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CHAPITRE I

INTRODUCTION GÉNÉRALE

Les perturbations naturelles ont depuis toujours affecté et configuré les écosystèmes, mais depuis le siècle dernier, on assiste à une augmentation continue des impacts anthropiques sur l'environnement ayant des conséquences sur le maintien du bon fonctionnement des écosystèmes (Naeem et al. 1994, Vitousek et al. 1997b). Avec l'augmentation des activités humaines à l'échelle planétaire, beaucoup d'écosystèmes subissent des perturbations qui modifient leurs propriétés abiotiques et biotiques qui les régulent (Vitousek et al. 1997b, Tilman and Lehman 2001). La zone côtière n'est évidemment pas épargnée par ces pressions (Vitousek et al. 1997b, Lotze et al. 2002, Thompson et al. 2002, Airoldi and Beck 2007). La destruction de l'habitat (Brooks et al. 2002, Tole 2002, Hanski 2005), la pollution (McNeely 1992, Oleksyn and Reich 1994) ainsi que l'altération des cycles biogéochimiques du carbone et de l'azote par les activités anthropiques (Vitousek et al. 1997a, Vitousek et al. 1997b, Rabouille et al. 2001) affectent de façon négative les structures (par ex.: richesse, abondance) et les fonctions (par ex.: productivité et respiration) des communautés (Vitousek et al. 1997b, Jackson et al. 2001, Hooper et al. 2005). Celles-ci sont également touchées par d'autres perturbations qui sont liées aux changements climatiques tels que l'augmentation de la température (Schiel et al. 2004, Keser et al. 2005, Mieszkowska et al. 2006, Hale et al. 2011) ou l'action des vagues causée par de fortes tempêtes (Dayton et al. 1992, Moring 1996, Byrnes et al. 2011), qui sont prédites d'augmenter dans le futur (Easterling et al. 2000, Meehl et al. 2000) ou de fluctuer davantage vers des extrêmes (Kerr 2011). On peut déjà assister à des changements du nombre, de l'identité et de l'abondance des espèces que ce soit au niveau local qu'au niveau global (Vitousek et al. 1997b, Tilman and Lehman 2001). Comprendre les conséquences des changements de la biodiversité

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(Sala et al. 2000, Tilman and Lehman 2001, Jenkins 2003, Lotze 2005, Solan et al. 2008) et de la perte de biodiversité (Grime 1997, Loreau et al. 2002, Worm and Lotze 2006) est devenu un axe majeur de recherche pour de nombreuses études. La perte de biodiversité a souvent des conséquences négatives, car les fonctions spécifiques des espèces perdues sont retirées en même temps (Tilman and Lehman 2001, Loreau et al. 2002, Jenkins 2003). Avec les extinctions envisagées, c'est donc une menace majeure pour le maintien du fonctionnement des écosystèmes (Hooper and Vitousek 1997, Tilman 1999, Hooper et al. 2005, Stachowicz et al. 2007); la perte de biodiversité étant considérée comme aussi importante que d'autres changements environnementaux majeurs (comme le changement climatique, l'eutrophisation) pour la santé de l'écosystème (Hooper et al. 2012).

Depuis de nombreuses années, le lien entre la biodiversité et la stabilité des écosystèmes a été largement étudié (MacArthur 1955, Elton 1958, Pimm 1984, Tilman 1996, Tilman 1999, Lehman and Tilman 2000). De manière générale, une plus grande diversité augmente la stabilité de l'écosystème (Tilman 1999, McCann 2000, Stachowicz et al. 2007) car un plus grand nombre d'espèces apportent une plus grande variabilité dans les stratégies et les traits fonctionnels, mais aussi dans les réponses aux perturbations (Tilman and Downing 1994, Tilman 1996, Tilman 1999, Yachi and Loreau 1999). La stabilité est un attribut essentiel de l'écosystème et elle peut être considérée de diverses manières (Grimm and Wissel 1997, Lehman and Tilman 2000). Pour permettre la comparaison entre les études de stabilité, il est donc important de définir préalablement quel type de stabilité est étudié. Elle peut être caractérisée comme des fluctuations temporelles de la structure et de la fonction de la communauté, définie alors comme la « variabilité naturelle » ; comme la capacité de rester inchangé, lorsque perturbée, qu'on appelle « résistance » (ou inertie *sensu* Underwood 1989), ou encore comme la capacité à retourner à son état initial après une perturbation, qui réfère à la « résilience » (voir Pimm 1991).

L'idée que des assemblages avec une plus grande biodiversité sont plus stables a amené plusieurs études sur l'importance de la richesse des espèces sur le maintien des communautés (Tilman et al. 1996, McCann 2000, Benedetti-Cecchi 2006, Hillebrand et al. 2008). Des assemblages plus diversifiés recouvrent plus rapidement que des assemblages appauvris après une perturbation grâce au plus grand pool de régénération (Sousa 1984b, Kim and DeWreede 1996a, Allison 2004, Hillebrand et al. 2008). Par exemple, Allison (2004) a manipulé la diversité macroalgale dans une communauté intertidale et, après avoir induit un stress de chaleur, il a observé que les assemblages où la diversité avait été réduite, les espèces retirées retournaient plus lentement et récupéraient plus difficilement du stress. Cependant, les effets de la richesse sur la résistance sont moins clairs. Une plus grande richesse peut contenir des espèces hautement résistantes tout autant que des espèces très sensibles à des perturbations (Allison 2004, Hillebrand et al. 2008). La résistance va donc dépendre de l'identité des espèces et de la dominance de celle-ci dans la communauté.

Certaines espèces particulièrement importantes pour les propriétés de l'écosystème (dites « espèces clés ») peuvent augmenter la stabilité et la résistance de la communauté (Maggi et al. 2009, Grman et al. 2010, Watson and Estes 2011). Dans le contexte d'une perte de la biodiversité, la disparition de ces espèces clés peut avoir des impacts majeurs sur le fonctionnement de l'écosystème. De ce point de vue, les espèces structurantes

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(«habitat forming species» ou espèces «bioingénieures» *sensu* Jones et al. 1994) ont une importance principale, car elles peuvent modifier la structure de l'habitat ainsi que le flux d'énergies et de matières, qui affectent la composition des espèces et la biomasse des populations environnantes (Eriksson et al. 2006a). De plus, la présence de telles espèces jouerait un rôle important en présence de perturbations (Eriksson et al. 2006b, Airoldi and Beck 2007). La réduction ou encore la perte de telles espèces structurantes peuvent avoir des effets négatifs directs sur la communauté environnante (perte de l'habitat, du refuge, des ressources) et indirects sur les interactions de compétition (Benedetti-Cecchi 2006, Smale and Wernberg 2013). Par exemple, la perte de zostères a amené une réduction de la richesse et de l'abondance des espèces associées (Rueda et al. 2009, Pillay et al. 2010).

Les macroalgues, telles les espèces du genre *Fucus* sp., qui dominent souvent les habitats rocheux intertidaux, sont considérées comme des espèces clés pour ces écosystèmes (Hawkins and Hartnoll 1983). Elles ont un rôle structurant pour la communauté (Jenkins et al. 1999a) et offrent un refuge pour la faune mobile et un substrat pour la faune sessile et les épiphytes. Elles sont également une source de nourriture pour les herbivores (Hawkins and Hartnoll 1983), modifient les conditions physiques et réduisent le stress (dessiccation et hydrodynamisme) (Bertness and Leonard 1997, Bertness et al. 1999). La perte d'espèces dominantes comme les macroalgues peut avoir des effets particulièrement importants et pourrait induire des changements rapides et importants dans la biodiversité locale (Worm and Duffy 2003): réduction de la richesse associée (Schiel and Lilley 2011, Watt and Scrosati 2013) et augmentation du recrutement des algues éphémères (Jenkins et al. 1999a, Bulleri et al.

2002, Schiel and Lilley 2007, 2011). Un changement de l'identité (par exemple de Fucales à des Ulvacées) et de l'abondance des macroalgues peut aussi affecter la fonction de la communauté en réduisant la production primaire (Tait and Schiel 2011b, Valdivia et al. 2012, Crowe et al. 2013). Un déclin des macrophytes est déjà observé depuis plusieurs années (Airoldi 2003, Airoldi and Beck 2007, Connell et al. 2008, Smale and Wernberg 2013) lié à une tendance à l'augmentation des algues éphémères ou filamenteuses (Eriksson et al. 1998, Benedetti-Cecchi et al. 2001b, Lotze 2005). Lorsque ces algues sont établies, elles inhibent la colonisation des algues de la canopée et d'autres organismes (Airoldi 1998).

Les brouteurs sont également des espèces importantes dans la structure de la communauté surtout durant le début de la succession, en pratiquant un contrôle « *top-down* » (c.-à-d. venant des consommateurs) sur le recrutement des algues (Hawkins and Hartnoll 1983, Anderson and Underwood 1997, Jenkins et al. 2005, Coleman et al. 2006, Aguilera and Navarrete 2012) et influençant la distribution et l'abondance des espèces algales qui s'installent. Par exemple, l'exclusion de gastéropodes montre une inhibition de la croissance des espèces pérennes (par ex. : *Fucus* spp.) causée par l'absence de broutage des espèces opportunistes établies comme *Ulva* spp. ou *Porphyra* spp. (Lubchenco 1983, Anderson and Underwood 1997, Jenkins et al. 1999b). Une augmentation des algues éphémères peut également être observée par une eutrophisation fréquente dans les milieux côtiers (Johansson et al. 1998, Korpinen 2010, Kraufvelin et al. 2010) effectuant alors un contrôle « *bottom-up* » (c.-à-d. venant des producteurs) sur les communautés.

Plusieurs études ont été effectuées pour évaluer la relation entre la présence des algues structurantes et l'aptitude des assemblages de résister ou de récupérer lorsque ces assemblages sont perturbés. Face à une eutrophisation, les macroalgues permettent d'augmenter la résistance de la communauté en réduisant la lumière (facteur souvent limitant) (Eriksson et al. 2006a) et la compétition pour l'espace (Korpinen and Jormamailen 2008), ce qui régule l'abondance des algues éphémères. (Eriksson et al. 2007). En absence de macroalgues, l'espace libre est colonisé par des colonisateurs précoces comme les algues éphémères ayant une croissance rapide (Sousa 1979, Lubchenco 1983). Ceci est d'autant plus vrai lorsque le milieu est enrichi (Kraufvelin 2007). Les brouteurs ont ce même effet protecteur face à une augmentation de nutriments surtout pour la résilience de la communauté (Eriksson et al. 2007, Korpinen et al. 2007, Guerry 2008) par le broutage des algues éphémères. Comme les perturbations arrivent rarement seules, étudier et comprendre les effets de multiples perturbations sur les espèces et les communautés permet d'avoir un aperçu plus réaliste des effets cumulatifs, qu'ils soient synergiques ou antagonistes. Cependant, peu d'études ont regardé les effets de multiples perturbations (Wernberg et al. 2012).

Les milieux intertidaux sont caractérisés par de nombreux habitats et une grande diversité d'espèces avec de nombreux niveaux trophiques. L'étude des milieux intertidaux offre la possibilité de travailler en deux dimensions et donc facilite les expériences en écologie fonctionnelle (Connell 1974). Les organismes intertidaux sont diversifiés et abondants, souvent avec des stades adultes sessiles ou peu mobiles qui sont très facilement manipulables et, les interactions se produisent à petite échelle spatiale et temporelle ce qui facilite les expériences sur le terrain (Allison 2004, Range et al. 2008). Malgré cela, les recherches en milieux terrestres sur la diversité en lien avec la stabilité furent plus fréquentes qu'en milieu marin (Loreau et al. 2001).

Le but de mon étude est d'évaluer la réponse à court terme des communautés benthiques intertidales soumises à diverses perturbations dans un contexte de stress multiples. Les perturbations considérées ici sont un enrichissement, une exclusion des brouteurs et un enlèvement de la canopée macroalgale. Ces perturbations peuvent représenter des facteurs importants dans l'établissement des communautés marines du Saint-Laurent (Québec, Canada). Les habitats côtiers de l'estuaire maritime du Saint-Laurent sont soumis à des perturbations multiples avec une abrasion fréquente par les glaces en hiver (Archambault and Bourget 1983, Bergeron and Bourget 1984), un hydrodynamisme élevé et en augmentation selon les modèles prévisionnels (Savard et al. 2008). Ces dernières perturbations, qui influencent fortement la présence des espèces clés dans l'intertidal, sont couplées avec une intensification de l'eutrophisation (Thibodeau et al. 2006, Gilbert et al. 2007). Ces facteurs étant appelés à être plus intense et fréquents pourront entraîner des modifications profondes chez les espèces macroalgales et affecter les relations consommateur-producteur. C'est entre autres pour ces raisons que nous avons choisi un site d'étude situé dans l'estuaire du Saint-Laurent. Le premier objectif de mon étude est de tester les conséquences de la perte d'espèces clés (c.-à-d. les macroalgues et les brouteurs) sur la structure et la fonction des communautés en présence d'un enrichissement. Puis de déterminer la résistance des communautés benthiques lorsque les perturbations sont cumulatives. Les réponses sont analysées tant sur le plan de la structure de la communauté (richesse, diversité, abondances) que sur le plan de sa fonction (productivité et respiration). Dans le cadre de ce mémoire, d'autres analyses sont également effectuées, mais vu le grand nombre de données présentées, nous avons choisi de les placer en annexes pour faciliter la lecture du chapitre principal de ce mémoire.

Ce projet va permettre de mieux comprendre la dynamique des populations et groupes fonctionnels macrobenthiques du milieu intertidal dans leurs structures et leurs fonctions via leur résistance (stabilité) face à des perturbations multiples. La vérification de savoir si les traitements de perturbations sont synergiques ou antagonistes va nécessairement permettre une meilleure gestion des écosystèmes.

CHAPITRE II

RESISTANCE OF BENTHIC COMMUNITIES TO MULTIPLES STRESSES

2.1 INTRODUCTION

In many systems, natural disturbances are coupled with human activities and affect abiotic and biotic properties of the ecosystems (Vitousek et al. 1997b, Tilman and Lehman 2001). Habitat destruction (Brooks et al. 2002, Tole 2002, Hanski 2005), pollution (McNeely 1992, Oleksyn and Reich 1994) and alterations of biogeochemical cycles (carbon and nitrogen) by human activities (Vitousek et al. 1997a, Vitousek et al. 1997b, Rabouille et al. 2001) are potential sources of stress and have negatively affected the structure and function within many ecosystems (Vitousek et al. 1997b, Hooper et al. 2005). Biodiversity loss is a major threat to the ecosystem functioning (Hooper and Vitousek 1997, Tilman 1999, Hooper et al. 2005, Stachowicz et al. 2007) and considered as important as other major environmental changes (e.g. climate warming, nutrient loading) on the ecosystems healthiness (Hooper et al. 2012). Therefore, understanding the consequences of biodiversity loss as a stress for the ecosystem has become a leading motivation in many ecological studies (Grime 1997, Loreau et al. 2002, Worm et al. 2006).

