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J. DESCHÊNES[1,2], G. DESROSIERS[1], J. FERRON[3], R. CLOUTIER[3], G. STORA[4]

[1] *Institut des sciences de la mer, Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec, Canada, G5L 3A1*
[2] *Groupe de recherche sur les écosystèmes aquatiques, Université du Québec à Trois-Rivières, département de chimie-biologie, 3351, b des Forges, C.P. 500, Trois-Rivières, Québec, Canada, G9A 5H7*
[3] *Département de Biologie, chimie et sciences de la santé, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec, Canada, G5L 3A1*
[4] *Laboratoire d'Océanographie et de Biogéochimie, Centre d'Océanologie de Marseille, Campus de Luminy, Case 901, 163 Avenue de Luminy, 13288 Marseille Cedex 09, France*
Corresponding author: gaston_desrosiers@uqar.qc.ca

BIOTURBATION
CARBON SEQUESTRATION
FEEDING STRATEGY
FOOD UTILIZATION
NEREIS VIRENS
INGESTION
SEASONAL VARIATIONS
STORAGE

ABSTRACT. – Seasonal variations in food utilisation, particularly storage, by *Nereis virens* are not well documented. This behaviour often results in carbon sequestration, the extent of which remains unknown. Observations on food utilisation by *Nereis virens* were conducted under experimental conditions of controlled temperature, food supply and photoperiod. The amount of ingested and stored food both increase with ration, but the latter does so more rapidly than the former. When food is rare, worms usually prioritise feeding over storing. However, immediate storage is more advantageous than feeding when worms are able to capture extra rations. This strategy is predominant when food is abundant because benefits far outweigh costs. The extrapolation of carbon storage under experimental conditions to natural populations suggests that storage mostly takes place between April and September. Summer storage is likely to be short term because of the predominance of algae, whereas autumn storage is likely to be long term because of vascular plants. The importance of storage on the carbon cycle is difficult to evaluate, but biogeographical distribution and densities of *Nereis virens* suggest a non-negligible effect.

BIOTURBATION
NEREIS VIRENS
INGESTION
STOCKAGE
SÉQUESTRATION DE CARBONE
STRATÉGIE D'ALIMENTATION
VARIATIONS SAISONNIÈRES

RÉSUMÉ. – Les variations saisonnières dans la stratégie d'utilisation de la nourriture, particulièrement du stokage, par *Nereis virens* sont peu documentées. La séquestration du carbone, dont l'étendue est encore inconnue, résulte directement de l'activité de stockage. Les stratégies d'alimentation de *Nereis virens* ont été observées sous des conditions contrôlées de température, d'abondance de nourriture et de photopériode. Les résultats démontrent que la quantité de nourriture mise en réserve augmente plus rapidement que la quantité ingérée en fonction de la ration fournie. Lorsque la nourriture se fait rare, les Vers semblent privilégier l'ingestion plutôt que le stockage. Cependant, le stockage immédiat peut s'avérer plus avantageux lorsque les Vers réussissent à capter plus de nourriture. Cette stratégie prédomine en abondance de nourriture puisque les bénéfices surpassent largement les coûts. L'extrapolation des valeurs expérimentales de séquestration de carbone aux populations naturelles suggère que la majorité du carbone est stockée entre avril et septembre. La mise en réserve estivale, principalement composée d'algues, semble être de courte durée, tandis que le stockage automnal, principalement composé de plantes vasculaires, semble être de plus longue durée. L'importance de ce comportement sur le cycle du carbone est difficile à évaluer. Par contre, la distribution biogéographique et les densités de populations de *Nereis virens* suggèrent un effet non négligeable.

INTRODUCTION

In marine ecosystems, the organic matter reaching the sediment surface is more or less degraded depending on its origin, its nature and its residence time in the water column. In coastal areas, since sites are usually shallow (< 50m), transit towards the bottom does not allow a complete mineralisation of the substrates by micro-organisms of the water column (Karl *et al.*1988). Therefore, mineralisation processes end at the water-sediment interface level and into the sedimentary column where degradation of organic matter is carried out by aerobic and/or anaerobic metabolites.

