Werner 2003). The quantity and the nutritive value of the food items as well as the length of the rich nutritive season (April - November) in the GSL region may account for the difference in the median size of *T. libellula* observed between the SLMS and Arctic seas.

Feeding ecology

This study is the first to examine and statistically test the diel feeding pattern of a macrozooplankton organism using generalized additive models (GAM). Based on the model results, *Themisto libellula* consumed prey mostly during the latter part of the night and the sunrise period, while much of the stomach content was digested during the daylight period. The graphical examination of the daily pattern of variation of the stomach fullness index (SFI) over a 24-h period, along with GAMs, suggested that *T. libellula* also acquired a small quantity of food during the afternoon and before the sunset period. This is supported by the observation that *Calanus finmarchicus* males were mostly found in the stomach contents sampled in the daylight period in the LSLE. The enhanced feeding of *T. libellula* during the sunrise and before the sunset periods is consistent with results obtained by Fortier et al. (2001). In that study, which was located at Barrow Strait and at the ice-water interface during the midnight sun period, the SFI of *T. libellula* was optimal in late evening when light intensity was near minimum, and in late morning when light was near maximum. In South Georgia (southern Atlantic Ocean) and in the Prince Edward Archipelago (southern Indian Ocean), *T. gaudichaudi* also has a diurnal feeding activity with two distinct peaks occurring just after sunrise and before sunset (Kane 1967, Pakhomov & Perissinotto 1996, Froneman et al. 2000). Another species, *T. japonica*, also has a diel feeding activity pattern with two distinct peaks except that it feeds more actively during the day than during the night—about half that of daytime (Yamashita et al. 1984).

The results of the stomach content analysis suggest a close relationship between the structure of the local zooplankton community and the diet composition of *Themisto libellula*. Stomach contents indicated that *T. libellula* occupies an important trophic status as zooplankton consumers in the SLMS. Zooplankton organisms, such as copepods, euphausiids, and chaetognaths, constituted the bulk of its diet during the fall season. Amphipods of the genus *Themisto* are known to be mainly carnivorous predators, principally of zooplankton (Kane 1967, Sheader & Evans 1975). The diverse dietary composition of *T. libellula* was in agreement with studies on *T. gaudichaudi*, which was recognized as a visual opportunistic predator, also consuming copepods, euphausiids, pteropods, and chaetognaths (Hopkins 1985, Pakhomov & Perissinotto 1996). Our study emphasized the dominance of copepods in the diet of *T. libellula* in the fall, and especially of *Calanus* copepods. This pattern has also been observed in Arctic regions (Dunbar 1946, Falk-Petersen et al. 1987, Scott et al. 1999, Fortier et al. 2001, Auel et al. 2002).

The results of stomach content analyses also showed a close relationship between the vertical distribution of the local zooplankton community and the diet composition of *Themisto libellula*. Its feeding pattern reflected the well-known diel migration pattern of mesozooplankton and of *T. libellula* itself. Indeed, in the SLMS, *T. libellula* lives in permanency in the CIL (isotherm < 3°C) and migrated from the lower (150 m) to the upper (25 m) limit of the CIL during the day and the night respectively (M. Harvey, unpublished data). At the same time, during the fall season, more than 50% of *Calanus finmarchicus* CIV-CV, the numerically dominant prey items found in the stomach contents of *T. libellula*, and 75 % of the *C. finmarchicus* females were also present in the CIL (between 25-150 m) during the day and migrated to the surface layer (between 0-25 m) during the night (Zakardjian et al. 1999). The migration of *C. finmarchicus* between the CIL and the surface layer probably occurred around sunrise (descending) and sunset (ascending) periods, and this coincided perfectly with the fact that *T. libellula* consumed *C. finmarchicus* CIV-CV in large and small quantities around sunrise and sunset periods, respectively. Among the other copepod species frequently observed in the stomach contents of *T. libellula* from both regions, *Metridia longa*, *Microcalanus* spp., and *Euchaeta norvegica* were likewise present in the CIL (between 25-150 m) during the day and migrated to the surface layer (between 0-25 m) during the night (Plourde et al. 2002, M. Harvey, unpublished data).

Compared to the other copepod species, *Calanus hyperboreus*, *Pseudocalanus* spp., *Acartia longiremis* and *Oithona* spp. were observed in relatively low frequency in the stomach contents of *T. libellula*. This could be explained by the fact that during the fall season, the greater part of these copepod populations were either in diapause in the deep layer between 200 and 300 m (*C. hyperboreus*) or residing in the surface layer during the daytime and the nighttime (*Pseudocalanus* spp., *Acartia longiremis* and *Oithona* spp.) (Plourde et al. 2002, Plourde et al. 2003). Only a small percentage of these populations (<10%) were present in the CIL (isotherm < 3°C) at this time of the year.