For many years, the link between biodiversity and stability of ecosystems has been well investigated (MacArthur 1955, Elton 1958, Pimm 1984, Tilman 1996, Tilman 1999, Lehman and Tilman 2000). Greater diversity generally increases the stability of ecosystem, since more species will have a broader range of functional traits and response strategies to disturbance (Tilman and Downing 1994, Tilman 1996, Tilman 1999, Yachi and Loreau 1999, Stachowicz et al. 2007). An essential attribute of ecosystem stability is resistance (or 'inertia' *sensu* Underwood 1989). Resistance is defined as the capacity of a system to remain unchanged when facing disturbances or stresses (Pimm 1991, Grimm and Wissel 1997, Lehman and Tilman 2000).

The presence of certain key species may increase the stability (and resistance) of the community (Maggi et al. 2009, Grman et al. 2010, Watson and Estes 2011). In the context of biodiversity loss, the disappearance of key species will likely have a major effect on the ecosystem functioning. For instance, habitat-forming species (or ecosystem engineers and bioengineers, *sensu* Jones et al, 1994) offer refuge and protection for numerous organisms and thus play a crucial role in the ecosystem functioning. A loss of habitat-forming species has a negative impact on the surrounding community, with a reduction of associated species richness and abundance (Rueda et al. 2009, Pillay et al. 2010, Schein et al. 2012, Do et al. 2013, Watt and Scrosati 2013).

Habitat-forming macroalgae, often dominating the intertidal zone of rocky shore habitats, are considered as key species for their ecosystem (Hawkins and Hartnoll 1983). They have an important role in structuring the community (Jenkins et al. 1999a), providing food supply (Hawkins and Hartnoll 1983), modifying physical conditions and reducing stress (e.g. desiccation and wave swept) for the understorey (Bertness and Leonard 1997, Bertness et al. 1999). However, macroalgae (i.e Fucoids) are facing a global decline (Eriksson et al. 1998, Walker and Kendrick 1998, Airoldi 2003, Airoldi and Beck 2007, Connell et al. 2008) caused by both climate and human impacts. Therefore, the loss of fucoids for the community would have major consequences for the understorey community (Worm and Duffy 2003). This loss will have subsequent effects on the community structure by reducing the species richness (Schiel and Lilley 2011, Watt and Scrosati 2013) and enhancing ephemeral algae recruitment (Jenkins et

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al. 1999a, Bulleri et al. 2002, Schiel and Lilley 2007, 2011). Moreover, changes in abundance of macroalgae could also affect community function by reducing primary production (Tait and Schiel 2011b, Valdivia et al. 2012, Crowe et al. 2013).

Grazers are also important in structuring intertidal communities, especially during early succession, applying a strong top-down control on algae recruits (Hawkins and Hartnoll 1983, Anderson and Underwood 1997, Jenkins et al. 2005, Coleman et al. 2006, Aguilera and Navarrete 2012), thereby influencing the course of settlement of species in the community. Grazer exclusion often leads to an inhibition of later successional taxa (like *Fucus* spp.) by ungrazed early settled ephemeral algae (like *Ulva* spp. or *Porphyra* spp.) (e.g. Lubchenco 1983, Anderson and Underwood 1997, Jenkins et al. 1999b). On the other hand, if top-down controls naturally occur in many habitats, human activities generate nutrient enrichment in coastal environments and may lead to increases in ephemeral algae (Johansson et al. 1998, Korpinen et al. 2007, Kraufvelin et al. 2010) which can exacerbate bottom-up controls within communities.

Communities are faced to multiple disturbances or stresses as they rarely act alone. Studying potential effects (synergic or antagonist) of those disturbances or stresses on communities (with examples of both anthropogenic and climatic impact) will help to understand summed effects that shape communities. Single effects of canopy or grazer removal and enrichment have been broadly studied; yet, few studies have looked simultaneously at these stresses. The aim of our study is to understand how *in situ* benthic communities react when faced to multiple stresses and determine (1) the consequences of key species loss (macroalgae canopy and grazers) on the ecosystem structure and function in the presence of nutrient enrichment and (2) the resistance of the benthic community when stresses are cumulative. Specifically, this study evaluates the response of subarctic benthic communities subjected to multiple stresses by investigating single and interactive effects of canopy removal, grazer exclusion and nutrient enrichment on community structure and function (by using community productivity and respiration) and on the resistance of community properties in intertidal rocky shore communities. Our study site is located in the marine section of the St. Lawrence Estuary. Among motivations in selecting this site is that the St. Lawrence estuary is subjected to a stressed environment with ice-scouring (Archambault and Bourget 1983, Bergeron and Bourget 1984), prediction of high hydrodynamic (Savard et al. 2008), and increasing eutrophication (Thibodeau et al. 2006, Gilbert et al. 2007) that may affect the abundance of macroalgae and grazers in benthic intertidal communities.

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2.2 MATERIALS AND METHODS

2.2.1 Study site

The experiment was conducted between May and September 2012 near the village of Sainte-Flavie on the south shore of the St-Lawrence Estuary, Quebec, Canada (N48°37'42,5" W068°11'55,7"). The study area is representative of flat rocky shores and can be considered as a subarctic habitat as it is subjected to ice-scouring during winter and early spring (Archambault and Bourget 1983, Bergeron and Bourget 1984). The intertidal fauna and flora are characteristic of a moderate wave disturbance environment (Archambault and Bourget 1983). In the mid intertidal zone, the macroalgae canopy was composed of *Fucus* spp. (*F. distichus edentatus* and *F. vesiculosus*) and the invertebrate assemblage was dominated by gastropod grazers (*Littorina obtusata* and *L. saxatilis,* Annex 1 for a complete list) and by filter feeder blue mussels (composed with *Mytilus edulis, M. trossulus* and hybrids, thereafter named *Mytilus* spp.). The shores of the estuary are often covered with ice during the winter (mid-December till end of March), which the ice foot provides protection against very cold period. The ice however may also act as indiscriminate disturbance on the flat rock and exposed crevices with heavy ice scouring (Bergeron and Bourget 1984, McKindsey and Bourget 2001).

2.2.2 Experimental design

We used an orthogonal factorial experiment design to evaluate the effects of biodiversity loss (canopy, 2 levels; grazer, 2 levels) and nutrient enrichment (2 levels) on the structure and function of the intertidal benthic communities. All 8 treatments from this design (see Figure 1), and a procedural control (for the grazer exclusion; see below) were replicated four times (n = 4) and randomly assigned to 36 experimental plots (50 x 50 cm) on emergent rocky substrates on our study area. Plots were placed at similar height in the mid-intertidal zone (average of 1.34 m ± 0.20 m), in a 400 m wide area. The experiment plots, marked with anchor screws, were haphazardly selected with the criteria of: homogenous flat substrate; without pools or large crevices; and with a minimum of 80% cover of *Fucus* spp.. A minimum distance of 3 meters between plots was respected to avoid treatment interaction.

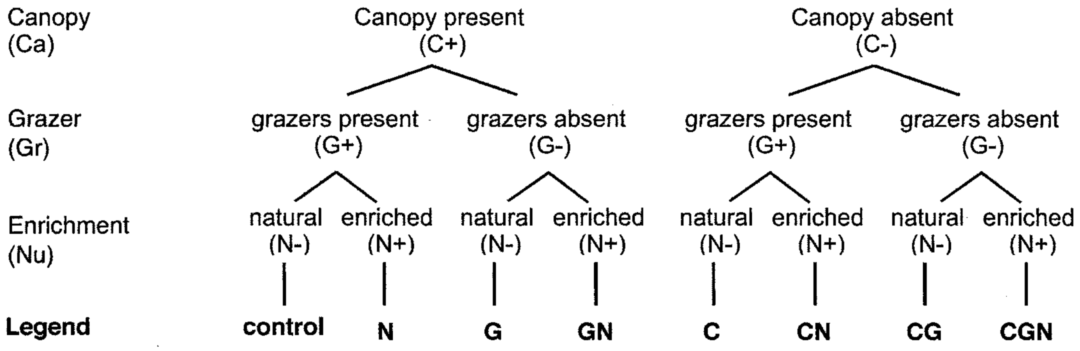

Figure 1. Experimental design with the 3 stress factors (canopy, grazer and nutrient enrichment) with 2 levels each (see text for more details). Four replicates (n = 4) for each treatment were used. The legend shows the letter codes that are used in the text and figures (2 to 8). One letter will represent one stress applied, two letters two stress and 3 letters a triple stress: «CGN» is a plot with all three applied stresses.

For the canopy treatment, we had two treatment levels: canopy present (C+) where the canopy was untouched, and canopy absent (C-) where all canopy taxa (i.e. *Fucus* spp.) holdfasts were removed in the 50 x 50 cm area (cf. Annex 2 for efficiency of the removal).

The grazer treatment had also two treatment levels: grazers present (G+) and grazers absent (G-). In the latter, grazers were *L. obtusata*, *L. saxatilis* and *L. littorea*, *Tectura testudinalis*, *Margarites* spp. and *Jaera marina* and were removed by handpicking. The exclusion treatment was made up with a physical barrier composed of a thin layer of natural sticky barrier (Tree Tanglefoot Insect Barrier, The Tanglefoot Company, Grand Rapids, USA) and a small twisted wire brush (2 cm in diameter) placed on cleared (~5 cm width) surface on the contour of the experimental plot. When needed, these surfaces were smoothed with small quantity of concrete (Poly-Plug Bomix, Daubois Inc. Saint-Léonard, Canada) and epoxy (West Systems Inc, Bay City, USA). Procedural controls (n = 4) with incomplete brushes were also implemented in natural communities. No difference was observed between control plots (canopy present, grazers present and no enrichment) and the procedural controls for all response variables with two exception (cf. Annex 3). At the study site, the abundance of small grazers (< 2mm) is large and the implementation of cages with small screen would certainly have had an effect on natural communities. Moreover, the cageless grazer treatment used in this study did not have the undesired effects of light and flow reduction and detritus retention commonly seen with cages (Range and Underwood 2008).

For the nutrient enrichment also two levels were used: natural conditions (N-) and enriched condition (N+) where an addition of controlled slow-release fertilizer pellets of

14% N (NO_3-N and NH_3-N), 14% P (P_2O_5) and 14% K (K_2O) (Smartcote® Plant Prod Canada) was used in the experimental plots. The enrichment with slow-release fertilizer pellets have been tested (Worm et al. 2000) and used in many habitats (Worm et al. 2000, Eriksson et al. 2006b, 2007, Korpinen et al. 2007, Jochum et al. 2012). This method produces independent nutrient treatment within a two meter distance from the source (Worm et al. 2000). Two mesh bags containing 100g of fertilizer were screwed in the opposite corners of the 50 x 50 cm plots and replaced every month. For all other experimental plots, inert control bags with washed pebbles were used to take into account any bag effects (e.g. as additional substrate). When replaced, the collected nutrient bags were weighed (dry weight loss) to estimate the amount of nutrient diffused into plots. An average of 31 % ± 0.15 of weight loss was observed, with a total estimated diffusion of 8.64 g (± 0.57 g) of total nitrogen per month in each plot. The nutrient enrichment would be a comparable moderate anticipated eutrophication into the St-Lawrence (Thibodeau et al. 2006, Gilbert et al. 2007). Pilot tests in the field showed a 3 to 6 times increase in total nitrogen concentrations for water samples in enriched quadrat compared to the natural concentration of the St. Lawrence. *F. distichus edentatus* tissues from the control plots and nutrient enriched plots were collected at the end of the experiment and compared in total nitrogen content (analyzed at INRS laboratory, Quebec City). The total nitrogen content values in the *Fucus* tissues from nutrient enriched plots were a little higher than those in controls (average of 1.06 ± SE 0.05%N and 0.95 ± SE 0.04 %N respectively; $F_{1,20}= 7.0725$; $p = 0.015$, see Annex 4 for details) providing evidence that the additional nutrients provided had been incorporated in the algae.

Canopy and grazer treatments were a « press » or continuous stress type (*sensu* Bender et al. 1984) as experimental conditions into plots were maintained and controlled every 9-11 days. During each inventory (see below) and during maintenances (between inventory periods) new *Fucus* spp. juveniles and grazers were estimated/ counted and thereafter removed from plots appropriately. Even when the grazer abundance was reduced for several days (up to 4 days; unpublished data from Joseph and Cusson; Cimon and Cusson), the grazer treatment (G-) failed to significantly reduce significantly the abundance during the period between two maintenance. However, although grazer removal efficiency failed (about 40% in time) at a bi-monthly scale, some statistically significant differences were observed for the grazer treatments and the treatment could not be removed from data analyses. In the text, the treatments with 'grazers absent' will be referred to as 'grazers reduced' and be interpreted accordingly.

2.2.3 Sampling

2.2.3.1 Structure of the community

The community in each plot was sampled using a 30 x 30 cm quadrat placed in the center of experimental plots. Non-destructive visual estimates of abundance as percent cover of all identified (> 1mm) taxa (usually species level) of each plot have been done at 4 distinct times: Date 1 (June 2-9, before establishment of the treatments), Date 2 (July 1-8), Date 3 (July 31- August 6) and Date 4 (August 29- September 4). Inventories were performed before any maintenance of the plot. The percent cover of macroalgae and mussels were estimated with the division of the 30 x 30 cm frame into 25 equal squares representing 4% of the total quadrat cover. Mobile invertebrates were counted and later transformed into % cover (conversion factors in Annex 5). This latter procedure is common (e.g. Scrosati et al. 2011) and the same unit among abundances is necessary to assess the community dominance profiles in our treatments. The cover was estimated per species, so the total summed % in a plot often exceeded 100%. Following the last visual inventory, a destructive sampling to collect all biomass (except crustose species) in the sampled 30 x 30 cm plot was done. The biomass samples were sieved (∅ 1 mm) and all individuals were identified under microscope and weighted (±0.00005 g). Biomass was converted into energy (kilo Joules) with conversion factors from Brey (2004) (used conversion coefficients are found in Annex 5).

2.2.3.2 Function of the community

To assess the effects of nutrient enrichment on the community function with or without canopy, measures of primary production were estimated at the end of July with CO_2 concentrations (ppm) variations using benthic chamber following the method described by Migné et al. (2002). The chamber consisted of a transparent dome and a base of Plexiglas placed over the 30 x 30 cm sampled community plot and airtight sealed to the ground with neutral silicon. The CO_2 variations in the chamber were measured with an infrared CO_2 gas analyzer (Li-800; LI-COR Inc., Lincoln, NE, USA) and recorded on a data logger (Li-400; LI-COR Inc.) every 15 seconds for 15- 20 min. Measures of CO_2 concentrations were done at ambient light (> 1000 µmol photon/m^2 measured in PAR 600-700nm) for net primary production (NPP) and with an opaque polyethylene sheet placed over the chamber to measure respiration (R). The CO_2 fluxes for net primary production and respiration were calculated with the following formula:

$$\text{Flux } (\text{mmolC.m}^{-2}.\text{h}^{-1}) = b\ (18.2 \bullet 60) / (22.4 \bullet 1000 \bullet 0{,}09)$$

where the slope b is obtained with a linear regression on the CO_2 variations recorded from the chambers; 18.2 = volume (liter) of air in the chamber; 60 = minutes in hours; 22.4 : molar air by liter in molar volume. The gross primary production (GPP) of the community is then calculated by adding NPP and R. Note that this method has no purpose to be used for global CO_2 budget but used only to give a metabolic state of the community in the same conditions and for comparison among treatments.

