Aquat. Living Resour. 23, 167–176 (2010)
© EDP Sciences, IFREMER, IRD 2010
DOI: 10.1051/alr/2010010
www.alr-journal.org

Aquatic
Living
Resources

The structure of subtidal food webs in the northern Gulf of St. Lawrence, Canada, as revealed by the analysis of stable isotopes

Marc-Olivier Nadon[1,2,a] and John H. Himmelman[2]

[1] Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149-1098, USA
[2] Département de Biologie & Québec-Océan, Université Laval, Québec, Québec, G1K 7P4, Canada

Received 22 July 2009; Accepted 23 February 2010

Abstract – We analyzed stable isotopes of carbon and nitrogen to investigate the trophic structure of the subtidal food web around the Mingan Islands, northern Gulf of St. Lawrence, eastern Canada. All benthic consumers were enriched in ^{13}C (mean δ^{13}C of –17.1‰) compared to particulate organic matter (POM: –23.3‰). Nitrogen stable isotope ratios ranged from 6‰ to 14‰ and the organisms studied fell into three distinct trophic groups, primary producers, primary consumers (herbivores), and predators. The sea star *Crossaster papposus* and the sculpin *Myoxocephalus scorpius*, known to be top level predators, had slightly higher δ^{15}N than other predators. Although the average isotope signature of the sea star *Solaster endeca* placed it among regular predators, the δ^{15}N increased with sea star size and large individuals could be considered as top predators. The relatively small number of organisms located at intermediate trophic levels suggests a low level of omnivory in the Mingan Islands' system, which contrasts with previously described benthic systems that exhibit a continuum between herbivores and predators. Low omnivory, in addition to low diversity, suggests that this ecosystem may be relatively unstable if exposed to natural and/or anthropogenic disturbances such as exploitation and climate change.

Key words: Stable isotopes / Food webs / Omnivory / Community structure / Trophic interaction / Gulf of St. Lawrence

Résumé – Nous avons analysé les isotopes stables du carbone et de l'azote pour définir la structure trophique du réseau alimentaire infralittoral (zone immergée subtidale) des îles Mingan situées dans la zone nord du golfe du Saint-Laurent, côte est du Canada. La quasi-totalité des consommateurs benthiques sont enrichis en carbone ^{13}C (δ^{13}C moyen : −17,1 ‰) comparés à la matière organique particulaire (POM : –23,3 ‰). Le rapport isotopique stable de l'azote se situe entre 6 ‰ et 14 ‰ et les organismes étudiés se classent en trois groupes trophiques distincts : les producteurs primaires, les consommateurs primaires (herbivores), et les prédateurs. L'étoile de mer, *Crossaster papposus,* et le poisson chaboisseau à épines courtes, *Myoxocephalus scorpius*, reconnus comme étant des prédateurs de niveau trophique supérieur, exhibent des rapports δ^{15}N supérieurs aux autres prédateurs. Bien que la signature isotopique moyenne de l'étoile de mer, *Solaster endeca,* la place ici comme prédateur typique, le rapport δ^{15}N augmente avec sa taille ; ce qui suggère que les individus de grande taille, chez cette espèce, peuvent être considérés comme des prédateurs de haut niveau. Le petit nombre d'organismes situés à des niveaux trophiques intermédiaires suggère un faible taux « d'omnivorie » dans le système des îles Mingan, ce qui contraste avec ce qui a été décrit précédemment pour d'autres écosystèmes marins (un continuum entre herbivores et prédateurs). Le faible taux « d'omnivorie », additionné à la faible diversité, suggère que cet écosystème peut être relativement instable face à d'éventuelles perturbations naturelles et/ou d'origine humaine, telles que le changement climatique et la surexploitation.

1 Introduction

Past research using stable isotopes to analyze temperate and Arctic nearshore food webs report (1) that benthic consumers almost always have a stable carbon isotope ratio enriched in ^{13}C compared to the phytoplankton δ^{13}C and (2) that the various consumer species are distributed roughly evenly along a trophic continuum spanning 3 or 4 trophic levels (i.e. few species located between trophic levels) (Fry 1988; Hobson and Welch 1992; Kaehler et al. 2000; Dunton 2001; Lesage et al. 2001; Fredriksen 2003). The first observation is usually interpreted as indicating the major importance of kelp detritus and microphytobenthos (e.g., benthic diatoms) as food sources for benthic consumers, since these primary producers have a stable carbon isotope ratio that is relatively enriched in ^{13}C. We recently questioned this interpretation as benthic

---

[a] Corresponding author: `marc.nadon@gmail.com`

consumers are always enriched in ^{13}C, even when individuals are located at sites far removed from benthic algae (Nadon and Himmelman 2006). The second point, an even distribution of consumers along the trophic gradient, is interesting as it suggests a high level of omnivory (i.e. consumers feeding on prey at different trophic levels) in benthic systems (if differences in δ^{15}N enrichment among different organisms are taken into account). The long-standing view among ecologists was that omnivory destabilizes food webs, and thus should be relatively rare in nature (Pimm 1982). However, more in-depth analyses of food webs have shown that omnivores are actually quite common (Diehl 1993), and theoretical works suggest that omnivory is a stabilizing factor in food webs (McCann and Hastings 1997; Emmerson and Yearsley 2004).

In recent years, the analysis of naturally occurring stable isotopes of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}N) has contributed to our understanding of energy transfers in marine ecosystems, especially at lower trophic levels where the flow of energy from primary producers to consumers is often difficult to evaluate using traditional methods (e.g., stomach contents). Different types of aquatic primary producers (e.g., phytoplankton vs. benthic algae) typically have well separated stable carbon isotope ratios which are conserved in their respective consumers, although with a slight (0.5–1.6‰) enrichment (i.e., an increase in the concentration of heavy isotopes) (Vander Zanden and Rasmussen 2001; McCutchan et al. 2003; Vanderklift and Ponsard 2003; Caut et al. 2009). Nitrogen stable isotope ratios are typically more similar among marine primary producers but are enriched by about 2–4‰ with each increase in trophic level (Vanderklift and Ponsard 2003; Caut et al. 2009). For this reason, carbon stable isotope ratios are typically used to determine the sources of primary production whereas nitrogen stable isotope ratios are more often used to investigate the trophic levels of organisms. Together, the two stable isotope ratios provide an effective tool in food web studies.