Bioturbation processes affect sediment properties (Rhoads & Boyer 1982, Hall 1994) and impact both sequestration and resuspension of organic matter (Clough *et al.* 1997). In the intertidal zone, particulate organic matter (i.e. phanerogams and algae detritus) can be exported towards the subtidal zone by the tides currents or, alternatively, sequestred into the sediments by means of benthic organism activities [food and bioturbation; Olivier (1994)]. For example, burrows of *Nereis virens* (Sars) filled with food may accidentally collapse or be sealed off by repeated scraping and reorganisation of the walls (maintenance behaviour; Miron *et al.* (1992), consequently sequestering organic carbon. Irrigation in open burrows allows microorganisms to colonise stored food and gradually mineralise the nutrients, which then return to the water column (Kristensen 1989, Kristensen *et al.* 1991, Kristensen *et al.* 1992). Therefore, benthic animals make up an important part of the biological pump and can sequester a great deal of carbon, ultimately influencing the carbon cycle (Demers & Therriault 1993).

Nereis virens belongs to the boreo-atlantic *Macoma balthica* community of the St. Lawrence lower estuary (Desrosiers & Brêthes 1984). Opportunistic, *N. virens* thrives on almost anything. However, immature worms prefer detritus, whereas adults prefer macro- and meiobenthos preys (Commito & Shrader 1985, Olivier *et al.* 1996, Tita *et al.* 2000). Although tidal flats are rich in organic matter, it may be exported from the system during tidal ebb flow (Valiela *et al.* 1978, Roman & Daiber 1989). To compensate for intermittent food shortage, some polychaetes (*Nereis vexillosa* and *Platynereis bicanaliculata*) attach living algae at the entrance of their burrow, providing food for the surrounding community (Woodin 1977). Other species, like *Nereis virens*, store their food by imbedding it in the burrow walls (Olivier 1994, Olivier *et al.* 1995). Readily available, algae may be stored for short periods, whereas vascular plants, which require decomposition before acquiring sufficient nutritional value, may be stored for longer periods (Hylleberg 1975, Mann 1988, Olivier *et al.* 1995).

Storage behaviour by *N. virens* has been reported and examined only recently (Olivier 1994, Deschênes 2001). Therefore, little is known of its seasonal variations. The present paper aims to experimentally examine the utilisation of organic matter and estimate the amount of organic carbon stored by *Nereis virens* in relation to three environmental factors associated to seasonal variations (temperature, photoperiod, and food supply).

MATERIAL AND METHODS

Experimental set-up: Laboratory experiments were conducted at the Institute of Marine Sciences Aquatic Centre in Pointe-au-Père (Québec, Canada) over the summer of 1999 to evaluate feeding and storing frequencies of *Nereis virens*. Observations were accomplished with 12 flat aquariums [adapted from Miron *et al.* (1992)]. Each aquarium combined two glass plates measuring 30 cm in height by 30 cm in length and set 0.5 cm apart. They were filled with sifted homogenised sediments (< 500 μm) that were left to settle for a week before introducing the worms. Immature animals of 1526.3 ± 454.0 mg (wet weight) (n=24) were captured from a small bay near the research centre and introduced into each aquarium randomly by groups of three. They were left without food for a week to avoid excessive activity and to let them build burrows.

Natural filtered seawater circulated openly through the aquariums by gravity. Four 38 L tanks supplied temperature-controlled water to each aquarium. Commercial aquarium heaters heated the water to 13 °C and 18 °C, whereas a coil water cooler (1 °C) and a temperature-controlled room (6 °C) cooled the other two tanks. Air tubes assured oxygen availability. Two light regimes created differences in photoperiod. The first, 12:12 (Light:Dark) hereafter referred to as LD 12 or long day, corresponds to spring and autumn equinox. The second, 6:18 (Light:Dark) hereafter referred to as LD 6 or short day, is not a condition found in nature but approximates the total quantity of light reaching the worms when ice covers the tidal flats. Two feeding regimes [59 ± 20 mg, n = 480 (limited) and 434 ± 90 mg, n = 480 (abundant) wet weight of *Enteromorpha intestinalis* per worm per day] were used to approximate seasonal changes in environmental conditions.

For each temperature, three aquariums were submitted to four consecutive treatments, which consisted of a 10-day combination of one photoperiod and one food regime. After each treatment, photoperiod was changed. However, worms were left without food for a week to avoid excessive activity and to let them adapt to the new photoperiod. Observations took place immediately after daily food provisioning and lasted 30 minutes which was deemed sufficient to obtain a reaction from the worms (Evans *et al.* 1974). Worms were fed every morning between 08:00 and 10:00.