Two of the more important macrozooplankton groups found in the stomach contents of *Themisto libellula* in both regions were the euphausiids and chaetognaths. These groups also resided in the CIL during the day and migrated to the surface layer during the night

(Sameoto & Jaroszynski 1973, Sameoto 1976, M. Harvey, unpublished data). In contrast, another group, the mysids, occupied the deep layer night and day, displaying little vertical displacement except in the NWGSL region, where a small proportion of the population would move up slightly to the lower part of the CIL during the nighttime (M. Harvey, unpublished data).

In conclusion, the high degree of overlap in the vertical distributions of prey as *Calanus finmarchicus* (CIV-CV and females), *Metridia longa*, *Microcalanus* spp. and euphausiids during both daytime and nighttime, were reflected by their high presence in the stomach contents of *Themisto libellula* in the SLMS. The high abundance of the CV stage, which was characterized by the *C. finmarchicus* population in autumn (Plourde et al. 2001), accounted for their dominance as prey. Thus, *T. libellula* was able to efficiently exploit the diel-migratory zooplankton community in these regions. The results of our stomach contents analyses lead to the conclusion that *T. libellula* is an opportunistic predator which can feed on any prey of appropriate size present in its habitat (CIL) during the day and the night periods. Furthermore, feeding activity and daily ingestion rates will be greatly influenced by the degree of overlap between the vertical distributions of *T. libellula* and its prey.

Daily ration

The digestion time (*DT*) of *Themisto libellula* obtained in the present study (13 h) is *ca*. 1.7 times higher than that seen in other *Themisto* species (*T. japonica* 6.5 h, Yamashita et al. 1985; *T. gaudichaudi* between 7.5 h and 8.1 h, Pakhomov & Perissinotto 1996, Froneman et al. 2000). In these studies, the *DT* was determined using the linear regression of change in SFI, which may account for the difference, although there are limits to this method (see Pakhomov & Perissinotto 1996). The effect of some factors, such as temperature, the number of prey in the stomach, prey size, and the influence of activity feeding may all affect the digestion time. Some of these factors have been reported to influence the value of *DT* in mysids (Murtaugh 1984, Cartes et al. 2001) and chaetognaths (Tönnesson & Tiselius 2005), but not in decapods (Maynou & Cartes 1998). The effects of these factors could not be tested with our approach; however, if there was ingestion of prey before sunrise or during daytime, the *DT* will be overestimated, and consequently the daily ingestion rates will be underestimated. For mysids, *DT* was inversely related to water temperature (Chipps 1998) and it is generally accepted that metabolic rates seen in a variety of taxa like fishes are lower with lower temperatures (Brett & Glass 1973, Karamushko & Shatunovskij 1993). The fact that *T. libellula* lives in the CIL at temperatures varying between -1 and +3°C, may thus explain its high estimated *DT*. Moreover, our estimate was close to the *DT* maxima found for *Euphausia superba* and *Boreomysis arctica* (equal to 10 h and 9 h, respectively), which also live in cold water (Pakhomov & Perissinotto 1997, Cartes & Maynou 2001).

In this study, the daily ingestion rate (*DIR*) of *Themisto libellula* was estimated using two different approaches, and a pronounced variability in the results was observed. The *DIR* on mesozooplankton and macrozooplankton using the second method was twice that when estimated with the first method. The *DIR* ranged from 6.32 to 9.54 % of body dry mass per day and from 17.02 to 19.97 with the first and the second method, respectively. These variations seem to be related to the two models founded on the Bajkov's equation. Most studies that used Bajkov's method were conducted using prey frequency (Øresland 1990, Froneman & Pakhomov 1998, Froneman et al. 1998, Øresland 2000). Less common were those that used biomass, or an index of biomass, as the SFI (Pakhomov & Perissinotto 1996, Froneman et al. 2000). Over the course of digestion, the number of prey does not change much until it is well advanced, unlike the prey biomass which changes progressively. This could explain the large difference seen between the two methods. In this case, the *DIR* from the SFI method will be underestimated.