The goal of the present study is to analyze the stable isotope ratios (carbon and nitrogen) of benthic organisms to investigate the trophic structure of the rocky subtidal food web around the Mingan Islands in the northern Gulf of St. Lawrence, eastern Canada. We used the isotope signatures first to identify the trophic level of common benthic organisms and secondly to examine the general distribution of organisms along the trophic level gradient. Numerous reports have described the subtidal community in the Mingan Islands but these studies have focused on the role of the major consumers in the system (e.g., urchins, ophiuroids, sea stars, whelks) (Himmelman and Dutil 1991; Rochette et al. 1995; Gaymer et al. 2001; Drolet et al. 2004; Gagnon et al. 2004). The knowledge of this system acquired from the past studies constitutes an interesting framework from which to explore relationships indicated by the stable isotope ratios.

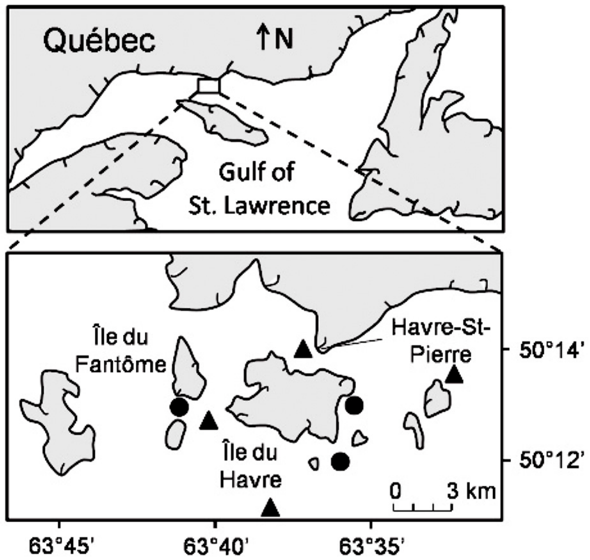

Fig. 1. Location of sampling sites in the Mingan Islands on the north shore of the Gulf of St. Lawrence, Canada. The circles are the main sampling sites where benthic microalgae, macroalgae, and animals were collected. The triangles are the locations where particulate organic matter (POM) samples were collected. A few POM samples were also taken further offshore at locations not shown on the map.

2 Materials and methods

2.1 Study area

Our study sites, located around the Mingan Islands in the northern Gulf of St. Lawrence (Fig. 1), are relatively protected from high wave energy due to the islands themselves and because of a large island (Anticosti Island) located 50 km to the south. The water in the region is unusually cold for this gulf, averaging only about 7 °C during summer. The cold water around these islands is due to intense vertical mixing by wind and tide, and makes this region representative of subarctic ecosystems at higher latitude. The subtidal area consists of two distinct zones (Himmelman 1991), (1) a macroalgal fringe, composed mainly of the fast growing kelp species *Alaria esculenta* and *Laminaria digitata*, in shallow water, and (2) extensive urchin barrens in deeper water. The density of the urchin, *Strongylocentrotus droebachiensis*, exceeds 100 individuals m^{-2} on most rocky surfaces. The lower limit of the macroalgal fringe is determined by the grazing of aggregations of large urchins at the lower edge of the fringe (Himmelman et al. 1983). The fringe extends to the greatest depths ($\sim$5 m) at exposed sites where wave action deters urchin grazing, but disappears completely at very sheltered sites, where urchins graze up into the intertidal zone (Himmelman 1991; Gagnon et al. 2004). The grazing resistant phaeophyte *Agarum cribrosum* occurs in patches on the upper barrens (down to 10–20 m), and individuals occasionally occur down to 30 m. On sandy bottoms, benthic microalgae form a thin but visible brown layer down to about 30 m (MO Nadon, unpubl. data). The main invertebrates within the barrens are a variety of suspension and deposit feeders, particularly sea cucumbers (e.g., *Cucumaria frondosa*), the soft coral, *Gersemia rubiformis*, and sponges. Also, bivalves (e.g., *Mya truncata*, *Chlamys islandica*) are abundant on soft bottoms and ophiuroids (e.g., *Ophiopholis aculeata*) occur in high densities on most rocky surfaces, particularly on vertical walls (Drolet et al. 2004). Grazers of algal films and coralline algae such as chitons (*Tonicella marmorea*) and limpets (Jenkins et al. 2001; Latyshev et al. 2004) are common on rocky surfaces. Four guilds of macropredators characterize this subtidal system (Himmelman 1991): (1) four sea stars (*Leptasterias polaris*, *Asterias vulgaris*, *Crossaster papposus*, and *Solaster endeca*), (2) the whelk *Buccinum undatum* (which is often a kleptoparasite) (3) two crabs (*Cancer irroratus* and *Hyas araneus*) and (4) fishes, the most conspicuous being the sculpin *Myoxocephalus scorpius*. Other predators may include sea birds (ex. several gull species), although these typically feed in the more accessible intertidal zone. The lobster *Homarus americanus* and the cunner *Tautoglaborous americanus*, important predators in communities further south, are absent in the cold waters of the Mingan Islands. Grey and harbor seals are relatively rare in the region and are mostly transients.

2.2 Sampling

Samples for isotopic analysis were collected from June to August in 2003. A few additional samples were also collected during the same months in 2004 (e.g., benthic microalgae, additional phytoplankton and sea urchin samples). We previously described our sampling of particulate organic matter (POM; Nadon and Himmelman 2006). In short, POM samples were obtained by pre-filtering up to 40 L of water through a 64-μm mesh screen and then onto either 5- or 10-μm Nitex mesh. The material remaining on the 5- or 10-μm screens, representing 5–64 μm and 10–64 μm size fractions, respectively, were collected and dried. For certain samples, a smaller size fraction (0.7–10 μm) was collected using GF/F filters in order to obtain stable isotope ratios for different parts of the POM. Water samples were collected at the surface and at a depth of 20 m at well separated sites haphazardly located at various distances from shore (Fig. 1) and at different time periods in both 2003 and 2004.

We dived at three nearshore sites (separated by at least 5 km) to sample the common benthic organisms (Fig. 1) and at least three individuals of each species were collected at each site. For most animals we took samples of the muscle tissues, but we sampled the podia of sea stars, the tunic of ascidians and whole body of sponges. Macroalgae samples were collected at both exposed and protected sites, and whole fronds were subsequently grounded up and then subsampled. We used syringes to collect samples of mats of benthic microalgae that were covering sediment bottoms. The samples were first filtered though a 64-μm mesh filter (to limit the amount of inorganic particles) and then though a 5-μm mesh filter, so that the filtrate was in the 5–64 μm size fraction. Within a few hours following collection, all plant and animal samples were dried at 60 °C for a minimum of 24 h. The rocky subtidal zones of the northern Gulf of St. Lawrence have relatively simple marine communities and the organisms collected during this study represent the vast majority of those present, with few omissions.