Food utilisation: Each capture event of food particles and their subsequent use was noted as: ingested, stored, or other. Under limited food conditions, each ration given consisted of one piece of *E. intestinalis* (59 ± 20 mg,
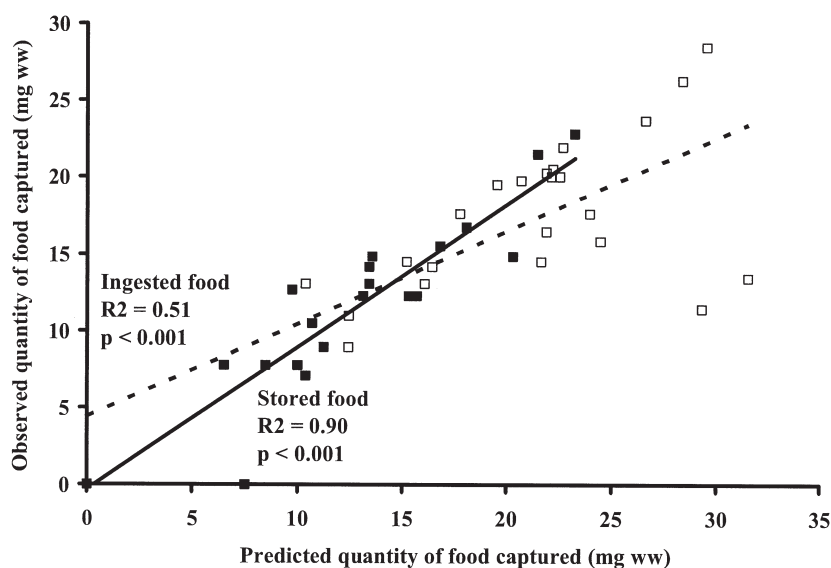
Fig. 1. – Observed amount of food used in relation to the predicted (calculated) amount for limited food conditions. Both observed and calculated amounts were square-root transformed.

n = 480). Therefore, it was possible to record the exact amount of food captured by each worm on every capture event. However, under abundant food conditions consisting of numerous pieces of *E. intestinalis* (10 to 20 pieces of 20 mg to 70 mg), worms nipped different-sized pieces of algae, preventing determination of the exact amount captured. An estimation of this amount was achieved by calculating the relative frequency of two behaviour patterns: feeding/capture and storing/capture, and multiplying it by the total weight of algae given (CIF: calculated amount of ingested food, CSF: calculated amount of stored food). These values were then compared with observed values for the limited food treatment by way of linear regression (Fig. 1). The amount of food used (abundant food treatment) was extrapolated from these regression equations:

$$OIF = 0.36*CIF + 5.34*CIF^{0.5} + 19.58 \qquad (1)$$

$$OSF = 0.86*CSF - 0.56*CSF^{0.5} + 0.09 \qquad (2)$$

where OIF and OSF represent the observed amount of ingested and stored food (mg wet weight), CIF and CSF the calculated amount of ingested and stored food (mg wet weight). Values for ingested food were logarithmically transformed to fit homoscedasticity and normality requirements.

Data was pooled for each trial over 10 days of experimentation. A stored to ingested food ratio [SI: amount of food stored (mg) / amount of food ingested (mg)] was calculated and used to evaluate the impact of several environmental conditions (temperature, photoperiod, food supply) on food utilisation. The ratio was log-transformed to fit the requirements of homoscedasticity and normality for a 3-factor ANOVA (Zar 1996). The relationship between the amount of food used and the ration given was also analysed by linear regression after a logarithmic transformation (Zar 1996). Statistical analyses were performed with SYSTAT 9.0 for Windows.

Carbon storage: Algae of different sizes were weighed (wet weight), dried at 50 °C for 24 hours, and weighed again to obtain the dry weight. Sub-samples of 2.5 ± 0.8 mg (n = 12) were submitted to a CHN analysis (Perkin-Elmer 2400 CHN) for total carbon assessment. Carbon content was expressed as a mean percentage of dry weight, and dry weight as a mean percentage of wet weight. The average amount of carbon sequestered per worm, per day was estimated for each treatment, which were then used to extrapolate values to worms under natural conditions.