Taking into account the fact that *Themisto libellula* is larger than other individuals of the genus *Themisto*, the in situ *DIR* estimated for zooplankton when using the SFI method was in reasonable agreement with those for *T. gaudichaudi* calculated with the same method (6.3% of body dry mass, Pakhomov & Perissinotto 1996; and 11.5% and 19.8%, respectively, for both offshore and inshore locations (Froneman et al. 2000) and for *T. japonica* calculated from in vitro experiments (6.6% of body dry mass, Ikeda & Shiga 1999). The *DIR* from the feeding rate method (second approach), estimated at 19.97% and 17.02% for the LSLE and the NWGSL respectively, corresponded to in vitro daily rations. The *DIR* obtained by in vitro incubations for *T. gaudichaudi* ranged from 8.5 to 21.8%

(Pakhomov & Perissinotto 1996) and 15.4 to 24.2% for *T. japonica* (Yamashita et al. 1985). Some of the differences in the *DIR* of *T. gaudichaudi* may be attributable to differences in its estimated *DT*, as well as differences in seawater temperature and its effects on metabolic processes. The degree of overlap between the vertical distributions of prey and these of the genus *Themisto* may also create disparity between these estimates (Gibbons & Painting 1992). In the second approach, incomplete ingestion of prey may cause bias or lower the precision of the *DIR* (Price et al. 1988, Beyer 1993, Båmstedt & Karlson 1998). Stomachs of *T. libellula* were sometimes observed to be completely filled by a very compact pink mass made up of eye, leg and gill fragments, suggesting that a whole individual had been ingested. Likewise, prey fragments were assumed to represent the remains of a single prey (see material and methods). Thus, the bias of incomplete prey ingestion may be negligible in our study. *T. libellula* is therefore seen as an active predator that exhibits a high *DIR*.

Very little is currently known about the rates of daily food consumption by *Themisto libellula*. The only daily ingestion rate available for this species was estimated by Auel & Werner (2003) in the Greenland Sea from predation experiments on *Calanus* copepods and respiration measurements. Their *DIR* was evaluated at 1.9% of body dry mass (Auel & Werner 2003). In the present study, using the second approach and considering only *Calanus finmarchicus*, the mean *DIR*, was estimated at 4.4 % of body dry mass in both regions. The different results seen in these studies are difficult to interpret because a variety of methods were used. However, our ingestion rate was determined in situ whereas that of Auel and Werner (2003) came from predation experiments that had several factors that may have biased their results. For example, factors like bottle effects or light intensity may influence prey or predator behaviour or prey availability. Furthermore, Auel and Werner (2003) did not exclude the possibility that stress during the catch could have led to a reduced feeding activity. Finally, the discrepancy in results might also be explained by the large difference in body length between GSL (e.g., SLMS: 5 to 39 mm) and Arctic specimens (e.g., Greenland Sea: 22 to 50 mm; Auel & Werner 2003).

Predation impact

Considering the high biomass and daily ingestion rates of *Themisto libellula* in the SML, impacts on the local zooplankton communities may be expected. As estimated by the first method, the daily predation impact of *T. libellula* on the zooplankton standing stock never exceeded 0.8%. On the other hand, the predation impacts estimated using the second method was higher and accounted for 2.2% and 0.5% of the zooplankton standing stock for the LSLE and the NWGSL, respectively. The predation impact is a function of both prey and predator biomass and the daily ingestion rate. Hence, all of the biases associated with *DIR* as well as abundance estimates may have an effect on this impact. In the SFI approach, predation impact should be regarded as an underestimate as the *DIR* was underestimated. Therefore, the impact of *T. libellula* predation may lie between these two estimates.