2.3 Sample analysis

We exposed POM and benthic microalgae samples to HCl fumes for 24 h prior to analyses to remove traces of carbonate. Also, we immersed the samples of sea star podia and urchin jaw muscle in a 2 N HCl solution to remove calcium carbonate particles. Samples were not defatted since only organs with low fat concentration were analyzed. Stable isotope samples were analyzed in an isotope mass ratio spectrometer (Fisons Instruments, model VG Prism Isotech) at the Commission Géologique du Canada laboratory in Quebec City. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) using the standard definition:

$$\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1000,$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. Pee Dee Belemnite was the standard for δ^{13}C and atmospheric N_2 for δ^{15}N. Replicates of internal standards showed that analytical errors were in the order of ±0.2‰ for both carbon and nitrogen.

We explored a variety of approaches in calculating the trophic levels (*TL*) of predators. As suggested by Vander Zanden and Rasmussen (2001), we used the primary consumers as the baseline for predator *TL* calculations using the following formula:

$$TL = \left(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}}\right)/\Delta^{15}N + 2 \tag{1}$$

where the baseline is the average nitrogen isotope value of primary consumers and Δ^{15}N is the trophic discrimination factor for nitrogen. Typical discrimination factors used in past studies are around 3.4‰ (Minagawa and Wada 1984). One problem with using a fixed value for Δ^{15}N is that nitrogen discrimination factors between consumers and their diets can vary substantially among consumer groups, mainly in relation to the biochemical form of nitrogen extraction of the consumers and the diet nutritional status (Vanderklift and Ponsard 2003). This shows that nitrogen discrimination factors need to be selected carefully for each consumer group when attempting to rebuild trophic relationships using stable isotopes. This can be difficult considering the relative paucity of controlled feeding experiments for certain taxonomic groups and the resulting lack of taxon-specific discrimination factors. To alleviate this issue, Caut et al. (2009) exploited the known linear relationship between diet δ^{15}N and discrimination factors to develop equations that provide discrimination factors by taxonomic group and tissue sampled. Two of these equations are of interest to us, the ones for whole-body invertebrates and fish muscles:
Whole-body invertebrate:

$$\Delta^{15}N = -0.311\delta^{15}N_{\text{diet}} + 4.065 \tag{2}$$

Fish muscle:

$$\Delta^{15}N = -0.281\delta^{15}N_{\text{diet}} + 5.879 \tag{3}$$

where Δ^{15}N is the discrimination factor between diet and consumers. These Δ^{15}N may replace a standard discrimination factor (e.g., 3.4‰) in Equation (1), if judged more appropriate.

We used primary consumers as a baseline for trophic calculations because primary producer δ^{15}N were slightly scattered (see Results section) and because of the uncertainties in associating various primary consumers with their specific diets (Nadon and Himmelman 2006; Caut et al. 2009). We did not attempt to measure the percent carbon originating from different benthic primary producers (as done in many food web studies) given the doubts raised in our accompanying study (Nadon and Himmelman 2006) about the interpretation that enriched δ^{13}C in consumers is due to feeding on enriched benthic algae.

3 Results

3.1 Primary producers

Our detailed results on the stable isotope ratios of particulate organic matter (POM) were reported in our previous study (Nadon and Himmelman 2006). In brief, we did not detect any significant variation related to size fraction, time period, depth or distance from shore in both δ^{13}C and δ^{15}N for POM, which suggests that POM was mostly composed of phytoplankton or phytoplankton-derived material. The average POM ratio (n = 20) was –23.3‰ for δ^{13}C and 8.1‰ for δ^{15}N. The three kelp species analyzed, the fast-growing fringe kelps *Alaria esculenta* and *Laminaria digitata*, and the grazer-resistant *Agarum cribrosum* from somewhat deeper water, had well separated δ^{13}C, –22.7‰, –18.9‰ and –15.9‰, respectively (i.e., no overlapping 95% confidence intervals); and similar δ^{15}N, 6.0‰, 6.7‰ and 6.8‰, respectively (Table 1). The kelp δ^{13}C showed high variability both within (mean SD = 1.3) and among sites (mean SD = 1.5). Finally, the δ^{13}C for benthic microalgae was –19.4‰ (SD = 0.2) and the δ^{15}N 6.0‰ (0.2). The overall average δ^{15}N of primary producers was 6.7 ± 0.9‰.

3.2 Consumers

For every consumer species, we pooled the samples collected at different sites because no differences were detected amongst individuals from various sites (ANOVA; $p > 0.05$). Most of the consumers studied had similar within-species δ^{13}C and δ^{15}N, which is reflected by their small 95% confidence intervals (an exception was *Solaster endeca*, as discussed below). The benthic consumers at all three sites were highly enriched in ^{13}C (Fig. 2), with δ^{13}C closer to those of benthic microalgae and the two fast growing kelps (*A. esculenta* and *L. digitata*) than to that of POM. However, values tending more towards values for POM were obtained for three consumers, the sponge *Haliclona oculata* (–20.6‰), the ascidian *Halocynthia pyriformis* (–20.1‰) and the sea anemone *Metridium senile* (–19.6‰). The soft coral Gersemia rubiformis was located halfway between the POM and *Laminaria digitata* δ^{13}C.

Overall, the benthic organism stable isotope ratios showed a coherent food web structure, with all ratios falling within the boundaries delimited by the primary producers. Almost all ratios fell into three distinct trophic levels, primary producers (trophic level = 1), primary consumers (2) and predators (3) (Fig. 2). The δ^{15}N values of the different primary producers were moderately separated, as δ^{15}N was 8.1‰ for POM, 6‰ for benthic microalgae, and the kelp ratios were intermediate between these values. Thus, there was no clear reference point for benthic primary producers which could be used for calculations of the trophic levels of the animals. Although some of the δ^{15}N values of primary consumers were slightly scattered (e.g., *Haliclona oculata* sponge), most of the main primary consumer values fell relatively close to a single level (average of 8.3 ± 1.0‰). The average predator δ^{15}N value was about 3.2‰ above the primary consumers. There were two predators which fell clearly above the third trophic level, the benthic fish *Myoxocephalus scorpius* and the sea star *Crossaster papposus*.