2.2.4 Data analysis

All analyses were performed on the associated community only (otherwise stated), the manipulated taxa (*Fucus* spp. and grazers species, see Annex 1 for a list) were excluded from the data prior analyses.

To test for the effects of the treatments and the interactions between and among them, analysis of variance (ANOVA) with 4 fixed factors (Date: 4 levels; Canopy, Grazer and Nutrient enrichment 2 levels each) were performed on total abundance (sum of all species in percent cover in the 30 x 30 cm sampled plots), richness (S) and Simpson's index of diversity ($1-\lambda$). If the factor Date was significant, a three-way ANOVA was performed at each date. A three-way ANOVA was performed for total abundance in biomass as this variable was only available for the last date. ANOVA assumptions were checked with a graphical examination of the residuals (Montgomery and Mastrangelo 1991, Quinn and Keough 2002). No transformation was necessary. When a factor was significant, a multiple comparison test (Tukey-HSD or if stated, *t*-Student) was performed to look at the differences between treatment levels.

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Comparisons between abundances for some taxa were investigated using *t*-test or Wilcoxon when assumption of normality and equality of variances were not met.

The effects of the treatments on the structure of the community (in percent cover and biomass data, based on Bray-Curtis similarities) were investigated using a permutational multivariate analysis of variance (PERMANOVA Anderson et al. 2008) with 999 permutations and with the same factors described above. Abundance data in percent cover and biomass were square root transformed and fourth root transformed, respectively, while data were transformed in presence-absence for effects on compositional community structure. The effects of the treatments were visualized with principal coordinate analysis (PCO). A similarity percentage analysis (SIMPER) was used to assess the percentage contribution of each taxon to the observed dissimilarities among treatments.

The effect of enrichment and canopy loss on gross- (GPP) and net- primary production (NPP) and respiration (R) were analyzed with a Kruskal-Wallis test (treatment fixed 4 levels) among control and N ($n = 3$) and C and CN ($n = 2$) treatments (see Figure 1 for legend).

Univariate analyses were done using JMP (version 10.0) while multivariate analyses and ordinations were done using PRIMER+PERMANOVA version 6.1.6 (Clark and Gorley 2006, Anderson et al. 2008). A significant level $\alpha = 0.05$ was used for all statistical tests. Observed *p*-levels close to significance were however carefully considered.

2.3 RESULTS

A total of thirty-five different taxa were observed at our site with an average (± SE) of 9.0 ± 0.3 species (min-max: 5-19) per sampled quadrat (30 x 30 cm). Eleven algal taxa were reported, the most abundant being *Fucus distichus edentatus* and *Ralfsia clavata*, while twenty-four taxa of invertebrates with grazers (e.g. *Littorina saxatilis, L. obtusata, Tectura testudinalis*) and filter feeders (e.g. *Mytilus* spp.) being the most common. A list of all observed taxa is presented in table A-1, Annex 1.

2.3.1 Effects of the single and multiple stresses on the community abundances and diversity indices

The canopy, grazer and nutrient enrichment treatments had different effects on the associated community. The total abundance in percent cover was not affected by the three stress types nor date, although the triple treatment (CaxGrxNu) interaction was marginally significant ($F_{3,127} = 34.512$; $p = 0.066$). When data from Date 1 (before treatments experiment started) were taken out of the analysis, this interaction term became significant (Table 1; Figure 2). Nutrient enrichment and the absence of grazers reduced the total percent cover of the associated community when compared to the unmanipulated controls. A marginal significant grazer treatment effect on total abundance was also observed ($p = 0.06$; Table 1): the total abundance in treatments with grazers present (25.64 ± 4.32) was 1.321 times higher than in treatments with grazers reduced (19.42 ± 4.61).

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Average richness values were significantly higher (more than twice) at the end of the experiment (Date 4) compared to the other dates ($F_{3,96} = 147$; $p < 0.0001$). This was due to the addition of cryptic taxa (originating e.g. from sediments or in between the mussels aggregations) that had been collected by the destructive sampling method after the last inventory. Diversity values were also significantly affected by date ($F_{3,96} = 4.939$; $p = 0.0031$), therefore each date was analyzed separately for both variables (Table 2 a and b).

Some significant effects were detected before the start of the experiments (Date 1; Table 2 a and b). This cannot be explained easily since the treatments were not implemented yet. Differences between the two categories of plots were however small by comparison of variation seen later in the course of the experiment. Plots where the canopy cover would remain had 3.75 species (± 0.323) and a 0.508 Simpson's index of diversity (± 0.028), while plots where canopy had to be removed had a lower richness with 2.86 species (± 0.10) and a diversity of 0.391 (± 0.032). Treatments were randomly assigned to plots along a 400m wide transect on the shore where some variability among natural communities can occur. However, no effects were observed on the structure (see next section below) and the significant effects observed at Date 1 dissipated at Date 2 (see Table 2).

Richness was significantly affected by the canopy treatment at both Date 3 and 4 (Table 2a). At the last date, average richness was lower (~ 3.5 species) when canopy was absent than present (Figure 3b). The grazer treatment affected richness differently between the enrichment treatment as shown by the significant grazer x enrichment interaction (Table 2a; Figure 3c). Diversity was significantly affected by the grazer treatment at the last inventory with higher values in grazer reduced plots (Figure 3e) however, at Date 3 and 4 this influence was significant only with the presence of canopy (Date 4 illustrated in Figure 3f).

Contrary to total abundance as percent cover, total abundance as biomass was significantly affected by the canopy treatment (Table 2c). When the canopy was removed, more than half of the total biomass of associated taxa disappeared (Figure 3h), with an average of 95% attributed to a loss of mussel biomass.

Table 1. Summary of the ANOVA showing the effects of Date (Da) and canopy (Ca), grazer (Gr) and nutrient enrichment (Nu) treatments and crossed effects on the total abundance in percent cover of the associated species. Date 1 was excluded in this analysis.

	df	*F* Ratio	*p*
Da	2	0.971	0.384
Ca	1	1.063	0.306
Gr	1	3.642	0.060
Nu	1	0.056	0.814
DaxCa	2	0.334	0.717
DaxGr	2	0.315	0.731
DaxNu	2	0.350	0.706
CaxGr	1	0.128	0.722
CaxNu	1	2.788	0.099
GrxNu	1	0.452	0.503
DaxCaxGr	2	0.328	0.721
DaxCaxNu	2	0.123	0.885
DaxGrxNu	2	0.997	0.374
CaxGrxNu	1	4.359	**0.040**
DaxCaxGrxNu	2	0.377	0.687
Residual	72		
C. Total	95		

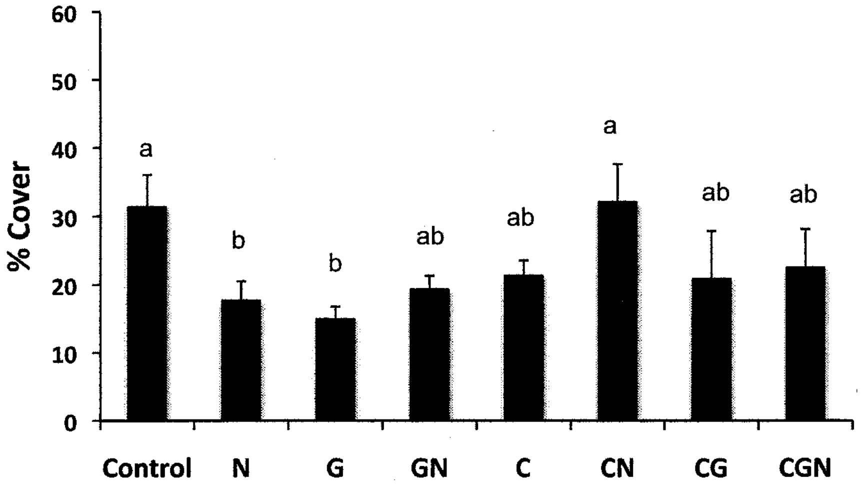

Figure 2. Average values (+SE, n = 12) of the abundance in percent cover of the associated species in the community among the various treatments for all dates, Date 1 excluded (see text for more detail). The legend for treatments is found in Figure 1; the numbers of letters used in the treatment label represent the quantity of stress applied. Bars with different letters are significantly different ($p < 0.05$).

Table 2. Summary of ANOVAs showing the effects of canopy (Ca), grazer (Gr) and nutrient enrichment (Nu) treatments and crossed factors on (a) richness, (b) Simpson's index of diversity and (c) biomass of the associated species of the community for all dates (expect for biomass). Significant values are shown bold.

		Date1		Date 2		Date 3		Date 4	
	df	***F* Ratio**	***p***	***F* Ratio**	***p***	***F* Ratio**	***p***	***F* Ratio**	***p***
a) Richness									
Ca	1	5.765	**0.025**	1.852	0.186	12.741	**0.002**	47.61	**< .0001**
Gr	1	0.471	0.499	0.000	1.000	0.318	0.578	0.831	0.371
Nu	1	0.118	0.735	0.074	0.788	0.035	0.853	0.017	0.898
CaxGr	1	4.235	0.051	1.852	0.186	0.882	0.357	0.831	0.371
CaxNu	1	0.118	0.735	0.000	1.000	0.882	0.357	2.051	0.165
GrxNu	1	0.000	1.000	3.63	0.069	0.318	0.578	8.966	**0.006**
CaxGrxNu	1	1.882	0.183	0.296	0.591	0.318	0.578	0.017	0.898
Residual	24								
C. Total	31								
b) Diversity									
Ca	1	6.626	**0.017**	0.012	0.914	3.296	0.082	0.54	0.470
Gr	1	0.058	0.812	0.269	0.608	0.571	0.457	5.875	**0.023**
Nu	1	0.032	0.859	0.303	0.587	0.099	0.756	0.278	0.603
CaxGr	1	0.176	0.679	2.850	0.104	5.183	**0.032**	6.566	**0.017**
CaxNu	1	1.698	0.205	1.523	0.229	0.210	0.651	0.123	0.729
GrxNu	1	0.078	0.782	0.207	0.653	0.414	0.526	0.229	0.637
CaxGrxNu	1	0.264	0.612	0.345	0.562	0.081	0.778	0.3	0.589
Residual	24								
C. Total	31								
c) Biomass									
Ca	1							14.697	**0.001**
Gr	1							1.217	0.281
Nu	1							0.698	0.412
CaxGr	1							2.067	0.163
CaxNu	1							0.292	0.594
GrxNu	1							0.002	0.965
CaxGrxNu	1							1.017	0.323
Error	24								
C. Total	31								

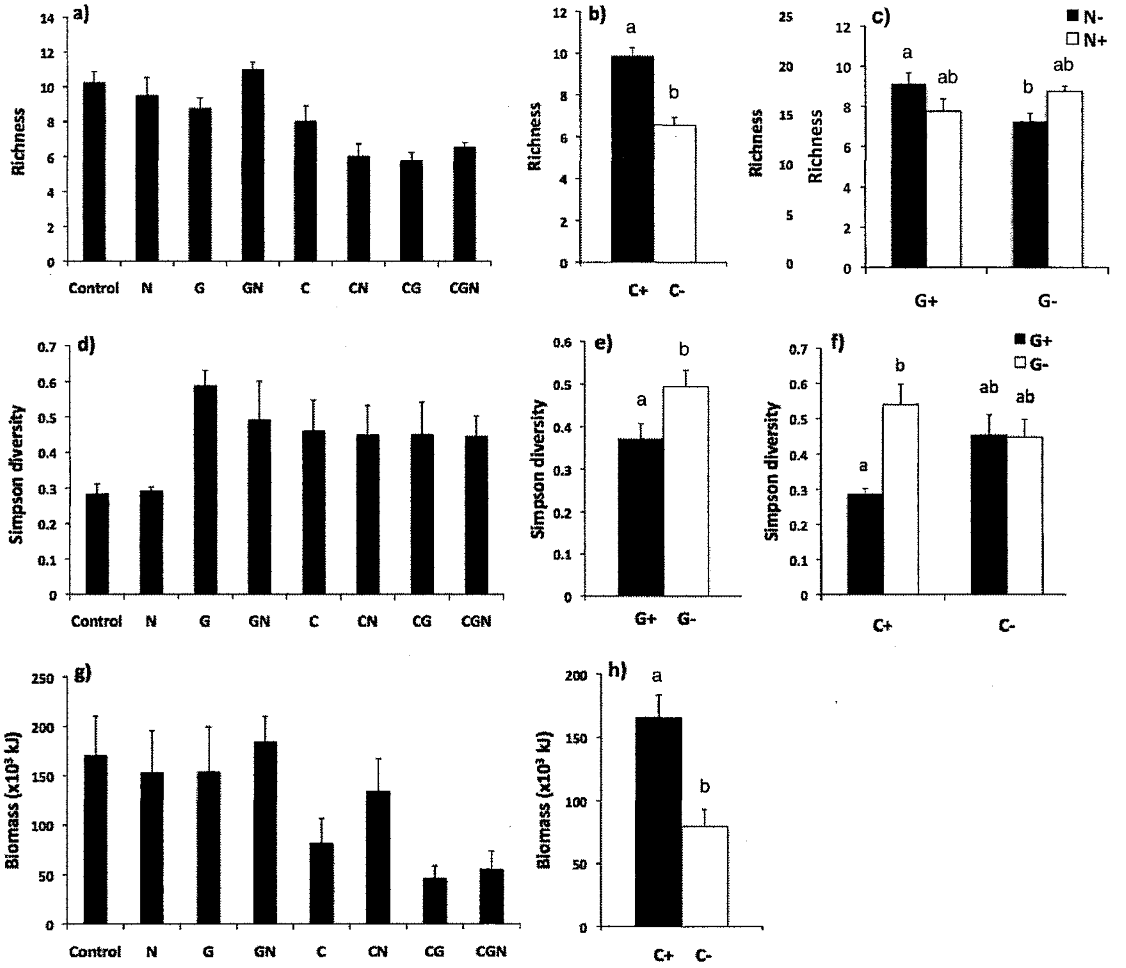

Figure 3. Average values (+SE) of richness (a, b, c), Simpson diversity index (d, e, f) and biomass (g, h) of the associated species of the community among the various treatments at the end of the experiment (i.e. Date 4). Black and white bars are treatments respectively with the canopy present (C+) and removed (C-) in graph b and h; grazers present (G+) and reduced (G-) in graphs e and f, while no (N-) and added (N+) nutrient in graph c. The legend for treatments is found in Figure 1; for graphs a, d and g the numbers of letters used in the treatment label represent the quantity of stress applied. Replicate numbers of averages are: n = 4 in graphs a, d, g; n = 8 in c and f and n = 16 in b, e and h. Bars with different letters are significantly different ($p < 0.05$).