A 365-day year was subdivided in 24 periods of 14 to 15 days, depending on the length of each month (Table II). The first half of each month was termed "early" and the second half was termed "late". A temperature and food abundance experimental category was assigned to each period according to sediment temperatures (Harvey & Vincent 1989) and food abundance (Breton-Provencher *et al.* 1979, Pocklington 1985, Thom & Albright 1990) in the St. Lawrence River. For example, from the 1st to the 15th of January (early January), water was considered to be 1 °C because sediment temperatures usually tend towards 0 °C at low tides in winter (Harvey & Vincent 1989); food was considered limited because of ice cover and limited winter primary production (Breton-Provencher *et al.* 1979, Pocklington 1985, Thom & Albright 1990).

These extrapolated values of sequestered carbon were then used to evaluate the annual amount of carbon stored per square meter by *Nereis virens* in Mercier and Ha! Ha! Bays (Bic provincial park, Québec, Canada). Experimental worms had a mean wet weight of 1526.3 ± 454.0 mg (n = 24) which is a similar size range to that of immature worms found in the lower beach of Mercier (1299.4 ± 135.4 mg) and Ha! Ha! (1597.7 ± 177.2 mg) bays (Caron *et al.* 1993). Corresponding mean densities are 79.8 ± 22.7 (Mercier) and 93.6 ± 33.4 worms·m⁻² [Ha! Ha!; Caron *et al.* (1993)].

Table I. – Assigned temperature and food categories to each of 24 periods of 14 to 15 days in a 365-day year.

Day	Month	Assigned temperature category (°C)	Assigned food category
1st to 15th	Early January	1	Limited
16th to 31st	Late January	1	Limited
1st to 14th	Early February	1	Limited
15th to 28th	Late February	1	Limited
1st to 15th	Early March	1	Limited
16th to 31st	Late March	1	Limited
1st to 15th	Early April	6	Abundant
16th to 30st	Late April	6	Abundant
1st to 15th	Early May	6	Abundant
16th to 31st	Late May	13	Abundant
1st to 15th	Early June	13	Abundant
16th to 30st	Late June	18	Limited
1st to 15th	Early July	18	Limited
16th to 31st	Late July	18	Abundant
1st to 15th	Early August	18	Abundant
16th to 31st	Early August	13	Abundant
1st to 15th	Early September	13	Abundant
16th to 30st	Late September	13	Abundant
1st to 15th	Early October	6	Limited
16th to 31st	Late October	1	Limited
1st to 15th	Early November	1	Limited
16th to 30st	Late November	1	Limited
1st to 15th	Early December	1	Limited
16th to 31st	Late December	1	Limited

Table II. – Three-way ANOVA results on the SI ratio. Te: temperature, Ph: photoperiod, and Fo: food supply. Significant results are highlighted in bold characters. Critical p (probability) considered is 0.05; sample size is 48; $R^2 = 0.832$; Te, FoTe, TePh, and FoTePh have 3 degrees of freedom. Ratio was log-transformed after adding 0.5.

Effect tested	F	p
Fo	117.320	**<0.001**
Te	3.219	**0.036**
Ph	0.862	0.360
FoTe	1.587	0.213
FoPh	0.476	0.495
TePh	4.161	**0.014**
FoTePh	1.343	0.278

RESULTS

Food ingestion vs storage

Temperature (F = 3.2; p = 0.036) and food supply (F = 117.3; p < 0.001) both significantly influence the SI ratio [SI: amount of food stored (mg) / amount of food ingested (mg)], while photoperiod has no significant effect (F = 0.9; NS). However, there is an interaction between photoperiod and temperature (F = 4.1; p = 0.014; Table II). An abundant food supply stimulates storage (SI > 1), whereas a limited food supply generally favours feeding (SI < 1; Fig. 2). An LD 6 photoperiod instigates storage at 1 °C and feeding at 6 °C, but only when food is abundant (Fig. 2). Worms store and ingest more food as rations increase (Table III).

However, the amount of food stored increases more rapidly than the amount ingested (Fig. 3a).