For most animals, variability in the δ^{15}N was low (standard deviations < 1‰), although the sea star *Solaster endeca* exhibited considerable variability (SD ~ 2‰). Most of the variation in two sea stars, *Solaster endeca* and *Leptasterias polaris*, was related to animal size (Fig. 3). Linear regressions of the δ^{15}N to sea star diameter showed that size explained 71% of the variation for *S. endeca* ($F_{1,4} = 9.7$, $r^2 = 0.71$, $p = 0.04$) and 76% of the variation for *L. polaris* ($F_{1,7} = 21.9$, $r^2 = 0.76$, $p = 0.002$) (Fig. 3). The other organisms did not show significant variation in stable isotope ratio related to size. In many cases, this may simply reflect the limited size range sampled.

The jaw muscles of the sea urchin *Strongylocentrotus droebachiensis* exhibited some unexpectedly elevated δ^{13}C (−13.4‰). Conversely, the δ^{15}N of the sea urchin gonads where fairly low (6.0‰). The average carbon and nitrogen stable isotope ratios of these two organs were taken for Figure 2.

4 Discussion

Our analysis showed three distinct trophic groups in the benthic community of the Mingan Islands, primary producers, primary consumers, and predators. A few organisms were located at a slightly higher level than the main group of predators and could be considered as top predators.

One important caveat to our study is the limited seasonal sampling period. Most organisms were collected during the summer months of 2003 (with a few extra individuals and/or species in 2004) due to logistical constraints. Since muscle tissue turnover rate in larger animals is between 1 and 3 months, the δ^{13}C values in the current study represent late spring – early summer diets (Tieszen et al. 1983; Riera and Richard 1997; Schaal et al. 2010). The main difference between winter and summer months in this ecosystem is the reduced availability of primary producers (kelp, microphytobenthos, and phytoplankton) due to reduced light intensity and expansive ice coverage. This may lead certain grazers, such as the green sea urchin, towards a more scavenger or predatory diet. Aside from these changes, we do not see a clear reason why other predators would drastically change their prey selection in the winter months.

The C and N stable isotope ratios for particulate organic matter in our study were close to the previously published values for the Gulf of St. Lawrence (Tan and Strain 1979; Martineau et al. 2004). The isotope values from the three kelp species were also similar to previously reported ratios (Stephenson et al. 1986; Fredriksen 2003), and showed a similar high variability. This variability is partly explained by the uneven storage of compounds with different stable isotope ratios within the plants (Stephenson et al. 1984). In addition, variations in water turbulence at different sites sampled probably affected the thickness of the boundary layer over kelp

Table 1. Mean isotopic ratios (± 95% confidence interval) for plants and animals collected at specific depths in the Mingan Islands, and the trophic level (TL) of predators as calculated based on the mean δ^{15}N of primary consumers and Equation (1). Equation (3) was used to obtain Δ^{15}N (see methods). A = autotrophs and PC = primary consumers. Figure 2 codes are also presented.

Samples	Code	n	Depth (m)	δ^{13}C (‰)	δ^{15}N (‰)	TL
Algae						
Phytoplankton (POM 0.7–64 µm)	POM	20	0–18	–23.3 ± 0.5	8.1 ± 0.3	A
Alaria esculenta	Alar	9	<5	–18.9 ± 1.0	6.7 ± 0.3	A
Laminaria digitata	Lami	6	<5	–15.9 ± 1.7	6.8 ± 0.2	A
Agarum cribrosum	Agar	9	10	–22.7 ± 1.6	6.0 ± 0.5	A
Benthic microalgae	*Same*	3	10–15	–19.4 ± 0.2	6.0 ± 0.2	A
Porifera						
Haliclona oculata	Hali	4	5–15	–20.6 ± 0.7	9.8 ± 0.7	PC
Cnidaria						
Gersemia rubiformis	Gers	4	15	–19.1 ± 0.9	8.8 ± 0.5	PC
Metridium senile	Metr	4	5–15	–19.6 ± 0.8	12.8 ± 1.1	3.2
Tealia felina	Teal	6	5–15	–16.8 ± 0.8	12.5 ± 0.6	3.1
Mollusca						
Aporrhais occidentalis	Apor	6	5–15	–17.0 ± 0.9	8.7 ± 0.3	PC
Buccinum undatum	Bucc	9	5–15	–16.5 ± 0.3	12.3 ± 0.7	3.1
Chlamys islandica	Chla	9	20–40	–18.1 ± 0.3	8.3 ± 0.3	PC
Mya truncata	Mya	3	5–15	–17.4 ± 08	7.7 ± 0.6	PC
Mytilus edulis	Myti	3	2	–17.8 ± 0.1	8.9 ± 0.5	PC
Tonicella marmorea	Toni	3	4–7	–15.5 ± 0.6	9.0 ± 0.1	PC
Crustacea						
Cancer irroratus	Canc	9	5–15	–16.6 ± 0.5	12.3 ± 0.2	3.1
Hyas araneus	Hyas	9	5–15	–17.5 ± 0.3	11.9 ± 0.1	2.9
Pagurus acadianus	Pagu	6	5–15	–16.3 ± 0.6	11.0 ± 0.3	2.7
Gammaridae	Gamm	3	5–10	–17.8 ± 0.3	7.2 ± 0.5	PC
Echinodermata						
Asterias vulgaris	Aste	8	5–15	–16.9 ± 0.4	12.2 ± 0.6	3.0
Crossaster papposus	Cross	6	5–15	–15.4 ± 1.1	14.0 ± 0.8	3.6
Cucumaria frondosa	Cucu	3	15	–17.9 ± 0.9	8.8 ± 0.6	PC
Leptasterias polaris	Lept	9	5–15	–16.5 ± 0.7	11.5 ± 0.3	2.8
Solaster endeca	Sola	6	5–15	–16.1 ± 0.9	11.8 ± 1.4	2.9
Strongylocentrotus droebachiensis (gonad)	Stron[t]	6	5–15	–18.8 ± 1.3	6.0 ± 0.6	PC
Strongylocentrotus droebachiensis (muscle)	Stron[t]	9	5–15	–13.4 ± 0.2	9.1 ± 0.1	PC
Ascidiacea						
Halocynthia pyriformis	Halo	4	5–15	–20.1 ± 0.3	9.1 ± 0.1	PC
Fish						
Myoxocephalus scorpius	Myox	6	5–15	–16.8 ± 0.5	13.7 ± 0.3	3.5
Stichaeus punctatus	Stic	2	15	–17.3 ± 0.4	12.4 ± 0.1	3.1

[t] This code in Figure 2 is the average for both organs.

fronds, which in turn would have affected how fast light carbon molecules become depleted (Simenstad et al. 1993). The slower growth rate of the grazer-resistant kelp *Agarum cribrosum* may explain why its δ^{13}C was close to POM as its capacity to deplete light carbon molecules in its boundary layer may have been limited.