2.3.2. Effects of single and multiple stresses on community structure

The associated community structure in percent cover changed among dates (Pseudo-$F_{3,96} = 14.88$; $p = 0.001$) where all dates differed significantly except between Date 2 and Date 3 (Pairwise tests among dates; results not shown). The treatment effects were thus analyzed at each date (Table 3a). All communities in the experiment plot categories were similar before the start of the experiment (Date 1). Only 50 days after the experimentation started (Date 3), the canopy treatment significantly affected the associated community structure (Pseudo-$F_{1,24} = 5.008$; $p = 0.004$; Table 3a) and remained significant until the end of the experiment (Date 4; illustrated in Figure 4a). This effect was also detected in the biomass structure (Table 3b; Figure 4b). The associated community structure (either in percent cover or biomass) was not affected by the grazer or nutrient enrichment treatment. We observed similar results in the compositional structure (all abundances transformed in presence-absence). The composition changed among dates and a significant effect of the canopy treatment was observed on Date 3 and Date 4, but no effect of the grazer nor nutrient enrichment treatments was observed (cf. Annex 6).

Of all treatments (single or in combination) those that included the canopy treatment had greater average dissimilarities over time when compared to natural assemblages (i.e control plots) (Figure 5). Four weeks after the start of the experiments (Date 2), dissimilarities between control plots and all other treatments generally increased. Only after two months (Date 3) did the treatments with the canopy treatment (i.e. CG, CGN, C and CN) become significantly more dissimilar from natural communities, while the other treatments (i.e. N, G and GN) became more similar to the control plots with time (smaller dissimilarity). At the end of the experiment, larger dissimilarities compared to controls were observed with the C, CG and CGN treatments (Figure 5). The main species (causing 90 % of the dissimilarities) at Date 3 were the mussel *Mytilus* spp., the encrusting algae *Ralfsia clavata* and the sea anemone *Aulactinaria stella*. At Date 4 those same species were still accounted for the dissimilarities with in addition Polychaeta and Oligochaeta. If the associated community was separated into two groups, understorey algae and invertebrates, and compared in total abundance (% cover) and in richness at Date 4, we observed that ephemeral algae had a higher percent cover when canopy was absent (Figure A-4.a), while a similar richness (solely due to the presence of *Ralfsia clavata*). For invertebrates, more abundant and higher richness was observed when canopy was present (cf. Annex 10; Figure A-4 and A-5).

For the community structure expressed in biomass, treatments with the canopy absent were significantly more dissimilar from the natural communities, CG and CGN treatments had the highest dissimilarities (Figure 6).

Table 3. Summary of PERMANOVAs showing the effects of canopy (Ca), grazer (Gr) and enrichment (Nu) treatments along with the crossed factors on the structure in abundance in (a) percent cover and (b) biomass of the associated species of the communities at each date. Data were square root transformed for % cover measures and fourth root transformed for biomass measures prior estimating the Bray-Curtis similarities. Significant values are shown bold. P-*F* stands for Pseudo-*F*.

		Date1		Date 2		Date 3		Date 4	
	df	**P-*F***	***p***	**P-*F***	***p***	**P-*F***	***p***	**P-*F***	***p***
a) % Cover									
Ca	1	1.971	0.117	0.774	0.525	5.008	**0.004**	9.536	**0.001**
Gr	1	1.814	0.152	2.085	0.118	0.869	0.452	1.279	0.312
Nu	1	0.591	0.608	0.983	0.401	0.440	0.735	0.224	0.894
CaxGr	1	0.285	0.848	0.710	0.584	1.604	0.196	1.216	0.297
CaxNu	1	0.431	0.717	1.089	0.376	0.254	0.859	1.373	0.260
GrxNu	1	0.760	0.499	0.767	0.515	0.435	0.717	1.254	0.305
CaxGrxNu	1	0.899	0.435	0.707	0.581	0.279	0.834	0.469	0.735
Residual	24								
Total	31								
b) Biomass									
Ca	1							21.614	**0.001**
Gr	1							0.767	0.556
Nu	1							1.357	0.230
CaxGr	1							1.313	0.270
CaxNu	1							0.272	0.899
GrxNu	1							0.585	0.719
CaxGrxNu	1							0.376	0.842
Res	24								
Total	31								

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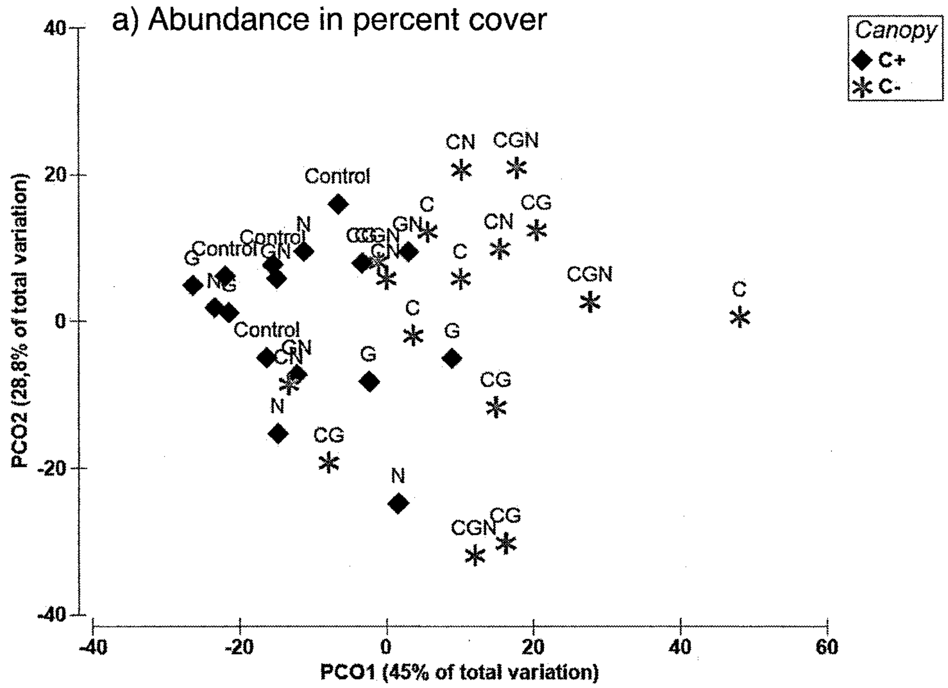
a) Abundance in percent cover

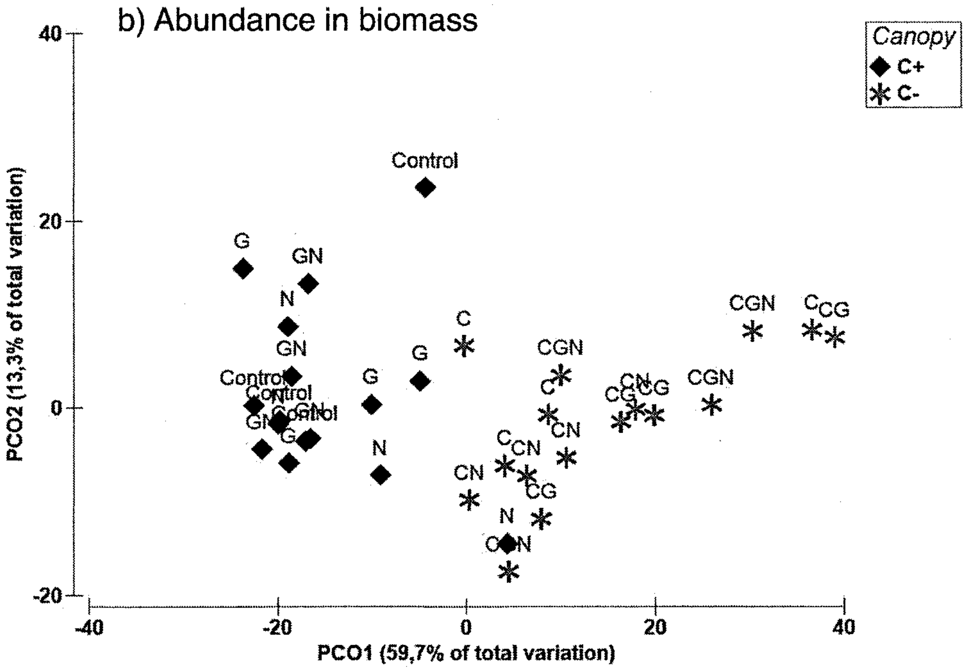
b) Abundance in biomass

Figure 4. PCO ordinations illustrating the effect of the canopy treatment (diamonds = C + or canopy present, asterisk = C- or canopy absent) at Date 4 on the community structure of the associated species in (a) percent cover, square root transformed, and in (b) biomass, fourth root transformed. The legend for treatment is found in Figure 1; the numbers of letters used in the treatment label represent the quantity of stress applied.

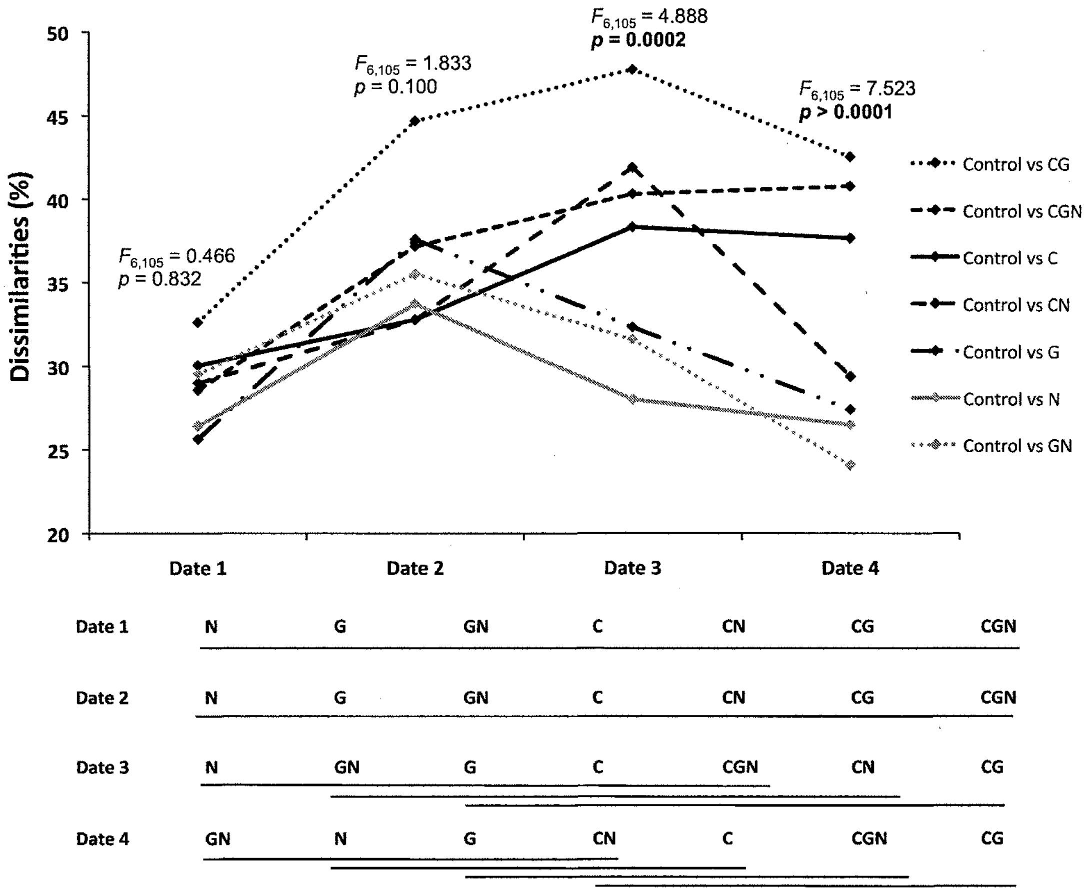

Figure 5. Average dissimilarities (n = 10) between control and treatments at each date for structure in abundance in percent cover of the associated species. Below the graph: treatments underlined with the same line are not significantly different ($p < 0.05$). The legend for the treatments is found in Figure 1; the numbers of letters used in the treatment label represent the quantity of stress applied.

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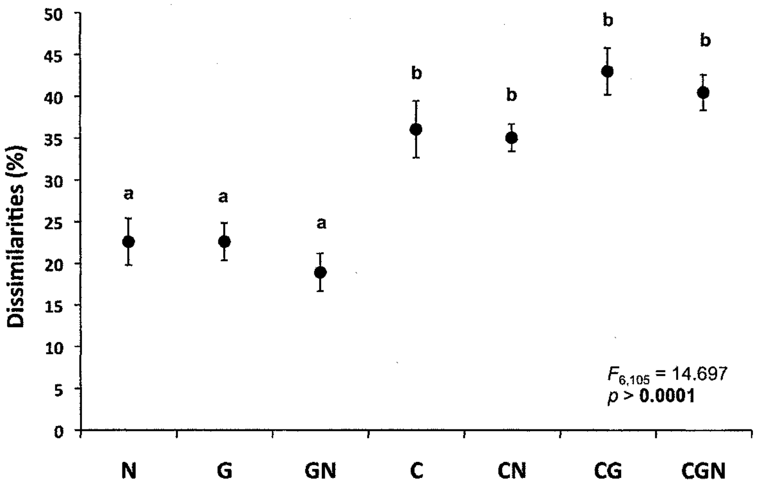

Figure 6. Average dissimilarities (± SE, n = 10) between control and other treatments at Date 4 in biomass structure of the associated species. The legend for the treatments is found in Figure 1; the numbers of letters used in the treatment label represent the quantity of stress applied. Average points with different letters are significantly different ($p < 0.05$).

As mentioned before, the grazer treatment using cageless techniques failed to significantly reduce the abundance (in % cover and biomass) of grazer species except for the first month of the experiment (cf. Annex 7). Yet, the abundances were reduced for several days (up to 4 out of 9-10 days; unpublished data from Joseph and Cusson; Cimon and Cusson). The non-accessibility of the plots at high tides restricted maintaining a constant removal or, at least, lower abundances.

We tried to understand the grazer abundance structure along with the other invertebrates when the canopy was removed. For the canopy treatment, the main species affected in their abundance in percent cover were *L. obtusata*, *Ralfsia clavata*, *Mytilus* spp., *Jaera marina*, *L. saxatilis* and *L. littorea* with an average dissimilarity of 7.54%, 7.38%, 5.29%, 3.35%, 2.92% and 2.83% respectively (cf. Annex 8 for full SIMPER analysis). Absence of canopy had a significantly negative effect on the abundance of *L. obstusata* and *J. marina* (Figure 7a, c), but not for *Mytilus* spp. (Figure 7e). Instead, it had a positive effect on the average abundance of the gasteropods *L. saxatilis* and *L. Littorea* (Figure 7b and d) as well as for the encrusting algae *R. clavata* that increased by 6 times its percent cover when the canopy was absent (Figure 7f). Using the biomass structure data, the main species affected by the loss of canopy were *L. obstusata*, *Nereis* sp., *Pectinaria gouldii, and Mytilus* spp. with an average dissimilarity of 5.48%, 3.40%, 3.15% and 3.02% respectively (cf. Annex 9 for full SIMPER analysis). The absence of canopy had a significantly negative effect on the biomass of those species (Figure 7a, c, e, g and h), except for *L. saxatilis* that had higher biomass when the canopy was removed (Figure 7b).