The predation impact of *Themisto libe*llula in the St. Lawrence marine system might appear insignificant over the whole of the zooplankton community. Nevertheless, our predation estimate is much greater than that of Auel and Werner (2003) in the Greenland Sea, who estimated that *T. libellula* removed only 0.03% of the mesozooplankton standing stock per day. The differing results could be related to differences in the abundance of *T. libellula* and in copepod biomass in the GSL and the Greenland Sea. The mean abundance of *T. libellula* varied between 1.5 10^{-2} and 4.3 10^{-2} ind. m^{-3} in the Greenland Sea and between 4.2 10^{-2} and 11.1 10^{-2} ind. m^{-3} in the LSLE and the NWGSL in 1998, 2003, and 2004. This discrepancy is probably not enough to justify such a difference between the predation impacts; rather, it may be due to the difference in the daily rations (see above) and to the degree of overlap between the vertical distributions of hyperiid amphipods and their prey. Predation impacts that have been determined for other hyperiid amphipods show that our estimates appeared to be in a good agreement with those investigations. In South Georgia, Pakhomov and Perissinotto (1996) revealed that the maximum predation impact of the Antarctic congener *Themisto gaudichaudi* was 2.1% of the total mesozooplankton standing stock when examined at its highest density (1.5 ind. m^{-3} corresponding to 2.8 g dm. m^{-2}). The predation impact we estimated for the LSLE with the second approach is close to this result, even if the biomass of *T. libellula* was lower than that of *T. gaudichaudi* (1.25 g dm. m^{-2}). When the abundance of *T. gaudichaudi* in the Prince Edward Archipelago was low (< 0.2 ind. m^{-3}), the predation impact of *T. gaudichaudi* never exceeded 0.2% of the mesozooplankton biomass (Froneman et al. 2000). The difference in the abundance of *T. gaudichaudi* in these latter studies reflected their variation in predation pressure (Froneman et al. 2000). Nevertheless, for the same zooplankton biomass and with a low predator biomass, *T. libellula* had almost the same predation impact as *T. gaudichaudi*, thus *T. libellula* seems to exert a higher predation pressure than *T. gaudichaudi*. With regards to *T. pacifica* and *T. japonica* in the Oyashio region (western subarctic Pacific), predation impacts on zooplankton biomass never exceeded 0.11% and 0.06% respectively (Yamada & Ikeda 2006). These estimates were lower than our results, which may be attributable to differences in amphipod biomasses or in their daily rations.

To date, predation pressure has only been examined for the mesozooplanktonic community and there are no reports of the predation impact of *Themisto* spp. on copepod species. As a result, it is difficult to compare the estimated predation impacts in the SLMS with other regions. Nevertheless, the second method used in this study probably constitutes the best method to assess the predation impact of *T. libellula* on its prey. Predation impacts were always highest when the high biomass of *T. libellula* coincided with the lowest mean biomass of zooplankton/copepod species. This might explain the variations we observed between regions and species. Consequently, although daily ration was higher on *C. finmarchicus* CV, predation impact was more important on *C. finmarchicus* CVI-F and CVI-M and on *Euchaeta norvegica.*

Themisto libellula is known to form dense swarms, like *T. gaudichaudi* (Gibbons et al. 1992, Vinogradov 1999), and thus is able to reach very high densities (Eiane & Daase 2002). Under such conditions, the potential impact of their predation may be substantial. Thus, *T. libellula* may play an important ecological role in the SLMS, exerting a significant control on the mesozooplanktonic populations, and more specifically, on *C. finmarchicus* and *Euchaeta norvegica.* The predation impact of *T. libellula* may be cyclical, undergoing seasonal variations, with higher or lower predation pressures at certain periods of the year. As a result, this species may influence the trophic structure of the SLMS. Likewise, due to its abundance and trophic level, these amphipods may be significant participants in the carbon flux of the GSL. Because of the pronounced importance of meso-zooplanktonic communities in the food chain, *T. libellula* may thus provide a key link in between pelagic secondary production and higher trophic levels, including fishes and mammals, and fisheries production in the SLMS.

3. CONCLUSION GÉNÉRALE

L'objectif de notre étude était de décrire quantitativement et qualitativement le trophodynamisme de l'amphipode hypéridé *Themisto libellula* dans l'écosystème marin du Saint-Laurent et principalement dans l'estuaire maritime (EM) et le nord-ouest du golfe du Saint-Laurent (NOGSL). Ce travail avait aussi pour objectif de mettre en évidence l'importance de *T. libellula* dans les flux énergétiques régissant le réseau trophique du Saint-Laurent. Ces objectifs ont pu être atteints en utilisant les spécimens de *T. libellula* échantillonnés lors de l'étude annuelle sur la biomasse macrozooplanctonique menée une fois par an au début du mois de septembre dans l'EM et le NOGSL depuis 1994 par l'Institut Maurice-Lamontagne (Pêches et Océans Canada). Les études menées en 1998, 2003 et 2004 ont été choisies en raison de leurs abondances élevées en *T. libellula*.