4.1 Primary consumers

In our study, we observed an enrichment of 2.1‰ between the average δ^{15}N of primary producers and primary consumers. As mentioned in the Methods section, we did not attempt to calculate the precise trophic levels of primary consumers because of the relatively wide range of primary producer δ^{15}N and the uncertainties in associating certain primary consumers, such as filter-feeders, with their respective diet (Nadon and Himmelman 2006).

The suspension and deposit feeders in our study (bivalves, sea cucumbers, soft corals, ascidians and sponges) had enriched δ^{13}C relative to POM and this is typically interpreted as indicating a strong dependence on benthic primary producers (kelp detritus and benthic microalgae) as a food source. Since

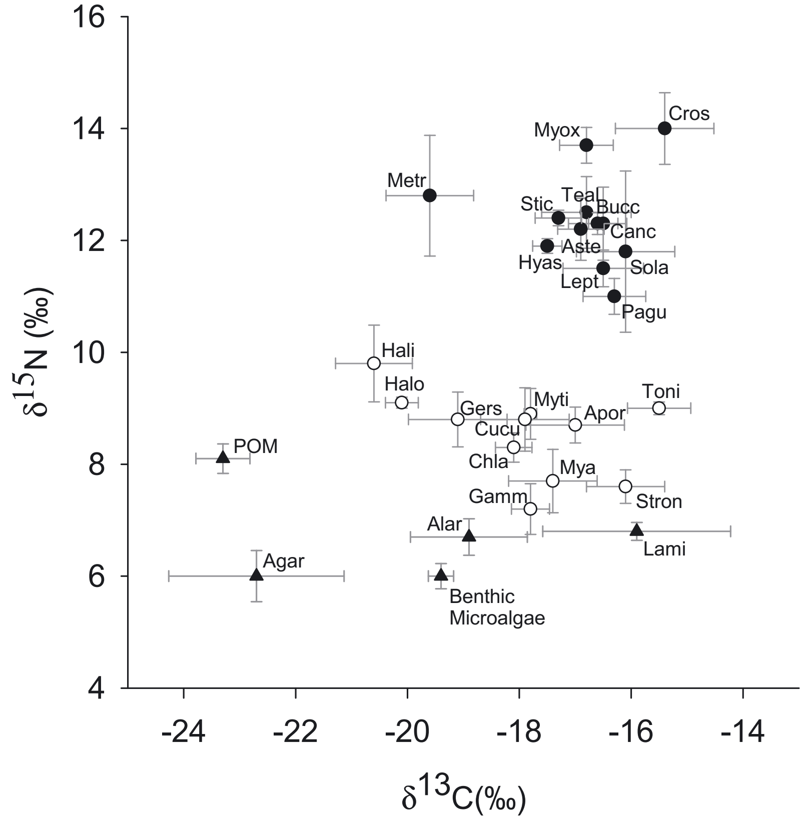

Fig. 2. Mean carbon and nitrogen stable isotope ratios for nearshore benthic primary producers (dark triangles), primary consumers (clear circles), and secondary/tertiary consumers (dark circles) in the subtidal community of the Mingan Islands. No trophic enrichment corrections were applied to these values. Error bars are 95% confidence intervals. Species are identified using the first four letters of the genus name and complete names are given in Table 1. *TL* = trophic level.

fast-growing kelp species and benthic microalgae are limited to shallow depths (by sea urchins grazing and light penetration) one would expect increased use of phytoplankton, and thus a decrease in δ^{13}C values, for benthic consumers living further offshore. In our companion study, we investigated this hypothesis and found no evidence, either in our field measurements or in a review of values in the literature, of a change in δ^{13}C in benthic consumers related to distance from benthic producers, even to great depths (e.g., >1000 m; Nadon and Himmelman 2006). Thus, we cannot evaluate the importance of benthic primary producers for nearshore suspension and deposit feeders in the northern Gulf of St. Lawrence. Other factors, such as the selective feeding on enriched carbon particles, could explain the heavy carbon found in these organisms, although this remains to be investigated. This was also recently suggested by van Oevelen et al. (2009). Studies combining stable isotope measurements with other methods will be needed to resolve this issue (i.e., HLPC pigment measurements, gut content analyses, isotope labeling). A promising approach combining DNA sequencing, microarrays, and stable isotope analysis is used in Hardy et al. (2010).

The jaw muscle tissues of the sea urchin *Strongylocentrotus droebachiensis* had a very heavy δ^{13}C that could not be explained by their main diet, kelp (Himmelman and Steele 1971; Himmelman 1991), and was different from values reported in other studies, which were usually similar to kelp. For example, the δ^{13}C for *S. droebachiensis* (from unspecified organs) in Nova Scotia, Canada, was similar to kelp ratios (Stephenson et al. 1986). Also, the stable isotope ratios of carbon and nitrogen for jaw muscle tissues of the Chilean urchin *Tetrapygus niger* were only 1‰ enriched compared to kelp (Rodriguez 2003). Our analysis of gonadal tissues of *S. droebachiensis* gave lighter, more reasonable δ^{13}C, but this was likely because lighter isotopes are more abundant in the gonads because of their high lipid content. Yatsuya and Nakahara (2004) showed a 2.5‰ increase in the δ^{13}C between the gonad and gut contents for the Japanese urchin *Anthocidaris crassispina*. A reduction by 2.5‰ of the δ^{13}C we obtained for the gonad of *S. droebachiensis* would give a value close to that of kelp (–16.3‰). The explanation for the enriched δ^{13}C for jaw muscles in our study is unclear. Possibly sea urchins were feeding on a food source which we did not analyze but which contained heavier δ^{13}C than kelp (e.g., coralline algae) or that there is some anomaly in the jaw muscles of the urchin in our area. Although we did not analyze the stable isotope composition of coralline algae, and could not find measurements for coralline algae in the literature, chitons, which are known to feed on coralline algae (Latyshev et al. 2004), did not have a particularly enriched δ^{13}C (–15.5‰ for *Tonicella marmorea*). Another surprising observation in our study was that sea urchin δ^{15}N (for both the muscles and gonads) fell slightly below the herbivore level. This was not expected given that sea