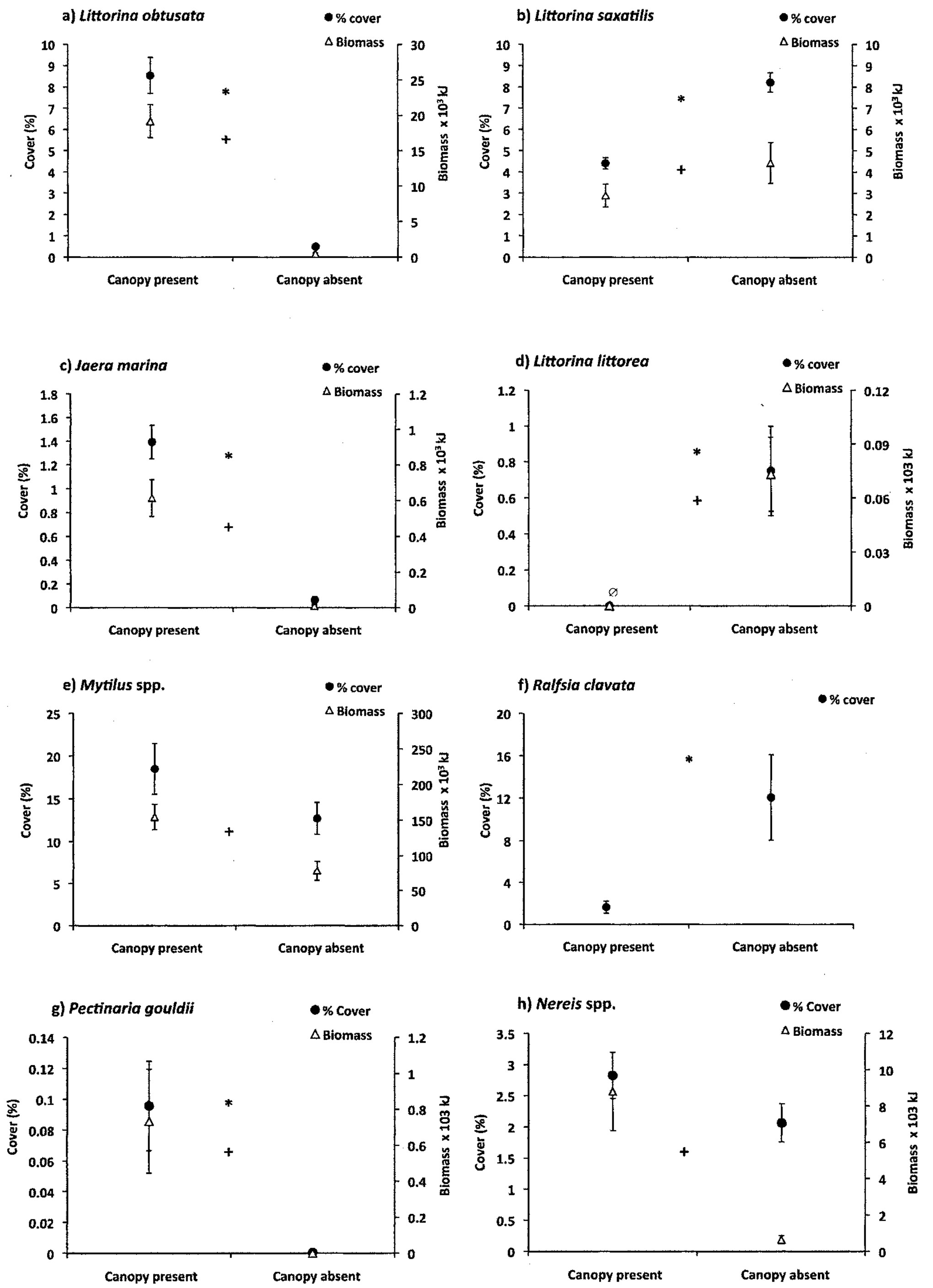

Figure 7. The average abundances of (a) *Littorina obtusata*, (b) *L. saxatilis*, (c) *Jaera marina*, (d) *Littorina littorea*, (e) *Mytilus* spp., (f) *Ralfsia clavata*, (g) *Pectinaria gouldii* and (h) *Nereis* sp.. Black dots represent abundances in % cover and open triangle represent abundances by biomass. Asterisks for % cover and plus sign for biomass show significantly differences (*t*-Student or Wilcoxon; $p < 0.05$). Note: quadrats with a grazer reduction were excluded for graphs a to d (n = 8) while all quadrats were used for graphs e to h (n = 16). ∅ = average of zero.

2.3.3 Effects of single and multiple stresses on community functions

Nutrient enrichment and canopy treatments had no effect on the NPP ($\chi^2 = 6.673$; $p = 0.083$) or respiration ($\chi^2 = 4.364$; $p = 0.225$) (Figure 8), while for GPP there was a difference observed for the canopy treatment but had no effect of the enrichment on the GPP ($\chi^2 = 8.018$; $p = 0.046$) (Figure 8). However, when the canopy was removed, there were very small values of NPP and GPP of the communities observed. Only positive CO_2 fluxes were observed (Figure 8) for treatments with canopy absent meaning that the productivity of the understorey algae species was negligible compared to the respiration of heterotrophic organisms.

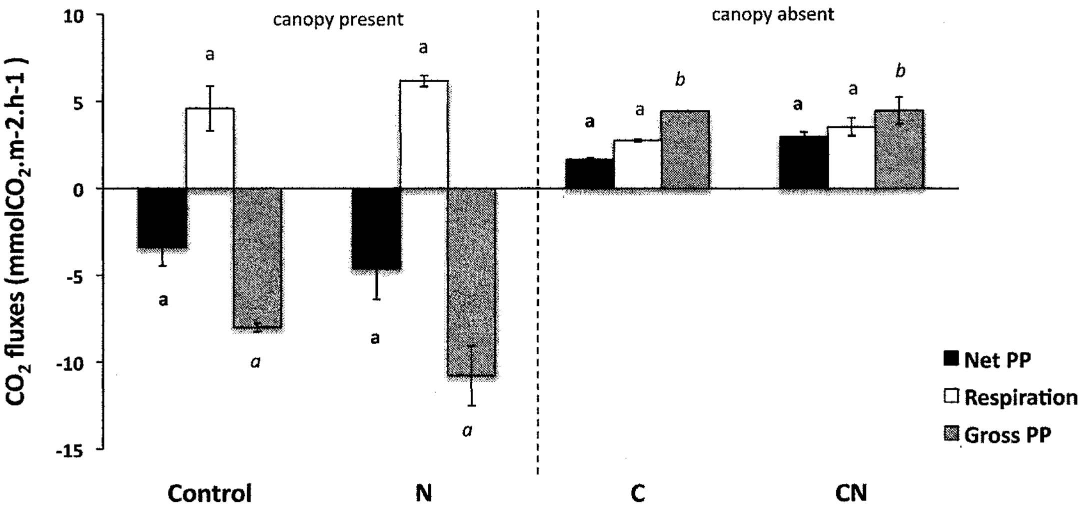

Figure 8. Average community net primary production (black bars), respiration (white bars) and gross primary production (gray bars) when canopy is present (left side of the graph; ± SE, n = 3) and when canopy is removed (right side of the graph; ± SE, n = 2). The legend of the treatments is found in Figure 1; the numbers of letters used in the treatment label represent the quantity of stress applied. For each variable, bars with different letters are significantly different ($p < 0.05$).

2.4 DISCUSSION

The objective of this study was to test the consequences of key species loss (i.e. macroalgae canopy and grazers) on the community structure and function in the presence of nutrient enrichment. Also, this study aimed to determine the resistance, or inertia, of the benthic community when stresses were cumulative. Overall, taken separately, canopy loss was the strongest single effect affecting the community structure and function, while community resistance was observed when grazers were reduced and nutrients were added. When these three stresses were cumulated various trends emerged suggesting a lower resistance of the community when facing multiple stresses. We discuss below the observed effects on the structure and the function of the community, as well as the resistance dimension.

2.4.1 Effects on community structure

The absence of canopy negatively affected the whole structure of the associated (unmanipulated) species abundance, both in percent cover and biomass. The aggregated properties of total abundance were marginally reduced in treatments with nutrient addition and grazers reduced, while in other treatments associated species compensated for the canopy loss. The loss of *Fucus* spp. as a habitat-forming species resulted in the disappearance of refuge and increases the stress level (e.g. in temperature, wave, etc.) for the understorey species (Bertness et al. 1999). We often observed > 10°C higher on substrates when canopy was removed (measured by infra-red camera; not shown in results). By improving conditions, the presence of the canopy cover may increase richness and diversity as shown by Schiel and Lilley (2007, 2011) and Watt and Scrosati (2013). Settling species need to be able to face physical impact of wave action, high temperature and whiplash (Lewis 1964). For example, whiplash by surrounding algae and high temperature (i.e. desiccation) can lead to a decrease in recruitment and growth of algal propagules (Kiirikki 1996, Kim and DeWreede 1996b, Irving and Connell 2006) and to higher mortality rate of settling species (Hawkins 1983, Kim and DeWreede 1996b, Ingolfsson 2008). Canopy loss can lead to bleaching of algae and the reduction of invertebrates due to exposition to light, high temperatures and wave action (Jenkins et al. 1999a, Jenkins et al. 1999b, Cervin et al. 2004). When canopy was removed, more ephemeral algae and fewer invertebrates were observed (cf. Figure A-4). This is in line within the literature-mentioned above. In our study, canopy absence lowered the species richness of the associated community, and negatively affected the diversity in the absence of grazers only. In addition, the reduced abundance of invertebrates (cf. Figure 7 and A-4) with canopy loss might also be caused by lower food supply. *Littorina obtusata*, the dominant grazer in the presence of a canopy was replaced by *L. saxatilis* when the canopy was removed. This change could be explained by their feeding habits, as both *L. obtusata* and *L. saxatilis* feed on *Fucus* spp. (Watson and Norton 1987, Barker and Chapman 1990, Laurand and Riera 2006) but *L. saxatilis* additionally feed on rocky surface biofilms (Sacchi et al. 1977).

The open space created by the removal of the canopy can be colonized by other species like turf-forming algae or ephemeral algae (Sousa 1979, Reed and Foster 1984, McCook and Chapman 1993, Lilley and Schiel 2006), however, in our study only *Ralfsia clavata* benefited from the absence of canopy by extending its cover (cf. Figure 7f and Figure A-4). Propagule availability (Sousa 1984a, Reed 1990) and timing of starting treatments in the season (Archambault and Bourget 1983) are critical for the recolonization. Even though *Fucus* spp. recruitment mostly happens during the summer (Archambault and Bourget 1983, Lamote and Johnson 2008), the delayed start of our experimentation (late spring) combined with a lack of efficient grazer exclusion likely explain the lack of ephemeral algae. However, Archambault and Bourget (1983) observed a rapid colonization of substrate by ephemeral algae after removing the canopy at the same period and in the same region as our study. In the St. Lawrence estuary, the abundance of ephemeral algae may vary among years since very few species were observed in our study while one year later (i.e. summer 2013), *Porphyra* spp. were very abundant and less fucoid juveniles (personal observations).

Herbivores have an important role in structuring the community by grazing on algae and recruits of different organisms (Hawkins and Hartnoll 1983, Anderson and Underwood 1997, Jenkins et al. 2005, Coleman et al. 2006, Korpinen et al. 2007, Aguilera and Navarrete 2012). Ephemeral algae are early colonizers and if not grazed, strong space competition may inhibit or delay the appearance of *Fucus* spp. (Lubchenco 1983), hence a canopy combined with a grazer treatment can lead to community structure changes with a dominance of ephemeral algae (Jenkins et al. 1999b, Benedetti-Cecchi et al. 2001a, Cervin et al. 2004, Phillips and Hutchison 2008, Aquilino and Stachowicz 2012, Atalah and Crowe 2012). As previously mentioned, no proliferation of ephemeral algae was observed in our study, although ephemeral species (e.g. *Porphyra* spp., *Ulva* spp. and *Chordaria* spp.) can be abundant in the lower part of the intertidal. However, the grazer treatment in our study led to reduced total abundance and richness values of associated species compared to other treatments, while increasing diversity. This seemed to be mainly caused by a small evenness *J'* in the treatments with grazers present due to the dominance by the mussels *Mytilus* spp. (results not shown). Other species accounted for the difference in diversity as the encrusted algae *Ralfsia clavata*, the polychaetes *Nereis* spp. and the sea anemone *Aulactinia stella* were more abundant in the treatments with grazers reduced (results not shown). This observation is however difficult to explain, as grazer treatment effects are mainly expected on algae and not on invertebrates. The fact that our grazer treatment was not as efficient as we expected between maintenance may explain the little effects that were observed in our study. Sticky barriers have been proved their efficiency reducing gastropods grazers in warmer environments (e.g. Australia: 10 x 10 cm plots, Range et al. 2008; California: 10 x 10 cm plots, Aquilino and Stachowicz 2012). In our study, the large size of the exclusion (50 x 50 cm) as well as the cold waters of the St. Lawrence estuary might consequently reduce the efficiency of the sticky barriers.

Nitrogen is known to be a limiting nutrient for algae in marine habitat. High level of nitrogen in water is used by algae for growth (Wheeler and North 1980) or storage (Chapman and Craigie 1977). Ephemeral algae are fast-growing species and will thereby use nutrients more rapidly than perennial algae like fucoids (Duarte 1995). Even if we did observe higher nitrogen content in macroalgae, the enrichment treatment did not affect the associated benthic community either in richness or in structure, which is contrary to other studies. Indeed, higher nutrient availability may enhance algal richness and diversity (Worm et al. 2002, Korpinen et al. 2007) and increase the abundance of ephemeral algae (Johansson et al. 1998, Eriksson et al. 2007, Kraufvelin et al. 2010) and propagules or periphyton (Eriksson et al. 2006a, Korpinen et al. 2007) leading to a higher food supply for the associated community. However in our study, the total

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abundance of the associated community was reduced by the addition of nutrients (Figure 2). An additional input of nutrients can modify the food preference of herbivores and change the competitive interactions of herbivores with grazing shifts (Worm et al. 1999, Russell and Connell 2005) and thereby influence the composition within the assemblage. Enrichment combined with canopy loss can lead to an increase in the abundance of macroalgae (Eriksson et al. 2007) or a change in dominance to opportunistic species and a decrease in invertebrates that had a refuge in the canopy (Benedetti-Cecchi et al. 2001b). Some studies have observed an increase in the abundance either of recruits or of mature macroalgae with nutrient enrichment when grazers were reduced (Guerry 2008, Atalah and Crowe 2012). Others have shown that under nutrient enriched conditions and in the absence of grazers, *Fucus* spp. failed to colonize the substrate and fast-growing ephemeral algae outcompeted, while with grazers present, those opportunistic algae were less abundant (Korpinen et al. 2007, Korpinen and Jormamailen 2008). Neither of those observations has been found in our study. A delayed response of the community to the nutrient input is possible. Kraufvelin et al. (2006) and Bokn et al. (2002) have observed a late response (16 months to 3 years) of fucoid species to enrichment even though rapid (few months) minor effects on the community structure were detected (increase of *Ulva* spp. and some grazers).