Carbon Storage

Experimental values of stored carbon were extrapolated to natural conditions revealed that late summer values are highest with 48.6 ± 13.4 mgC·worm^{-1} (n = 12) in August and 57.9 ± 4.6 mgC·worm^{-1} (n = 12) in September (Fig. 3b). Spring and summer values are lower, varying between 20.2 ± 21.1 (n = 12) and 41.8 ± 16.7 mgC·worm^{-1} (n = 12). Ninety per cent of the annual sequestered carbon (242.5 ± 103.7 mgC·worm^{-1}, n = 12) is stored in a period of
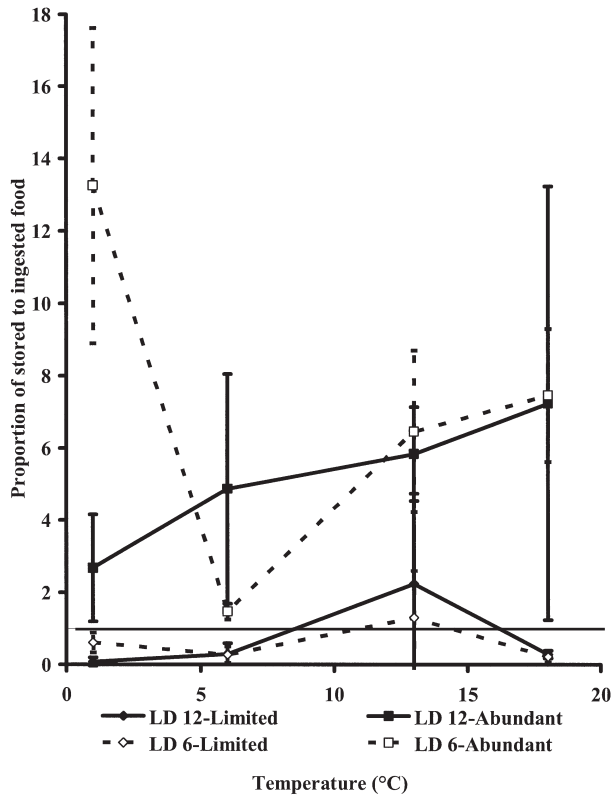

Fig. 2. – Variations of the stored to ingested ratio in relation to temperature, food supply and photoperiod (mean $\pm$ SD, n = 48). Horizontal line represents a one to one ratio of stored to ingested food.

Table III. – Relationship between food used and ration given.

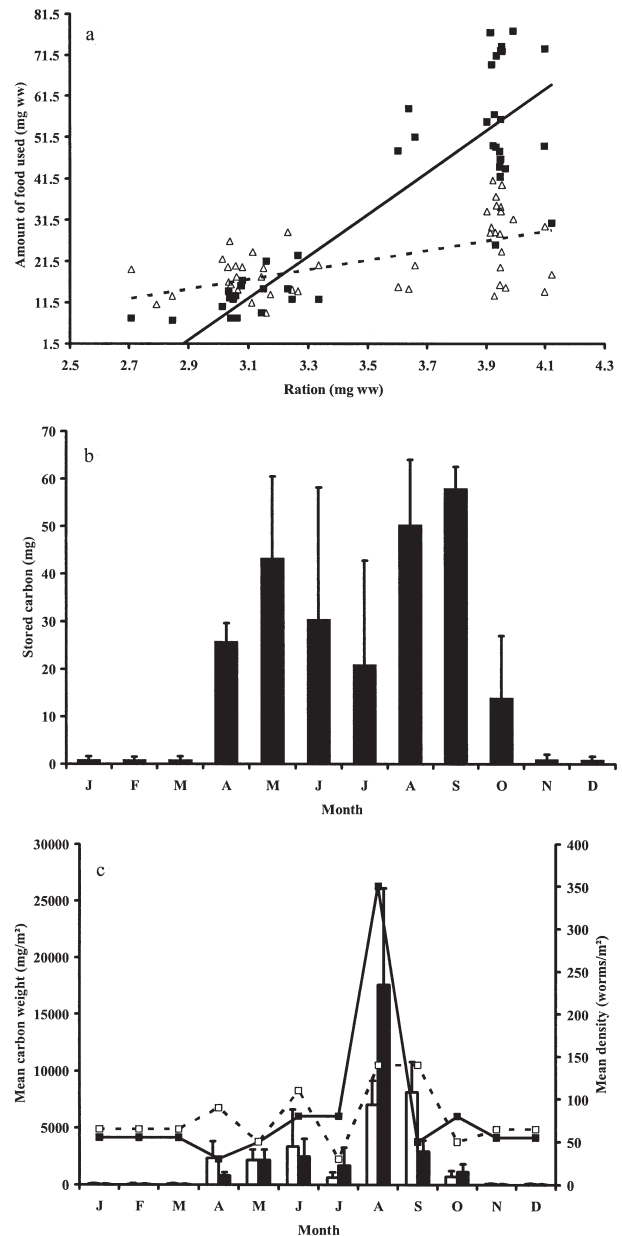|	Effect tested	Value	t or F-ratio	p
Ingested food	Constant	1.201	3.547	**0.001**
	Slope	0.407	4.148	**0.001**
	Regression		18.044 (F-Ratio)	**<0.001**
Stored food	Constant	2.752	-5.776	**<0.001**
	Slope	1.616	12.176	**<0.001**
	Regression		148.260 (F-Ratio)	**<0.001**