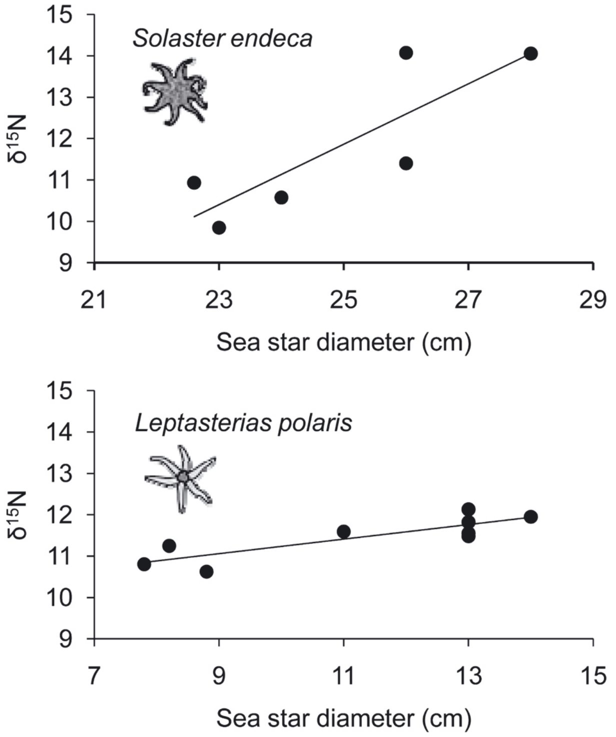

Fig. 3. Relationship between sea star size and nitrogen stable isotope ratio. Statistically significant regression lines are shown ($p < 0.05$).

urchins also occasionally feed on animal tissue (Himmelman and Steele 1971). Our nitrogen values suggest that animal tissues are not an important component of the diet of urchins. The study of Hobson and Welch (1992) in the high Arctic also found that the δ^{15}N of *S. droebachiensis* clearly placed it as a herbivore.

Little is known about the gastropod *Aporrhais occidentalis* that is exclusively found on sand and mud slopes below the rock zone. We have never seen it feeding on drift macroalgae or animal tissues. Perron (1978) indicates that it feeds on benthic microalgal films and this appears to be confirmed by its stable isotope ratio which places it amongst herbivores, with a δ^{13}C close to that of benthic microalgae.

4.2 Predators

We observed an average enrichment of 3.2‰ between primary consumers and predators. This value is very close to the discrimination factor of 3.4‰ suggested in Equation (1) (Minagawa and Wada 1984). This indicates that this value is appropriate to calculate the trophic level of the predators in the current study. Alternatively, we also evaluated the diet-dependent discrimination factor approach described in Caut et al. (2009). We tried both the whole-body invertebrate and fish muscle formulas in order to obtain potentially more appropriate discrimination factors (see Methods section). The invertebrate formula (Eq. (2)) gave unrealistic nitrogen discrimination factors when applied to the invertebrate predators in this study. This equation provided a relatively low nitrogen discrimination factor of 1.4‰ for these predators, which, when used in Equation (1), gave an unlikely average predator trophic level of 4.7. However, the fish muscle formula (Eq. (3)) provided a discrimination factor of 3.5‰, which is much closer to the average enrichment found in this study between predators and preys (3.2‰). For this reason, we used Equation (2) to calculate the discrimination factor and average trophic level of predators in this system (Table 1). One potential explanation for the inappropriateness of Equation (2) is that only whole-body invertebrate δ^{15}N were measured in the controlled feeding experiments from which this equation is derived. If feeding experiments measuring invertebrate muscle δ^{15}N were available, it is likely that that a discrimination factor formula close to the fish muscle formula (Eq. (3)) would be derived, as suggested by the results in the current study. For this reason, we suggest using the fish muscle formula to obtain discrimination factors for invertebrate muscle tissue (Caut et al. 2009).

The whelk *Buccinum undatum* is the most abundant carnivore in the Mingan Islands. Until recently, it was not clear which food sources were supporting the high densities of whelks, since these animals are rarely seen feeding and stomach analyses usually revealed empty stomachs or sometimes unrecognizable materials (Himmelman and Hamel 1993). Rochette et al. (1995) indicate that bivalve tissues stolen from feeding sea stars *Lepasterias polaris* represent a substantial portion of the diet of adult whelks. The stable isotope ratio of *B. undatum* lends support to this hypothesis since their stable isotope ratio fell in the predators/scavengers group (TL = 3.1) and close to the δ^{13}C for bivalves. The northern red sea anemone *Tealia felina* commonly feeds on detached macroinvertebrates, most often urchins, and it is most abundant in depressions and at the base of vertical faces where the probability of encountering dislodged animals is increased (JHH, pers. observ.). Its elevated δ^{15}N, placing it high in the main predator group (TL = 3.1), suggests that it may be feeding on carnivores (e.g., whelks and crabs) as well as on herbivores. The much lighter δ^{13}C of the sea anemone *Metridium senile* compared to other predators is probably because this anemone, with its fine tentacles, mainly feeds on pelagic organisms, such as zooplankton (Sebens and Koehl 1984), which typically have δ^{13}C close to phytoplankton in oceanic systems (Martineau et al. 2004). The three crabs in our study, *Hyas araneus*, *Cancer irroratus* and the hermit crab *Pagurus acadianus*, were clearly positioned at the level of carnivores (TL equal to 2.9, 3.1, and 2.7, respectively). This is somewhat surprising for *C. irroratus* and *H. araneus* as stomach analyses by Bérubé (1989) show that both crabs commonly ingest algae (algae represent 10% of the average stomach content of *C. irroratus* and 5% for *H. araneus*). The isotope data suggest that ingested algae contribute little to tissue growth in these species. As hermit crabs are scavengers, the position of *P. acadianus* within the predator group is not surprising. The small fish *Stichaeus punctatus* (Arctic shanny) has a diet of mainly amphipods (~65% of diet), complemented by a mix of polychaetes and caridean shrimps (Thomas 1988). As amphipods have a δ^{13}C of –16.5‰, the ratio of *S. punctatus* (–17.3‰) seems to reflect its diet.

The stable isotope ratio of the sea star *Asterias vulgaris* positioned it amongst the main predator group (TL = 3.0), reflecting its diet of bivalves and sea urchins as inferred from feeding observation studies (Dutil et al. 2004). The trophic level of the polar sea star *Lepasterias polaris* varied significantly with size, although none of the individuals analyzed fell much higher than the predator level. We expected a higher trophic position for *L. polaris*, as previous feeding studies showed that large individuals (diameter > 20 cm) commonly feed on predatory whelks (between 9 and 20% of diet) in addition to its mostly bivalve diet (Himmelman 1991; Rochette et al. 1995).