L'étude de la distribution de taille des individus *Themisto libellula* du golfe Saint-Laurent révèle la présence de deux classes d'âge. Contrairement aux régions arctiques et au détroit d'Hudson, où une cohorte d'individus juvéniles est présente en Août – Septembre (Percy & Fife 1993, Auel & Werner 2003), cette catégorie de petits individus n'a jamais été observée lors de l'étude sur la biomasse macrozooplanctonique effectuée début septembre dans l'EM et le NOGSL depuis 1994. La plus grande classe de taille de *T. libellula* échantillonnés à l'automne dans le golfe du Saint-Laurent est quant à elle plus grande que celle observée dans les diverses régions que peuple cette espèce (Percy & Fife 1993, Dalpadado 2002, Auel & Werner 2003). Notre étude serait la première à révéler d'aussi grandes tailles d'individus échantillonnés avec un BIONESS. En effet, des individus aussi grands n'ont été répertoriés dans les régions arctiques que dans les estomacs de phoques et de morues (Dunbar 1957, Dalpadado et al. 2001). La différence entre la taille médiane des grands *T. libellula* provenant du système marin du Saint-Laurent et ceux des mers arctiques ne semble pas être attribuable à l'évitement possible des filets d'échantillonnage ni à la température de l'eau. Par contre, la meilleure quantité et valeur nutritive des proies ainsi que la longueur de la saison nutritive dans la région du golfe du Saint-Laurent pourraient expliquer cette différence.

Le cycle circadien de l'activité nutritive de *Themisto libellula* dans l'écosystème marin du Saint-Laurent obtenu avec les GAMs (generalized additive model) a ensuite dévoilé une consommation de la plupart des proies pendant la seconde partie de la nuit et pendant le lever du soleil. Les GAMs ont également suggéré que *T. libellula* pouvait acquérir de petites quantités de nourriture pendant l'après-midi et avant le coucher du soleil. L'augmentation de l'alimentation de cette espèce au coucher et au lever du soleil a été observée par Fortier et al. (2001) dans le détroit de Barrow. De même, à South Georgia (sud de l'océan Atlantique) et dans l'archipel du Prince Édouard (sud de l'océan Indien) *T. gaudichaudi* a également une activité nutritive cyclique avec deux pics distincts qui sont présents juste après le lever du soleil et avant le coucher du soleil (Kane 1967, Pakhomov & Perissinotto 1996, Froneman et al. 2000). Tout comme *T. libellula* et *T. gaudichaudi*, *T. japonica* possède aussi une activité nutritive avec deux pics distincts excepté qu'il se nourrit plus activement pendant le jour que la nuit (Yamashita et al. 1984).

Une étroite relation entre la structure des communautés zooplanctoniques locales et le régime alimentaire de *Themisto libellula* a été découverte lors de notre étude. Les contenus stomacaux ont indiqué que *T. libellula* occupe une place trophique importante en tant que consommateur de zooplancton dans le SMSL. Les organismes zooplanctoniques tels que les copépodes, les euphausiacés et les chaetognathes constituent ainsi la majeure partie de son alimentation pendant l'automne. Cette diversité alimentaire se retrouve également chez *T. gaudichaudi* (Hopkins 1985, Pakhomov & Perissinotto 1996). Notre étude a également souligné la dominance des copépodes *Calanus* spp. dans l'alimentation de *T. libellula*. Cette dominance a aussi été observée dans les régions arctiques (Dunbar 1946, Falk-Petersen et al. 1987, Scott et al. 1999, Fortier et al. 2001, Auel et al. 2002). Aucune preuve de cannibalisme n'a été trouvée dans notre étude, contrairement aux observations faites par Dunbar (1946) et Pakhomov & Perissinotto (1996). Le cannibalisme pourrait être saisonnier et apparaître pendant la période de couvée. Une relation étroite existe également entre la distribution verticale des communautés zooplanctoniques locales et la composition de l'alimentation de *T. libellula*. En effet, dans le système marin du Saint-Laurent, *T. libellula* vit en permanence dans la CIF (isotherme < 3°C), et migre des limites inférieures (150 m) aux limites supérieures (25 m) de la CIF pendant le jour et la nuit respectivement (M. Harvey, données non publiées). Ses proies sont plus ou moins présentes dans cette zone pendant certaines périodes de la journée en raison de leurs migrations nycthémérales (Sameoto & Jaroszynski 1973, Sameoto 1976, Zakardjian et al. 1999, Plourde et al. 2002, Plourde et al. 2003).