Although the grazer reduction treatment had almost no effect on the community abundance structure, when it was combined with the canopy treatment, at the end of the experience it showed trend of larger differences with controls than other single treatments (cf. Figure 5). This suggests that multiple stresses may act in synergy leading to stronger effects than when alone. This may highlight the need to analyze the interactions among treatments as they might be important in field situations.

2.4.2 Effects on community functions

It is known that macroalgae primary production can be positively affected by nutrient addition (Bucolo et al., 2008; Krause-Jensen et al., 2012; Ylla et al., 2007, but not in Kraufvelin et al., 2010). Still we did not find an enrichment effect on the primary production. If higher storage of the nutrients was observed, primary production measures were not higher with enrichment. On the other hand, a strong negative effect of canopy loss on the gross primary production (GPP) was observed in our study. With a community affected by canopy loss, changes in functioning were expected through lower abundances and low productivity of the understorey community (Gollety et al. 2008, Tait and Schiel 2011a, Valdivia et al. 2012, Crowe et al. 2013). In our study only *Ralfsia clavata* was present as crustose algae and its production was probably not enough to compensate for the respiration of other heterotrophic organisms present. The lack of increasing ephemeral algae led to an unsignificant increase in total abundance and richness of understorey algae for enriched plots (Figure A-6), creating no enhancement of the productivity. Higher diversity may lead to higher productivity in many systems (Naeem et al. 1994). However, some studies in shallow marine habitat systems have shown no increase in primary production with enrichment due to changes in the macrophyte community (Sandjensen and Borum 1991, Nixon et al. 2001).

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2.4.3 Resistance of the community

High resistance of the benthic community to nutrient enrichment and periodic grazer reduction has been observed in this study. The absence of Canopy, on the contrary, strongly affected the resistance of the associated species. Undoubtedly, the canopy macroalgae played a key role in the stability of the structure and function of the benthic community. Interestingly, the effects of the absence of canopy appeared only after 2 months of treatment, showing a temporary resistance probably due to the large number of *Fucus* spp. juveniles that appeared and grew fast (with an average cover of 41% ± 24% Figure A-1) and perhaps still gave some protection for the understorey species. This «pulse» perturbation (after one single event) was not enough to induce changes; while maintaining the removal longer, or applying «press» perturbation, caused the changes. After 1 month of stress, all treatments increased their dissimilarity from controls but thereafter, treatments where canopy was present decreased, while most treatments with canopy removed continued to increase their dissimilarities, suggesting less resistance to canopy removal (i.e. Figure 5).

Conclusion remarks

In response to different stress sources, a community may resist, or fail and change. Obviously, the benthic communities were not resistant to canopy loss, which lead to strong changes in community structure and composition. Our study reconfirms the important role of the dominant habitat-forming species *Fucus* spp. influencing the structure and the function of their associated community. However, following enrichment and grazer reduction, the marine benthic communities of the mid-intertidal zone of the St. Lawrence estuary remained mostly unaffected. Grazer reduction combined with other treatments, gave various responses with effects on the structure in abundance (both in percent cover and biomass) while little or no effect on richness, diversity and total abundances. Moreover, our study also gave new insight on the possible interactions among treatments, highlighting the importance to test for the potential synergetic or antagonistic effects of multiple stressors. Natural coastal communities are often facing multiple threats, therefore, understanding the antagonist and the additive effects of stresses may help identify the ecological mechanisms that cause the changes in community structure and function. Studying these interactions will also help policy managers for mitigation and conservation priorities.

CHAPITRE III

CONCLUSION GÉNÉRALE

Ce mémoire a été réalisé dans le but d'acquérir de nouvelles connaissances sur le fonctionnement des écosystèmes et notamment sur l'importance des espèces clés pour les écosystèmes et des impacts de la perte de telles espèces sur le reste de leurs communautés. De plus, mon étude a permis d'obtenir des connaissances supplémentaires sur l'écosystème et les communautés benthiques de la zone intertidale de l'estuaire du Saint-Laurent. La recherche menée pour ce mémoire a donc mesuré les réponses des communautés benthiques face à des perturbations pouvant être liées à des changements climatiques et environnementaux, tant sur le plan de la structure que sur le plan de la fonction des communautés pour connaître leur résistance. Ces perturbations étaient un enlèvement de la canopée macroalgale, une exclusion des brouteurs et un enrichissement. On a ainsi testé les conséquences de la perte d'espèces clés (c.-à-d. les macroalgues et les brouteurs) sur la structure et la fonction des communautés en présence d'un enrichissement et de déterminer la résistance des communautés benthiques lorsque les perturbations sont cumulatives. Ce projet fut innovateur dans le sens que celui-ci fut effectué dans un contexte de multi-stress. De fait, peu d'études regardent les effets de perturbations multiples sur tant de paramètres (c.-à-d. la richesse, la diversité, la structure en abondance, etc.) à l'échelle de la communauté. Comme les perturbations peuvent avoir des effets antagonistes, il est important de pouvoir mesurer sur le terrain les effets de plus d'un seul stress.

Les résultats obtenus ont démontré de manière très claire l'importance de la canopée macroalgale pour les espèces associées de la communauté. Lorsque celle-ci disparaissait, des changements importants ont été observés avec une perte en richesse, en biomasse et en productivité ainsi qu'une modification dans les abondances avec des espèces qui sont plus susceptibles de résister à des stress physiques, tels *Littorina saxatilis* et *Ralfsia clavata*. Cette importance de la canopée fut déjà démontrée dans de nombreuses études. Cependant, l'absence d'algues éphémères qui est très régulièrement observée avec une disparition de la canopée n'a pas été observée durant l'expérience. Le moment auquel les traitements ont débuté et le taux de recrutement ont surement été des facteurs qui ont influencé les réponses observées.

Les résultats montrent une résistance des communautés à l'enrichissement et à l'exclusion des brouteurs. Cependant une réponse négative a été observée pour l'abondance totale face à un enrichissement et à une réduction des brouteurs alors qu'une réponse positive a été observée pour la diversité face à la réduction des brouteurs. L'apport en nutriments apporté aux quadrats a été stocké dans les tissus des macroalgues, mais n'a pas induit de changements majeurs dans la structure ni dans la productivité. Il est fort probable que la zone intertidale offre un environnement déjà riche en azote, et que donc, l'apport supplémentaire soit stocké dans les tissus des algues. De plus, aucun effet n'a été observé sur la communauté associée que ce soit sur les algues éphémères ou sur les invertébrés. Il est donc possible qu'une augmentation modérée du taux d'azote dans l'estuaire du Saint-Laurent ait peu d'effet à court terme sur les communautés benthiques. Cependant, d'autres études étalées sur plusieurs années devraient être effectuées pour en vérifier les effets à long terme, car il se peut qu'un délai dans les réponses soit possible et qu'un éventuel changement important dans la communauté se produise tel qu'observé dans la littérature. En ce qui concerne l'exclusion des brouteurs, il a été difficile de réduire de manière importante l'abondance des brouteurs dans les quadrats plus longtemps que 3 à 4 jours. La technique utilisée combinant une barrière collante à une brosse a été novatrice, même si la barrière collante seule fut déjà utilisée dans des études et a été efficace dans la réduction de l'abondance des brouteurs, spécialement les patelles. Les patelles sur notre site sont moins nombreuses que les littorines, plus mobiles. Ces dernières peuvent avoir été transportées par les vagues et courants et passer les barrières d'exclusion. De plus, la barrière collante peut avoir été affectée par les températures froides des eaux du Saint-Laurent, la rendant ainsi moins collante. À l'avenir, d'autres techniques devraient être envisagées, car les cages, même si elles permettent une exclusion efficace, ont un effet trop important sur les communautés sous-jacentes.

Néanmoins, la réduction des brouteurs et l'enrichissement couplés à l'enlèvement de la canopée pouvaient montrer des effets marginaux. Les communautés qui faisaient face à deux ou trois perturbations avaient tendance à être moins résistantes (soit plus différentes que celles des contrôles). Les effets doubles et triples (comprenant l'enlèvement de la canopée) étaient marginalement plus affectés que les traitements simples. Ce qui montre que l'accumulation de perturbations peut avoir des effets plus importants que des effets simples tels qu'observés pour la richesse, l'abondance totale en biomasse et la structure d'abondance en recouvrement et en biomasse.

Ce projet a confirmé l'importance des espèces clés (c.-à-d. macroalgues) pour les communautés et a montré un avant-gout des impacts que peuvent avoir plusieurs perturbations sur le bon fonctionnement de l'écosystème. Dans le cadre actuel de perte de biodiversité et de perturbations multiples sur l'environnement, mon étude rejoint d'autres recherches qui montrent qu'il est important de comprendre les effets de perturbations afin d'identifier les mécanismes écologiques qui amènent aux changements au sein de la structure et de la fonction des communautés. Les réponses observées conduisent vers la nécessité d'aller approfondir ces résultats, car il y a une tendance qui est observée pour les effets multiples. La poursuite des recherches dans ce domaine pourra, je l'espère, y répondre et être utile dans les prises de décision pour la gestion et la protection des écosystèmes et plus spécifiquement pour celui du Saint-Laurent marin.

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ANNEXES

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LE NUMERO 1 MONDIAL DU MÉMOIRES

ANNEXE 1

Table A-1. Taxa list (with classification) found during the sampling period at Sainte-Flavie, Quebec, Canada. Taxa marked with * were removed in the canopy ~~removal~~ treatments, and taxa with ** were removed in the grazer exclusion treatments.

Species	**Type**	**Phylum**	**Class**	**Order**	**Family**
Algae					
Chordaria flagelliformis	Brown algae	Ochrophyta	Phaeophyceae	Ectocarpales	Chordariaceae
Ectocarpus sp.	Brown algae	Ochrophyta	Phaeophyceae	Ectocarpales	Ectocarpaceae
*Fucus distichus edentatus**	Brown algae	Ochrophyta	Phaeophyceae	Fucales	Fucaceae
*Fucus vesiculosus**	Brown algae	Ochrophyta	Phaeophyceae	Fucales	Fucaceae
Laminaria sp.	Brown algae	Ochrophyta	Phaeophyceae	Laminariales	Laminariaceae
Ralfsia fungiformis	Brown algae	Ochrophyta	Phaeophyceae	Ralfsiales	Ralfsiaceae
Stragularia clavata	Brown algae	Ochrophyta	Phaeophyceae	Scytosiphonales	Scytosiphonaceae
Clathromorphum circumscriptum	Red algae	Rhodophyta	Florideophyceae	Corallinales	Hapalidiaceae
Rhodomela confervoides	Red algae	Rhodophyta	Florideophyceae	Ceramiales	Rhodomelaceae
Hildenbrandia rubra	Red algae	Rhodophyta	Rhodophyceae	Hildenbrandiales	Hildenbrandiaceae
Ulvaceae	Green algae	Chlorophyta	Ulvophyceae	Ulvales	Ulvaceae
Invertebrates					
*Lacuna vincta***	Animals	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Littorina obtusata***	Animals	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Littorina saxatilis***	Animals	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
*Littorina littorea***	Animals	Mollusca	Gastropoda	Littorinimorpha	Littorinidae
Margarites sp.**	Animals	Mollusca	Gastropoda	Archaeogastropoda	Trochidae
Nudibranchia	Animals	Mollusca	Gastropoda	Nudibranchia	
*Skeneopsis planorbis***	Animals	Mollusca	Gastropoda	Littorinimorpha	Skeneopsidae
*Tectura Testudinalis***	Animals	Mollusca	Gastropoda	Patellogastropoda	Lottidae
Macoma Balthica	Animals	Mollusca	Bivalva	Veneroida	Tellinidae
Mya arenaria	Animals	Mollusca	Bivalva	Myoida	Myidae
Mytillus edulis	Animals	Mollusca	Bivalva	Mytiloida	Mytilidae
Balanus sp.	Animals	Arthropoda	Maxillopoda	Sessilia	Balanidae
*Jaera marina***	Animals	Arthropoda	Malacostraca	Isopoda	Janiridae
Etone sp.	Animals	Annelida	Polychaeta	Phyllodocida	Phyllodocidae
Fabricia sabella	Animals	Annelida	Polychaeta	Sabellida	Fabriciidae
Lepidonotus squamatus	Animals	Annelida	Polychaeta	Phyllodocida	Polynoidae
Nereis sp.	Animals	Annelida	Polychaeta	Phyllodocida	Nereididae
Pectinaria gouldii	Animals	Annelida	Polychaeta	Terebellida	Pectinariidae
Phyllodocidae	Animals	Annelida	Polychaeta	Phyllodocida	
Phyllodoce maculata	Animals	Annelida	Polychaeta	Phyllodocida	Phyllodocidae
Oligochaeta sp.	Animals	Annelida	Clitellata (oligochaeta)		
Cyanophthalma obscura	Animals	Nermertea	Enopla	Monostilifera	Tetrastemmatidae
Nemerta	Animals	Nermertea			
Aulactinia stella	Animals	Cnidaria	Anthozoa	Actiniaria	Actiniidae

ANNEXE 2

Canopy juveniles decreased significantly over time (Table A-2 and Fig. A-1; quadrats with canopy present had an average cover of 99.11% ± 2). Those results illustrate the efficiency of the canopy treatment that was performed during the experiment.

Table A-2. Summary of two-way ANOVA showing the effects of Date and Treatment and crossed factor on *Fucus* spp. Significant values are shown bold.

Source	**df**	***F* Ratio**	***p***
Date	3	164.191	**<.0001**
Treatment	3	1.310	0.282
Date xTreatment	9	0.466	0.890
Error	48		
C. Total	63		

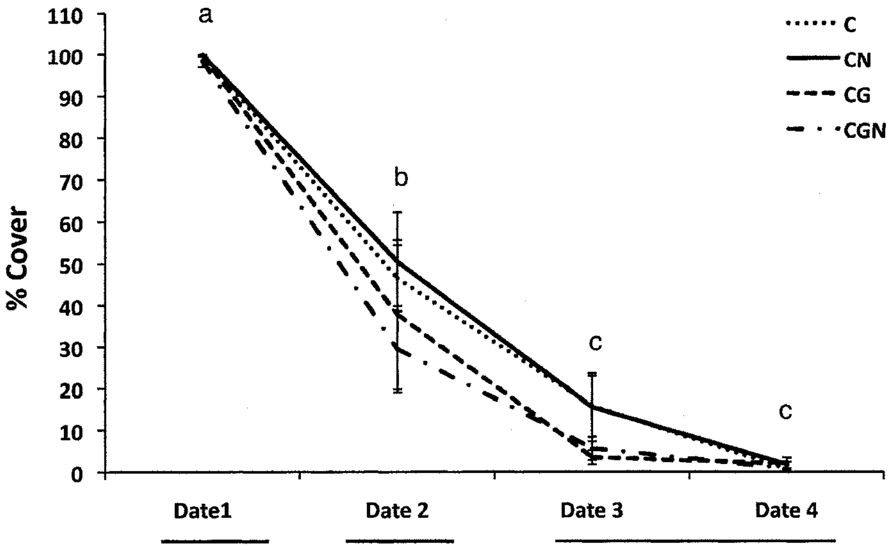

Figure A-1. Average percent cover (± SE, n = 4) of canopy at date 1, and canopy juveniles at Date 2, 3 and 4 for the canopy treatments . The legend of the treatments is found in Figure 2. Dates with different bars under the graph are significantly different ($p < 0.05$).