Fig. 3. – a, amount of food used in relation to ration given. Filled squares and solid line: stored food, empty triangles and dotted line: ingested food, squares: limited food, triangles: abundant food. Dotted regression line: ingested food; solid regression line: stored food. b, estimation of monthly total carbon sequestration per worm (mean $\pm$ SD, n = 12), c, Monthly variation of total carbon sequestration (mean $\pm$ SD, n = 12) and population densities for the lower beach of two bays. White bars: Mercier Bay carbon storage; white squares: Mercier Bay densities, black bars: Ha!Ha! Bay carbon storage, black squares: Ha!Ha! Bay densities.

less than six months, from April to September (Fig. 3b).

Likewise, estimated values of carbon sequestration in Mercier and Ha! Ha! Bays have marked seasonal variations (Fig. 3c). Most of the storage occurs in late spring and summer, during which storage frequencies and worm densities are the highest. Worm densities are similar in both bays except in August where they rise to 350 worms·m^{-2} in Ha! Ha! and to 140 worms·m^{-2} in Mercier (Fig. 3c). The annual amount of carbon stored by worms on the lower beach in Mercier and Ha! Ha! Bays was estimated at 24.6 ± 11.6 gC·m^{-2}·year^{-1} (n = 12) and 28.9 ± 14.7 gC·m^{-2}·year^{-1} (n = 12) respectively.

DISCUSSION

Food utilisation

Both photoperiods tested being at or under a threshold (LD 12), we found no difference in the SI ratio, thus supporting the findings of Last *et al.* (1999). With increasing food availability, the amount stored rises more rapidly than the amount ingested. Variations in ratio values may be mostly attributed to variations in stored food. The ratio may also be underestimated at high temperature (13 °C and 18 °C) due to the length of the observation period. Indeed, with a limited food supply, 30 minutes of observation were sufficient to determine the amount of food used. However, when food was abundant, worms spent most of the period capturing and storing algae. As little or no stored food was left on the next day, feeding necessarily took place after the observation period. Therefore, *Nereis virens* exhibits a clear hoarding behaviour, possibly anticipating short or long-term food shortage (Olivier *et al.* 1995).

Maintenance ration was not likely to have caused starvation. Indeed, the average maintenance ration for *Nereis virens* between 1500 mg to 4000 mg (wet weight) feeding on *Nephtys hombergii* is 10.7 cal·worm^{-1}·day^{-1} [at 15 °C; Kay & Brafield (1973)]. In the present study, the average ration given in limited food conditions was 31.0 ± 16.5 cal·worm^{-1}·day^{-1} of *E. intestinalis* [according to calorific values of Haroon & Szaniawska (1995)]. Storage behaviour is also exhibited under our limited food conditions, although less frequently than feeding. By storing food immediately, worms may return faster to their foraging activity. In doing so, some worms were able to capture extra rations. The advantage of this strategy is an overall energy gain, despite an immediate energy loss due to increased foraging. Hunger may also influence the use of this strategy (Krebs &

Davies 1993). Hungry worms may be more "risk-prone" than satiated ones in order to gain more food. Activity costs also increase with temperature in polychaetes (Mangum & Sassaman 1969, Newell & Branch 1980). Therefore, worms may be hungrier at high temperatures (13 °C and 18 °C) and incorporate more storage in their foraging strategy.