Notre étude a ensuite permis de calculer le temps de digestion (TD) de *Themisto libellula* dans le GSL. Ce TD a été estimé à 13 h à l'aide du GAMs. Il est assez élevé comparé à la moyenne des TD de ses congénères *Themisto* spp. qui est de 7,15 h

(Yamashita et al. 1985, Pakhomov & Perissinotto 1996, Froneman et al. 2000). Toutefois, il doit être interprété avec beaucoup de prudence. En effet, la température, le nombre de proies dans le contenu stomacal, la taille des proies ainsi que l'activité de nutrition pourraient affecter le temps de digestion ainsi que les estimations des taux d'ingestion. Le temps de digestion de *T. libellula* semblerait s'expliquer par la basse température de son habitat (la couche intermédiaire d'eau froide). Il est généralement admis que les taux métaboliques dans une variété de taxons tels que les poissons sont faibles quand la température est faible (Brett & Glass 1973, Karamushko & Shatunovskij 1993). De plus, chez les mysidacés, le temps de digestion est inversement corrélé à la température de l'eau (Chipps 1998).

Dans cette étude, deux approches ont été utilisées pour estimer les taux quotidiens d'ingestion (TQI) de *Themisto libellula* et une grande variabilité a été observée dans les résultats. Ces variations semblent être liées aux deux modèles basés sur l'équation de Bajkov. La plupart des études l'ont appliquée en utilisant un nombre de proies (Øresland 1990, Froneman & Pakhomov 1998, Froneman et al. 1998, Øresland 2000) mais très peu l'ont utilisée avec une biomasse ou un indice de biomasse comme l'indice de remplissage stomacal (Pakhomov & Perissinotto 1996, Froneman et al. 2000). Le nombre de proies ne change pas beaucoup pendant la digestion, sauf quand elle est avancée, alors que les indices de biomasse changent progressivement. Ceci pourrait expliquer la grande différence entre nos deux méthodes d'estimation. Dans ce cas, les TQI provenant de la première méthode (méthode de l'indice de remplissage stomacal) seront sous-estimés.

Avec nos deux approches d'étude, les taux quotidiens d'ingestion de *Themisto libellula* sur le zooplancton sont en accord avec ceux observés pour *T. gaudichaudi* (Sheader & Evans 1975, Pakhomov & Perissinotto 1996, Froneman et al. 2000), pour *T. japonica* (Yamashita et al. 1985, Ikeda & Shiga 1999) et également avec ceux obtenus par méthodes *in vitro* (Yamashita et al. 1985, Pakhomov & Perissinotto 1996) même si *T. libellula* est plus grand que les autres individus du genre *Themisto*. Nos TQI provenant de la deuxième approche ont été estimés à 19,97% de la masse sèche corporelle pour l'EM et à 17,02% pour le NOGSL. Les TQI obtenus pour *T. gaudichaudi* par méthode *in situ* (méthode de l'indice de remplissage stomacal) révèlent des taux variant entre 11,5% et 19,8% (Froneman et al. 2000) et par méthode *in vitro* (expériences de prédation) entre 8,5 et 21,8% (Pakhomov & Perissinotto 1996). L'activité nutritive journalière de *T. libellula*, son temps de digestion, mais aussi des différences dans la température de l'eau et les effets de cette température sur les processus métaboliques semblent être responsables des quelques différences observées dans les TQI. L'existence d'un haut degré de chevauchement entre les distributions verticales des proies et celles des prédateurs peut également créer des disparités entre ces estimations (Gibbons & Painting 1992). *T. libellula* semble donc être un prédateur actif, exhibant des taux quotidiens d'ingestion élevés.

Nos résultats ont ensuite mis en évidence un taux quotidien d'ingestion (TQI) de *Themisto libellula* sur *Calanus finmarchicus* plus grand que celui estimé pour des individus vivant dans la mer du Groënland (Auel & Werner 2003). La moyenne de nos TQI pour nos deux régions a été estimée à 4,4% de masse sèche corporelle et celui calculé par Auel et Werner (2003) est égal à 1,9%. Cette différence semble s'expliquer par une disparité dans les approches expérimentales employées. Dans les expériences de prédation utilisées par Auel et Werner (2003), des facteurs comme les effets « de mise en bouteille », l'intensité lumineuse peuvent avoir influencé le comportement des proies et des prédateurs ou bien encore la disponibilité des proies. De plus, il semble que la différence de longueur entre les spécimens du GLS et ceux des régions arctiques puisse expliquer également la différence entre les TQI.