ANNEXE 3

For diversity measures (Richness, Simpson's index of diversity and Total abundance in percent cover and biomass), no significant differences were observed between control and procedural control plots, except for diversity at Date 1 before the treatments had started and Richness at Date 4 (Table A-3). For the structure in abundances (percent cover and biomass) no significant differences were observed (Table A-4). All species were considered for these analysis.

Table A-3. Summary of ANOVA showing the effect of grazer exclusion on richness, diversity (Simpson index) and total abundance (in percent cover and biomass) between control and procedural treatments (partial exclusion, see Methods) at each date. Significant values are shown bold.

		Date 1		Date 2		Date 3		Date 4	
	df	***F* Ratio**	***p***	***F* Ratio**	***p***	***F* Ratio**	***p***	***F* Ratio**	***p***
a) Richness									
Procedure	1	0,3418	0,5801	0,6667	0,4454	0,3253	0,5891	78,387	**0.0312**
Error	6								
C. Total	7								
b) Diversity									
Procedure	1	61.600	**0.0477**	13.553	0,2886	18.363	0,2242	13.650	0.287
Error	6								
C. Total	7								
c) Total % cover									
Procedure	1	44.960	0,0782	20.006	0,2070	27.490	0,1484	0,4728	0,5174
Error	6								
C. Total	7								
d) Total biomass									
Procedure	1							0,111	0,7503
Error	6								
C. Total	7								

Table A-4. Summary of PERMANOVAs showing the effects of the procedure for grazer exclusion on the structure in abundance in percent cover of the associated species at each dates. Data were square root transformed for percent cover and four root transformed for biomass prior estimating the Bray-Curtis similarities. Significant values are shown bold. MC stand for Monte-Carlo procedure for probabilities.

		Date 1		Date 2		Date 3		Date 4	
	df	**Pseudo-*F***	***p* (MC)**	**Pseudo-*F***	***p* (MC)**	**Pseudo-*F***	***p* (MC)**	**Pseudo-*F***	***p* (MC)**
a) % cover									
Procedure	1	1,3885	0,281	0,49956	0,661	2,8962	0,065	1,098	0,352
Res	6								
Tot	7								
b) Biomass									
Procedure	1							0,67276	0,619
Res	6								
Tot	7								

ANNEXE 4

The results of the two-way ANOVA show that algae in enriched plot did significantly incorporate more nutrients compared to algae in control plot (Table A-5). The average total nitrogen content of enriched algae was higher than of control algae (1.058 %N; SE ± 0.0526 and 0.951 %N; SE ± 0.0439 respectively).

Table A-5. Summary of two-way ANOVA showing the effects of Treatment (n = 4) and replicates (n = 8) on the nitrogen content of algae. The Replicates factor has been incorporated in the ANOVA test for samples that were not independent. Significant values are shown bold.

Source	**df**	***F* Ratio**	***p***
Treatment	1	7.073	**0.015**
Replicates	2	0.557	0.581
Error	20		
C. Total	23		

ANNEXE 5

Data of invertebrates were taken in numbers of individuals. To obtain data in percent cover, those data were transformed using equations found in Table A-6. These equations were established in our lab with large amount of independent observations.

Table A-6. Equations used to transform the data of invertebrates from abundances in numbers (nb) to percent cover.

Percent cover for species:	Equation
Littorinids	(0.0276*nb) + 0.3633
T. testudinalis, L. littorea, A. stella, Nereis sp.	nb*0.25
L.vincta, Margarites sp.	nb*0.1
J. marina, S. planorbis, oligochetae and other polychetae *M. baltica and M. arenaria,* Balanus sp.	nb*0.01

Furthermore, some species were stored in ethanol 70% prior identification and weight.. Therefore an adjustment had to be done to obtain fresh weight (grams) with a correction of + 30% for invertebrates (Leuchs and Koop 2005, Leuven et al. 1985).

Table A-7. Factors used to transform the data from gram to kiloJoule (Brey 2004).

	J/mgWM	J/mg(WM+shell)
Fucus distichus	2.7273645	
Fucus vesiculosus	3.38054025	
Mollusc (Gastropods and bivalves)		1.27957147
Polychetea	3.70082872	
Oligochetea	3.348	
Crustaceans	3.10609352	
Actiniaria	2.03032607	

ANNEXE 6

Table A-8. PERMANOVAs results analyzing the effects of canopy (Ca), grazer (Gr) and enrichment (Nu) treatmentson the composition of the associated species (grazers excluded) of the community at all dates. Data were transformed in presence-absence prior to Bray-Curtis similarities. Significant values are shown bold.

		Datel		Date 2		Date 3		Date 4	
	df	**Pseudo-F**	***p***	**Pseudo-F**	***p***	**Pseudo-F**	***p***	**Pseudo-F**	***p***
Source									
Ca	1	2.386	0.07	1.076	0.367	7.315	**0.006**	22.838	**0.001**
Gr	1	2.508	0.059	0.454	0.697	0.604	0.505	0.634	0.579
Nu	1	0.916	0.472	1.719	0.198	0.253	0.704	0.412	0.683
CaxGr	1	0.661	0.594	0.744	0.536	0.923	0.374	8.73E-02	0.825
CaxNu	1	0.341	0.791	negative		0.213	0.732	0.341	0.738
GrxNu	1	0.805	0.533	1.246	0.293	0.849	0.418	0.34	0.71
CaxGrxNu	1	1.406	0.238	1.106	0.363	negative		0.351	0.724
Residual	24								
Total	31								

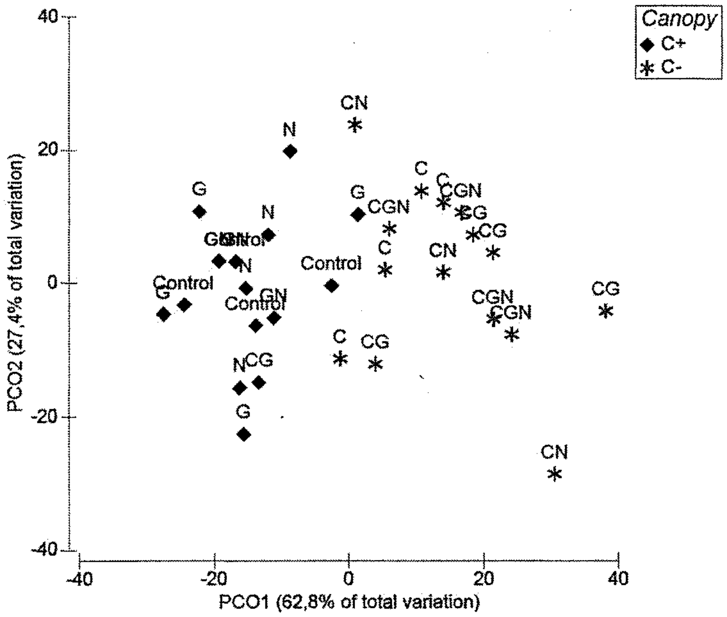

Figure A-2. PCO ordination illustrating the effect of the canopy treatment (diamonds = C+ or canopy present, asterisk = C- or canopy absent) on the composition of the associated species at Date 4, data transformed for presence-absence. The legend for treatments is found in Figure 2.

ANNEXE 7

To test if grazers were efficiently excluded, total abundance of the grazers present in each plot was analyzed. A 4 factorial ANOVA revealed that date was significant for total abundance in % cover ($F_{3,96}$= 103.011; p <0.001) and richness ($F_{3,96}$= 189.114; p <0.001) thus effects of the grazer exclusion efficiency on the grazers community was done by dates separately (Table A-9). There was no significant grazer exclusion over time. From Date 1 to Date 2 there is though a reduction in the abundance of grazers (Figure A-3).

Table A-9. Summary of ANOVAs showing the effect of the grazer exclusion (Gr) of (a) the total abundance of grazers (in % cover) and (b) Richness for the grazer exclusion efficiency. Significant values are shown bold.

		Date1		Date 2		Date 3		Date 4	
	df	***F* Ratio**	***p***	***F* Ratio**	***p***	***F* Ratio**	***p***	***F* Ratio**	***p***
a) Total Abundance									
Gr	1	6.217	**0.0184**	4.9403	**0.034**	0.447	0.501	0.172	0.6811
Error	30								
C. Total	31								
b) Richness									
Gr	1	0.033	0.8565	1.111	0.300	0.921	0.345	3.045	0.091
Error	30								
C. Total	31								

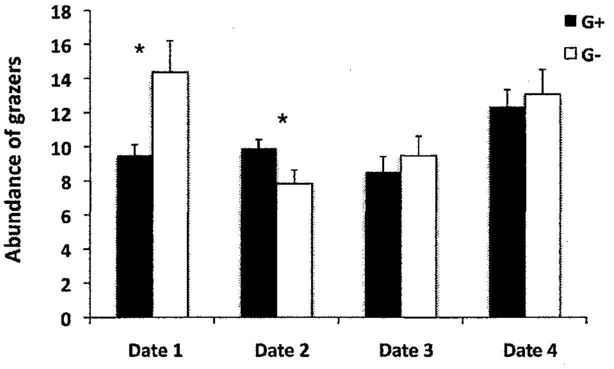

Figure A-3. Average abundance of grazers (+ SE, n=16) at each date for grazers present (G+; black bars) and grazers absent (G-; white bars). Asterisk above bars indicate differences ($p < 0.05$).

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ANNEXE 8

Table A-10. Relative contribution of the associated species + grazers in percent cover to the presence (C+) or not (C-) of canopy from a SIMPER analysis. Data were square root transformed. Note: Canopy present = Control+N treatment; Canopy absent = C and CN treatments; all G- treatments were excluded.

Groups C+ & C-

Average dissimilarity = 40.79

Species	Group C+ Av.Abund	Group C- Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Littorina obtusata	0,70	2,90	7,54	4,62	18,48	18,48
Ralfsia clavata	2,66	0,69	7,38	1,67	18,10	36,58
Mytilus edulis	3,73	4,66	5,29	1,26	12,96	49,54
Jaera marina	0,19	1,17	3,35	3,78	8,21	57,75
Littorina saxatilis	2,83	2,07	2,92	1,82	7,16	64,91
Littorina littorea	0,82	0,00	2,83	2,08	6,94	71,86
Aulactinaria stella	0,00	0,61	2,13	1,44	5,23	77,08
Nereis sp.	1,49	1,44	1,81	1,19	4,43	81,51
Tectura Testudinalis	0,29	0,36	1,44	1,06	3,52	85,03
Lacuna vincta	0,00	0,36	1,24	1,50	3,04	88,07
Lepidonotus squamatus	0,07	0,31	0,85	1,83	2,10	90,17

ANNEXE 9

Table A-11. Relative contribution of the associated species + grazers in biomass to the presence (C+) or not (C-) of canopy from a SIMPER analysis. Data were four root transformed Note: Canopy present = Control+N treatment; Canopy absent = C and CN treatments; all G- treatments were excluded.

Groups C+ & C-
Average dissimilarity = 36.07

Species	**Group C+ Av.Abund**	**Group C- Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Littorina obtusata	4,74	11,67	5,48	2,07	15,19	15,19
Nereis sp.	4,73	8,08	3,40	1,66	9,42	24,60
Pectinaria gouldii	0,15	4,23	3,15	3,70	8,72	33,33
Mytilus edulis	17,33	19,12	3,02	1,26	8,39	41,72
Aulactinaria stella	0,00	3,42	2,61	1,53	7,23	48,95
Balanus sp.	1,41	4,06	2,55	1,53	7,08	56,03
Jaera marina	1,63	4,92	2,55	2,54	7,07	63,09
Littorina littorea	2,80	0,00	2,18	4,93	6,05	69,14
Lacuna vincta	0,00	2,07	1,56	1,60	4,32	73,45
Tectura Testudinalis	0,76	1,70	1,42	1,01	3,95	77,40
Lepidonotus squatamus	0,65	2,26	1,30	1,81	3,61	81,01
Oligochaeta spp.	1,22	1,49	1,18	1,23	3,28	84,29
Mya arenaria	2,89	3,63	1,12	1,20	3,11	87,40
Littorina saxatilis	8,50	7,16	1,04	1,68	2,89	90,30

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ANNEXE 10

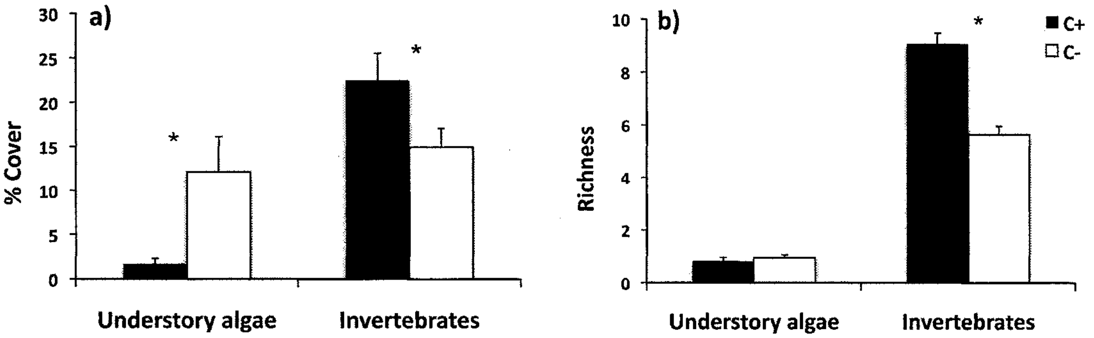

Figure A-4. Average (a) percent cover and (b) richness (+SE, n = 16) of understory algae and invertebrates (without grazers) among the canopy treatment at Date 4 (dark bar: C+ or canopy present and white bar: C- or canopy absent).