Two predators had heavier δ^{15}N than the main group of predators. One was the sea star *Crossaster papposus* (TL = 3.6), which mainly feeds on green sea urchins and sand dollars (50% of its diet) and is also an important predator of sea stars, including conspecifics (Himmelman 1991; Dutil et al. 2004). The other was the shorthorn sculpin *Myoxocephalus scorpius* (TL = 3.5). The sculpin mainly feeds on capelin (*Mallotus villosus*) and its diet also includes predatory crabs (Thomas 1988); thus, its diet is consistent with the observed enriched δ^{15}N. Surprisingly, the average stable isotope signature of the sea star *Solaster endeca* did not classify it among the top predators, even though feeding observations show that it occasionally feeds on other sea stars (~10% of feeding observations for large individuals), with its main diet of sea cucumbers (Himmelman 1991; Dutil et al. 2004). Nevertheless, larger individuals had significantly higher δ^{15}N, suggesting an ontogenetic shift to feeding at a higher trophic level. Thus, large *S. endeca* (diameter > 25 cm) should also be considered as top predators.

The correlation between size and trophic level (as indicated by the δ^{15}N), which was revealed in two species of sea stars (*L. polaris and S. endeca*), even though very small individuals were not examined, indicated that the isotope technique is a potentially powerful tool for studying ontogenetic shifts in diet for invertebrates. Such shifts have previously been documented in fishes using this method (Deudero et al. 2004). For many species (e.g., sea stars, whelks, crabs), the food resources used by small individuals is hard to determine, because they are cryptic and more difficult to find or because it is more difficult to dissect than small individuals. In such cases, isotope analyses would be a very useful tool for detecting situations where shifts in diet occur.

4.3 General food web structure

The subtidal food webs in the northern Gulf of St. Lawrence have a fairly low species richness and a low level of omnivory, as suggested by the small number of organisms located in-between the three main trophic levels (i.e. organisms feeding on prey from more than one trophic level). Both of these observations can have profound effects on the stability of this ecosystem, especially in the face of human exploitation as well as the ongoing changes to the Earth's climate and its impacts on nearshore systems (e.g., increased sea temperature, increased wave energy, decreased winter ice coverage, rising sea level, increased ocean acidification, etc.). Diversity and omnivory can affect the stability of an ecosystem in several ways. First, low diversity systems are usually less stable due to a lower functional redundancy (e.g., species capable of compensating the decline in an ecosystem function caused by the loss of another species). Furthermore, higher diversity increases the chances that a community contains species that are capable of adapting to a new environment, thus insuring the persistence of this community (McCann 2000). Finally, the distribution of interaction strengths in low diversity communities is typically skewed towards a few strong ones, as opposed to numerous weak ones in diverse systems. This has been suggested to make communities more prone to invasions and other destabilizing forces (McCann 2000).

Simulation studies have shown that weak omnivorous links enhance community stability and persistence by dampening the oscillations between consumers and producers (McCann and Hastings 1997; Emmerson and Yearsley 2004; Namba et al. 2008, although see (Tanabe and Namba 2005). Weak omnivorous links can be seen as consumers complementing their main diet with occasional preys located at a different trophic level than their main diet (ex. intraguild predation of the whelk *B. undulatum* by large *L. polaris* sea stars, consumption of macroalgae by crabs, scavenging *S. centrotus* sea urchins). The low level of omnivory found in the current system contrasts with the general pattern reported by previous studies of temperate and polar benthic systems, which show a continuum in organisms from the level of herbivores through to the level of predators and higher order predators (Hobson and Welch 1992; Kaehler et al. 2000; Dunton 2001; Fredriksen 2003). This apparent trophic continuum may be due to variable nitrogen discrimination factors among organisms in these studies which may cause two species with different δ^{15}N to be classified at different trophic levels, even when it is not the case. A better understanding of nitrogen discrimination factors through more feeding experiment may help clarify this issue, along with innovative approaches based on diet δ^{15}N (Caut et al. 2009).

Acknowledgements. We are most thankful to Myles Thompson, Catherine Vallières, Isabelle Deschênes, Pierre Grondin, François Praira, Jean-Philippe Parent, Jean-Sébastien Roy and Émilie Castonguay who aided us in the field work. Also, we are indebted to Ladd E. Johnson and Warwick F. Vincent for their many helpful comments throughout the project. Anna Smirnoff at the Commission Géologique du Canada helped with the isotope analysis. This study was supported by an operating grant from the National Sciences and Engineering Research Council of Canada to J.H. Himmelman and M.-O. Nadon received support from Québec-Océan. All experiments were carried in accordance to Canadian laws.

References

Bérubé M., 1989, Partage des ressources entre le crabe tourteau, *Cancer irroratus*, et le crabe araignée, *Hyas araneus*, au nord du golfe du Saint-Laurent. M.Sc. Thesis. Université Laval, Canada. Département de biologie.

Caut S., Angulo E., Courchamp F., 2009, Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. 46, 443–453.

Deudero S., Pinnegar J.K., Polunin N.V.C., Morey G., Morales-Nin B., 2004, Spatial variation and ontogenic shifts in the isotopic composition of Mediterranean littoral fishes. Mar. Biol. 145, 971–981.

Diehl S., 1993, Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. Oikos 68, 151–157.

Drolet D., Himmelman J.H., Rochette R., 2004, Use of refuges by the ophiuroid *Ophiopholis aculeata*: contrasting effects of substratum complexity on predation risk from two predators. Mar. Ecol. Prog. Ser. 284, 173–183.

Dunton K.H., 2001, δ^{15}N and δ^{13}C measurements of Antarctic peninsula fauna: Trophic relationships and assimilation of benthic seaweeds. Am. Zool. 41, 99–112.

Dutil C., Gaymer C.F., Himmelman J.H., 2004, Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community. J. Exp. Mar. Biol. Ecol. 313, 353–374.

Emmerson M., Yearsley J.M., 2004, Weak interactions, omnivory and emergent food-web properties. Proc. R. Soc. Lond. B Biol. Sci. 271, 397–405.

Fredriksen S., 2003, Food web studies in a Norwegian kelp forest based on stable isotope (δ^{13}C and δ^{15}N) analysis. Mar. Ecol. Prog. Ser. 260, 71–81.

Fry B., 1988, Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 33, 1182–1190.

Gagnon P., Himmelman J.H., Johnson L.E., 2004, Temporal variation in community interfaces: kelp-bed boundary dynamics adjacent to persistent urchin barrens. Mar. Biol. 144, 1191–1203.