Avec des taux d'ingestion quotidiens élevés, il est attendu que *Themisto libellula* exerce un impact important sur les communautés zooplanctoniques. En considérant la première méthode de calcul (indice de remplissage stomacal), l'impact est sous-estimé car il a été calculé à partir de TQI sous-estimés. Cet impact se situe donc entre les valeurs de ces deux approches soit entre 0,34% et 0,49% de la biomasse de mésozooplancton par jour pour le NOGLS et entre 0,59% et 2,18% pour l'EM. L'impact quotidien de prédation estimé pour *T. libellula* dans la mer du Groënland est égal à 0,03% de la biomasse mésozooplanctonique (Auel & Werner 2003). Il est plus bas que nos résultats obtenus avec nos deux méthodes. La différence entre les résultats de ces deux études pourrait être liée aux variations dans l'abondance de *T. libellula* ainsi que dans la biomasse des copépodes dans le golfe du Saint-Laurent et dans la mer du Groënland. Néanmoins, cette différence dans les impacts de prédation serait plutôt due à l'écart entre les taux d'ingestion et au degré de chevauchement entre les distributions verticales des proies et des amphipodes (Pakhomov & Perissinotto 1996). Dans le GLS, *T. libellula* exerce une pression de prédation quotidienne plus importante que *T. gaudichaudi* (maximum *ca.* 2,1% de la biomasse mésozooplanctonique par jour, Pakhomov & Perissinotto 1996), *T. pacifica* et

T. japonica (0,11% et 0,06%, Yamada & Ikeda 2006), vivant à South Georgia et dans la région de Oyashio, respectivement. Une différence dans la biomasse des amphipodes ou dans les taux d'ingestion semblerait refléter la variation entre ces pressions de prédation (Froneman et al. 2000).

À ce jour, la pression de prédation a seulement été examinée sur la communauté mésozooplanctonique et il n'y a aucun rapport sur l'impact de prédation de *Themisto* spp. au niveau de chacune des espèces de copépodes. Il est donc difficile de comparer les impacts de prédation que nous avons estimé pour le SMSL. Néanmoins, la seconde méthode utilisée dans notre étude constitue la meilleure méthode disponible pour exprimer l'impact de prédation sur des espèces et des stades de copépodes. Nos impacts de prédation sont toujours plus élevés quand il y a chevauchement entre la biomasse de *Themisto libellula* et de faibles biomasses de zooplancton ou d'espèces de copépodes, ce qui explique les variations entre nos deux régions et entre les espèces de copépodes. De ce fait, bien que le taux d'ingestion soit élevé pour *C. finmarchicus* CV, l'impact de prédation est beaucoup plus important sur *C. finmarchicus* CVI-F et CVI-M et sur *Euchaeta norvegica.*

Les principales conclusions qui émanent de notre étude sont que les spécimens *Themisto libellula* du GSL sont plus grands que les individus des régions arctiques. L'étude a ensuite montré que *T. libellula* se nourrissait majoritairement à la fin de la nuit et au lever du soleil et qu'il pouvait acquérir de petites quantités de nourriture l'après-midi jusqu'au coucher du soleil. L'alimentation de ce prédateur est basée principalement sur les copépodes et plus spécifiquement les individus de stades CIV-CV de la population de

Calanus finmarchicus. Les taux quotidiens d'ingestion ainsi que l'impact de prédation de *T. libellula* ont été calculés et se sont révélés plus élevés que ceux trouvés pour *T. libellula* vivant dans les régions arctiques et pour d'autres espèces du même genre. Les taux quotidiens d'ingestion de *T. libellula* les plus importants, ont été estimés à 19,97 % de sa masse corporelle sèche pour le zooplancton et à 5,50% pour *C. finmarchicus*. *T. libellula* est ainsi capable d'ingérer quotidiennement 2,18% de la biomasse de zooplancton et 3,39% de celle de *C. finmarchicus*. Les variations observées au niveau des taux quotidiens d'ingestion avec les autres espèces du genre *Themisto* semblent être liées à la différence de taille des amphipodes mais également à d'autres facteurs tels que l'activité nutritive journalière, le temps de digestion et à l'existence d'un chevauchement des biomasses proie/prédateur. De plus, quand la biomasse de *T. libellula* est présente avec des faibles biomasses de copépodes, l'impact de prédation est toujours plus important, ce qui explique les variations entre nos deux régions.