When food is abundant, foraging time decreases (Deschênes 2001) and, with it, the cost of foraging. Storage therefore becomes more frequent especially at high temperatures. However, food stored at 1 °C and 6 °C is sequestered for over 24 hours as opposed to food stored at 13 °C and 18 °C, which is eaten within the same day. At high temperatures, energetic costs and growth rates are high (Newell & Branch 1980, Atkinson 1994). Most of the food stored is therefore eaten within 24 hours (at 13 °C and 18 °C) unless the burrow collapses.

Feeding is predominant over storage at cold temperatures and low food abundance during late autumn, winter and early spring. In contrast, storage supersedes feeding at hot temperatures and high food abundance during late spring, summer, and early autumn. Cold temperatures favour nutrient absorption (Neuhoff 1979), as well as weight gain (Atkinson 1994). Priority given to feeding in autumn may therefore increase survival probability of immature *Nereis virens* through winter. Priority feeding in spring may result from winter weight loss (Snow & Marsden 1974), especially in younger worms. As this species is semelparous, spring feeding may be associated with costs of gametogenesis for older mature worms (Garwood & Olive 1981, Desrosiers *et al.* 1994).

Storage during summer is likely to be on a short-term basis due to high energy demands (Newell & Branch 1980) and high degradability of algae (Mann 1988). Summer food is mostly composed of algae because of its abundance and availability (Breton-Provencher *et al.* 1979). As *Nereis virens* reaches its maximum growth rate in summer (Desrosiers *et al.* 1994), it may store food for short periods at a time in order to maximise food intake. Early autumn storage, on the other hand, is likely to be long-term. Vascular plant detritus are more abundant due to increasing frequency and intensity of storms (Roman & Daiber 1989). In autumn, vascular plants are already decomposing, rendering nutrients available to macroconsumers (Mann 1988). Moreover, cold temperatures (Harvey & Vincent 1989) decrease decomposition of sequestered organic matter (Kristensen *et al.* 1992). Although winter induces quiescence, worms under experimental winter conditions continue to ingest food within their burrow (Deschênes 2001). Organic matter is much less available during winter (Pocklington 1985) and worms must rely on food reserves (Olivier *et al.* 1995); they may therefore anticipate winter food shortage.

Carbon storage

Increase in total carbon sequestration during summer seems to result from the arrival of recruitment. In fact, reproduction usually occurs between late April and early June in populations of the St. Lawrence River (Desrosiers *et al.* 1994). Larvae are then transported to areas of low hydrodynamism, where they settle on fine sediments. In bays of North and North-East orientation, along the south shore of the St. Lawrence estuary, adult *Nereis virens* are mostly found in the lower beaches and migrate to the upper beach to reproduce (Caron *et al.* 1993). Recruitment therefore emanates from the upper beaches. After two to three years, immature worms, in turn, migrate to the lower beaches in search of more space (Kay & Brafield 1973). High mortality ensues reproduction and migration as larvae and juvenile become prey for established benthic organisms (Desrosiers *et al.* 1994). In contrast to these bays, Mercier and Ha! Ha! Bays have a SO orientation which induces a circular current (Caron *et al.* 1993). In these systems, adults are most abundant in upper beaches, juveniles in lower beaches and larval recruitment emanates from the center (Caron *et al.* 1993). Although this circular current mixes juveniles and adults, there is segregation and recruitment increases population densities for a short while. Considering variations in density, *Nereis virens* of the lower Mercier and Ha! Ha! beaches may sequester an average of approximately 267 ± 132 kgC·ha^{-1}·year^{-1} in the sediments of both bays.

From our observations on seasonal variations in carbon sequestration and food use, we can predict that *Nereis virens* will store food for short and long-term periods, anticipating upcoming food shortages. The next step will be to verify its validity in natural populations. However, determination of food use or carbon storage in natural populations of *N. virens* is difficult, as it is necessary to observe them within their burrows. The effects of climatic and environmental conditions on this behaviour also need to be examined. A close relationship exists between the amount of food available and the amount of food stored. However, this relation was observed for worms under laboratory-controlled conditions and its validity in natural populations still needs to be verified.

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