Gaymer C.F., Himmelman J.H., Johnson L.E., 2001, Distribution and feeding ecology of the seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St. Lawrence, Canada. J. Mar. Biol. Assoc. UK 81, 827–843.

Hardy C.M., Krull E.S., Hartley D.M., Oliver R.L., 2010, Carbon source accounting for fish using combined DNA and stable isotope analyses in a regulated lowland river weir pool. Mol. Ecol. 19, 197–212.

Himmelman J.H., 1991, Diving observations of subtidal communities in the northern Gulf of St. Lawrence. Can. Spec. Publ. Fish. Aquat. Sci. 113, 319–332.

Himmelman J.H., Cardinal A., Bourget E., 1983, Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. Oecologia 59, 27–39.

Himmelman J.H., Dutil C., 1991, Distribution, population structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 76, 61–72.

Himmelman J.H., Hamel J.-R., 1993, Diet, behavior and reproduction of the whelk *Buccinum undatum* in the northern Gulf of St. Lawrence, eastern Canada. Mar. Biol. 116, 423–430.

Himmelman J.H., Steele D.H., 1971, Foods and predators of the green sea urchin *Strongylocentrotus droebachiensis* in Newfoundland waters. Mar. Biol. 9, 315–322.

Hobson K.A., Welch H.E., 1992, Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Mar. Ecol. Prog. Ser. 84, 9–18.

Jenkins S.R., Arenas F., Arrontes J., Bussell J., Castro J., Coleman R.A., Hawkins S.J., Kay S., Martinez B., Oliveros J., Roberts M.F., Sousa S., Thompson R.C., Hartnoll R.G., 2001, European-scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. Mar. Ecol. Prog. Ser. 211, 193–203.

Kaehler S., Pakhomov E.A., McQuaid C.D., 2000, Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by δ^{13}C and δ^{15}N analysis. Mar. Ecol. Prog. Ser. 208, 13–20.

Latyshev N.A., Khardin A.S., Kasyanov S.P., Ivanova M.B., 2004, A study on the feeding ecology of chitons using analysis of gut contents and fatty acid markers. J. Molluscan Stud. 70, 225–230.

Lesage V., Hammill M.O., Kovacs K.M., 2001, Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. Mar. Ecol. Prog. Ser. 210, 203–221.

Martineau C., Vincent W.F., Frenette J.-J., Dodson J.J., 2004, Primary consumers and particulate organic matter: Isotopic evidence of strong selectivity in the estuarine transition zone. Limnol. Oceanogr. 49, 1679–1686.

McCann K., Hastings A., 1997, Re-evaluating the omnivory-stability relationship in food webs. Proc. R. Soc. Lond. B Biol. Sci. 264, 1249–1254.

McCann K.S., 2000, The diversity-stability debate. Nature 405, 228–233.

McCutchan J.H., Lewis W.M., Kendall C., McGrath C.C., 2003, Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378–390.

Minagawa M., Wada E., 1984, Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim. Cosmochim. Acta 48, 1135–1140.

Nadon M.-O., Himmelman J.H., 2006, Stable isotopes in subtidal food webs: Have enriched carbon ratios in benthic consumers been misinterpreted? Limnol. Oceanogr. 51, 2828–2836.

Namba T., Tanabe K., Maeda N., 2008, Omnivory and stability of food webs. Ecol. complex. 5, 73–85.

Perron F.E., 1978, Seasonal burrowing behavior and ecology of *Aporrhais-occidentalis* (Gastropoda Strombacea). Biol. Bull. 154, 463–471.

Pimm S.L., 1982, Food webs. London, Chapman & Hall. Population and community biology series.

Riera P., Richard P., 1997, Temporal variation of δ^{13}C in particulate organic matter and oyster *Crassostrea gigas* in Marennes-Oléron Bay (France): effect of freshwater inflow. Mar. Ecol. Prog. Ser. 147, 105–115.

Rochette R., Morissette S., Himmelman J.H., 1995, A flexible response to a major predator provides the whelk *Buccinum undatum* L. with nutritional gains. J. Exp. Mar. Biol. Ecol. 185, 167–180.

Rodriguez S.R., 2003, Consumption of drift kelp by intertidal populations of the sea urchin Tetrapygus niger on the central Chilean coast: possible consequences at different ecological levels. Mar. Ecol. Prog. Ser. 251, 141–151.

Schaal G., Riera P., Leroux C., Grall J., 2010, A seasonal stable isotope survey of the food web associated to a peri-urban rocky shore. Mar. Biol. 157, 283–294.

Sebens K.P., Koehl M.A.R., 1984, Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actiniaria) in the New England subtidal. Mar. Biol. 81, 255–271.

Simenstad C.A., Duggins D.O., Quay P.D., 1993, High turnover of inorganic carbon in kelp habitats as a cause of δ^{13}C variability in marine food webs. Mar. Biol. 116, 147–160.

Stephenson R.L., Tan F.C., Mann K.H., 1984, Stable carbon isotope variability in marine macrophytes and its implications for food web studies. Mar. Biol. 81, 223–230.

Stephenson R.L., Tan F.C., Mann K.H., 1986, Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and a kelp bed in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 30, 1–7.

Tan F.C., Strain P.M., 1979, Carbon isotope ratios of particulate organic matter in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 36, 678–682.

Tanabe K., Namba T., 2005, Omnivory creates chaos in simple food web models. Ecology 86, 3411–3414.

Thomas B., 1988, L'utilisation des ressources infralittorales par une communauté de poissons démersaux. M.Sc. Laval Univ. Département de biologie.

Tieszen L.L., Boutton T.W., Tesdahl K.G., Slade N.A., 1983, Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for δ^{13}C analysis of diet. Oecologia 57, 32–37.

van Oevelen D., Soetaert K., Franco M.A., Moodley L., van Ijzerloo L., Vincx,M., Vanaverbeke J., 2009, Organic matter input and processing in two contrasting North Sea sediments: insights from stable isotope and biomass data. Mar. Ecol. Prog. Ser. 380, 19–32.

Vander Zanden M.J., Rasmussen J.B., 2001, Variation in δ^{15}N and δ^{13}C trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. 46, 2061–2066.

Vanderklift M.A., Ponsard S., 2003, Sources of variation in consumer-diet delta N-15 enrichment: a meta-analysis. Oecologia 136, 169–182.

Yatsuya K., Nakahara H., 2004, Diet and stable isotope ratios of gut contents and gonad of the sea urchin *Anthocidaris crassispina* (A. Agassiz) in two different adjacent habitats, the *Sargassum* area and *Corallina* area. Fish. Sci. 70, 285–292.