Selon notre hypothèse principale, *T. libellula* serait capable de contrôler la communauté mésozooplanctonique locale dans le système marin du Saint-Laurent. En effet, sa dynamique d'alimentation et son impact de prédation élevé, font de cet amphipode hypéridé, un organisme zooplanctonique carnivore a surveillé. *Themisto libellula* est connu pour être capable de former des essaims comme *T. gaudichaudi* (Gibbons et al. 1992, Vinogradov 1999) et ainsi atteindre de très hautes densités (Eiane & Daase 2002). Sous de telles conditions, l'impact potentiel peut être substantiel et *T. libellula* peut jouer un rôle écologique important dans le SMSL, en exerçant un contrôle significatif sur les populations mésozooplanctoniques et plus spécifiquement sur *C. finmarchicus* et *Euchaeta norvegica*.

L'impact de prédation de *T. libellula* pourrait être cyclique, subir des variations saisonnières qui entraîneraient des pressions de prédation plus élevées ou plus basses à certaines périodes de l'année. Cette espèce peut toutefois contribuer à modifier la structure trophique dans cet écosystème. De plus, à cause de son abondance et de son niveau trophique, cette espèce peut participer significativement au flux de carbone dans le GSL. À cause de l'importance prononcée des communautés mésozooplanctoniques dans les chaînes alimentaires, *T. libellula* semble donc devenir un lien clé entre la production secondaire pélagique et les hauts niveaux trophiques, incluant les poissons et les mammifères marins, dans le SMSL. Cependant, quelques interrogations qui ont émané de cette étude, persistent à son sujet et tendent à être étudiées dans de futures investigations.

En effet, à travers notre étude, nous avons constaté de grandes variations dans les classes de taille, dans les taux d'ingestion et dans les taux de prédation entre les individus *Themisto libellula* vivant dans le golfe du Saint-Laurent et ceux des régions arctiques. Une étude comparative entre les cycles de vie de *T. libellula* vivant dans les régions arctiques et ceux vivant dans le SMSL pourrait être entreprise afin de déterminer s'il existe des différences régionales importantes qui expliqueraient nos variations. Il serait ainsi intéressant d'étudier s'il existe des variations intra-spécifiques à cette espèce qui pourraient expliquer nos différences. En effet, il serait possible que *T. libellula* soit devenue une espèce résidente du SMSL. Cette région serait ainsi probablement peuplée de *T. libellula* provenant de l'advection d'eau froide du plateau du Labrador (Harvey et al. 2005) et de *T. libellula* résidant de façon permanente dans le SMSL.

Il serait également intéressant d'étudier l'apparition de cette nouvelle espèce carnivore macrozooplanctonique dans le golfe du Saint-Laurent pour comprendre si cette arrivée serait liée aux résultats d'un changement à large échelle dans la circulation des eaux arctiques associé au changement climatique global (Morison et al. 2000).

De plus, en ayant mis en évidence le taux élevé d'ingestion de *Themisto libellula*, il serait intéressant d'observer si, depuis l'apparition de cette espèce dans le Saint-Laurent, les compositions mésozooplanctoniques et macrozooplanctoniques de cet écosystème auraient commencé à être affectées par la présence de cet amphipode. Si tel était le cas, le réseau trophique du Saint-Laurent pourrait être perturbé et subir des changements à long terme.

Lors de ce projet de recherche, différentes expériences de prédation ont été effectuées avec *T. libellula*, cependant ces dernières n'ont pas été probantes. Malgré cela, il serait intéressant de persévérer dans cette recherche en incluant un système de vidéosurveillance qui permettrait d'analyser le comportement alimentaire de *T. libellula* et d'approfondir cette étude afin de comparer et de corroborer nos résultats *in situ* (résultats obtenus avec nos deux méthodes d'étude) avec des résultats *in vitro* (résultats obtenus avec des expériences de prédation). Une étude utilisant des biomarqueurs lipidiques pourrait également être entreprise pour appuyer nos résultats sur l'écologie de l'alimentation de *T. libellula* et fournir ainsi la possibilité de témoigner de la présence ou non de phytoplancton dans le régime alimentaire de cet amphipode (Auel et al. 2002). Pour donner une meilleure estimation de l'impact de prédation de *T. libellula*, un monitorage du déclin du contenu stomacal pourrait être effectué à différents intervalles de temps tels que 15 min, 30 min, 1 h, 2h, 4h, 6h, 10 h, 14h, et 24h, afin de déterminer plus précisément son temps de digestion. Et finalement, il serait aussi intéressant de poursuivre l'étude des contenus stomacaux sur différentes saisons pour observer l'existence d'un changement saisonnier dans l'alimentation et le cycle circadien de l'activité nutritive de *T. libellula* et ainsi connaître les variations de sa pression de prédation sur la biomasse mésozooplanctonique du Saint-Laurent au cours des saisons.

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