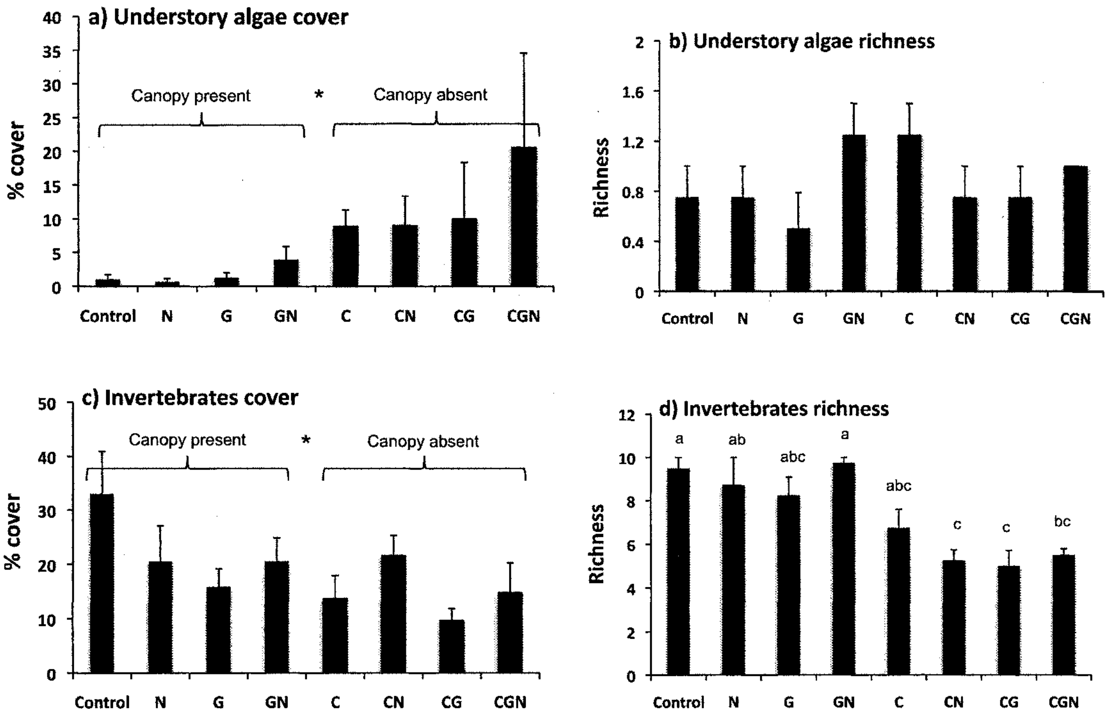

Figure A-5. Average values of (a,c) total abundance in percent cover and (b,d) richness (+SE, n = 4) for ephemeral algae (a,b) and for invertebrates (without grazers) (c,d) among treatments at Date 4. The legend of the treatments is found in Figure 2. One-way ANVOA with the treatment canopy was also performed (brackets). For each variable, bars with asterisks or different letters are significantly different ($p < 0.05$) depending on the test done.

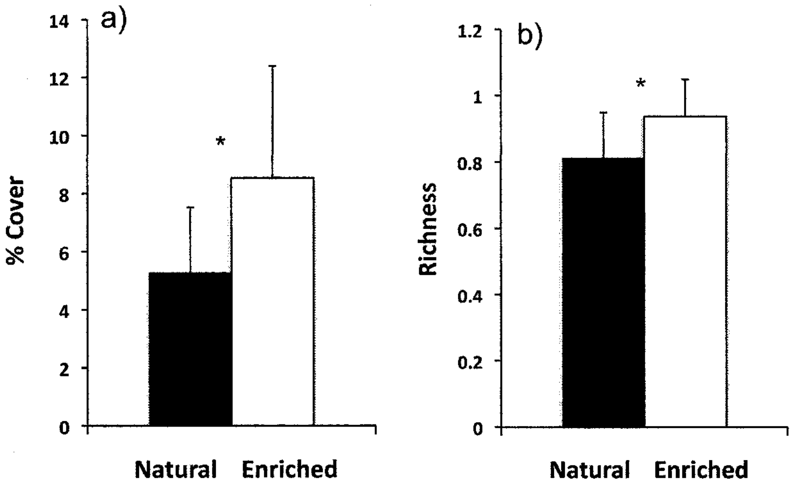

Figure A-6. Average (a) percent cover and (b) richness (+SE, n = 16) of understorey algae among the enrichment at Date 4 (dark bar: natural and white bar: enriched). Bars with asterisks are significantly different ($p < 0.05$).

ANNEXE 11

Abundance-Biomass Comparison (ABC) plots were generated for all plots at Date 4 and the *W* statistic values, that represent the sum of the ranked species abundances differences in biomass and percent cover, (see Clarke 1990) obtained from the plots were compared among treatments (3 factors ANOVA). The *W* value displays a range from -1 to 1, where in theory undisturbed communities tend to have a *W* value > 0 and disturbed communities a *W* value < 0.

The derived Abundance-Biomass Comparison (ABC) statistic *W* using the whole community (i.e. canopy and grazers included in the analysis) showed a significant effect of the canopy treatment at the end of the experiment (Table A-12; Figure A-7), and communities with canopy had a *W* statistic twice as small than communities without canopy. Examples of ABC plots for each treatment are shown in Figure A-8. Biomass curves were always above the abundance curve indicating that none of the communities were disturbed.

Table A-12. Summary of ANOVAs showing the effects of canopy (Ca), grazer (Gr) and enrichment (Nu) treatment and crossed factors on the *W* statistic issued from the ABC curves. Significant values are shown bold.

	df	***F* Ratio**	***p***
Ca	1	61.4704	**< .0001**
Gr	1	0.0528	0.8202
Nu	1	0.0705	0.7929
CaxGr	1	1.0796	0.3091
CaxNu	1	2.5395	0.1241
GrxNu	1	0.3029	0.5871
CaxGrxNu	1	0.3663	0.5507
Error	24		
C. Total	31		

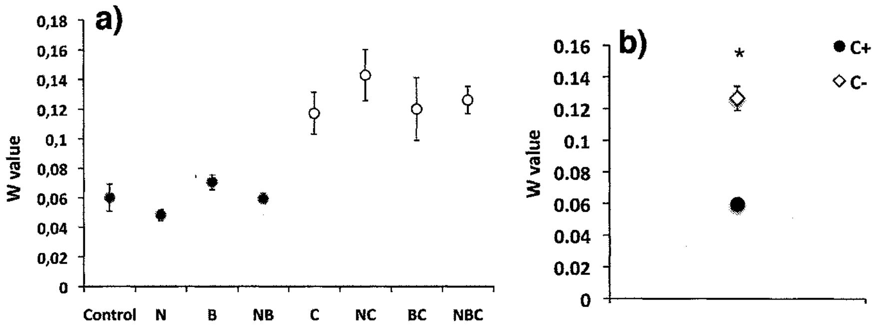

Figure A-7. Average *W* statistic from the ABC plots of the whole community (all species included) among (a) the various treatments (± SE, n = 4; black dots are treatments with the canopy present, and white dots with canopy removed) and (b) the canopy treatment (± SE, n = 16; C+ black bars: canopy present; C- white bars: canopy absent). Asterisk above bars indicate differences ($p < 0.05$). The legend of the treatments is found in Figure 2.

Somewhat unexpected, the Abundances-Biomass Comparison method indicated that none of the communities were disturbed since no negative *W* values were observed. The *W* statistic has been used as indicator of human impacts on ecosystems (Munari and Mistri 2006, 2007, 2008, Puente and Diaz 2008) where low values of *W* indicate disturbed communities. On the contrary, in this study, low *W* values are attributed to natural communities while disturbed communities that included the strongest disturbance C- had higher *W* values. This inaccurate evaluation could be attributed to an uneven abundance distribution across species. Canopy is largely dominant (Figure A-9) in plots with canopy present (Control, N, G and GN) and might explain the low *W* values observed. Furthermore, the *W* statistic is a measure sensitive to low samples or replicate size (Bilkovic et al. 2006). Four replicates might not be sufficient to obtain a clear response with the *W* statistic.

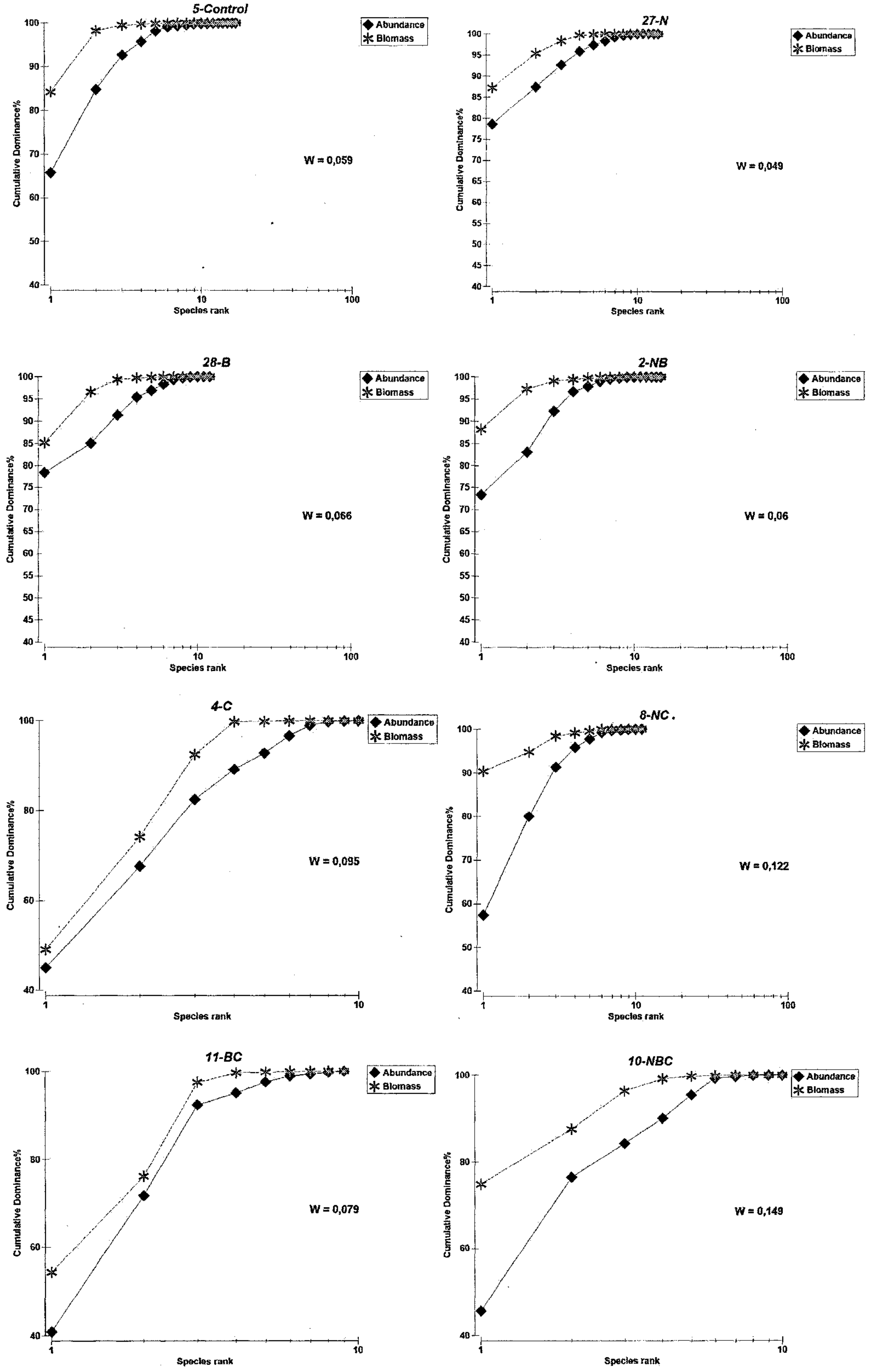

Figure A-8. Examples of ABC plots for all 8 treatments. The number of the quadrat is indicated with its associated treatment (e.g. # - control).

The average contribution of the *Fucus* spp. to the total abundance in percent cover for plots with canopy present is 71.31% while plots with absent canopy is 4.52%. For grazers, the average contribution is 11.71% for plots with canopy present and 29.12% with absent canopy.

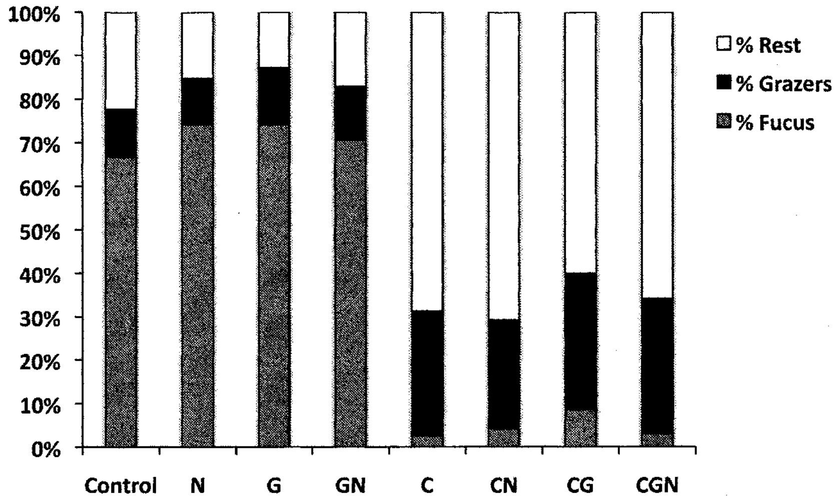

Figure A-9: Average percent of contribution of the *Fucus* spp. (gray) species and the grazers (black) to the whole community. The «Rest» (white) are all the associated species. The legend of the treatments is shown in Figure 2.

ANNEXE 12

Temporal abundance stability, *S*, defined as the mean abundance over time, μ, divided by the standard deviation, σ, that is $S = \mu/\sigma$ (Lehman and Tilman 2000), was calculated for each individual quadrat (over 2 months, including dates 2, 3 and 4) and compared among treatments (3 factors ANOVA). After graphical examination of the residuals, data were log transformed to satisfy the ANOVA assumptions.

Temporal abundance (in percent cover) stability was not affected by any treatment (Table A-13). Even the triple treatment didn't affect the stability of the associated community (Figure A-9).

Table A-13. Summary of ANOVAs showing the effects of canopy (Ca), grazer (Gr) and enrichment (Nu) treatments and crossed factors on the Temporal Stability. Data were log transformed. Significant values are shown bold.

	df	***F* Ratio**	*p*
Ca	1	0.8233	0.3732
Gr	1	2.0445	0.1656
Nu	1	0.0288	0.8666
CaxGr	1	2.2535	0.1464
CaxNu	1	0.4594	0.5044
GrxNu	1	0.136	0.7155
CaxGrxNu	1	0.8118	0.3765
Error	24		
C. Total	31		

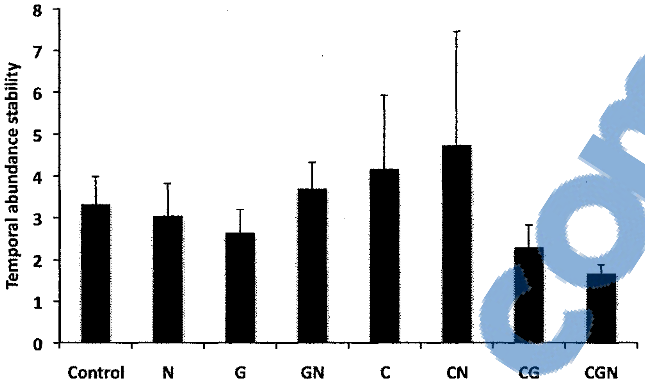

Figure A-9. Average temporal stability of the associated species among the various treatments (± SE, n = 4). The legend of the treatments is found in Figure 2.

Surprisinly, none of the temporal stability within the associated communities was affected by any treatment. The loss of habitat-forming species like the fucoids canopy is known to have a major role in enhancing the stability of the community (Bulleri et al. 2002, Crowe et al. 2013). An increase in the abundance of dominant species provided for the conservation of the stability of the community (Grman et al. 2010, Sasaki and Lauenroth 2011).

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