TROPHIC ECOLOGY OF SOUTHERN OCEAN SEA STARS

Influence of environmental drivers on trophic diversity

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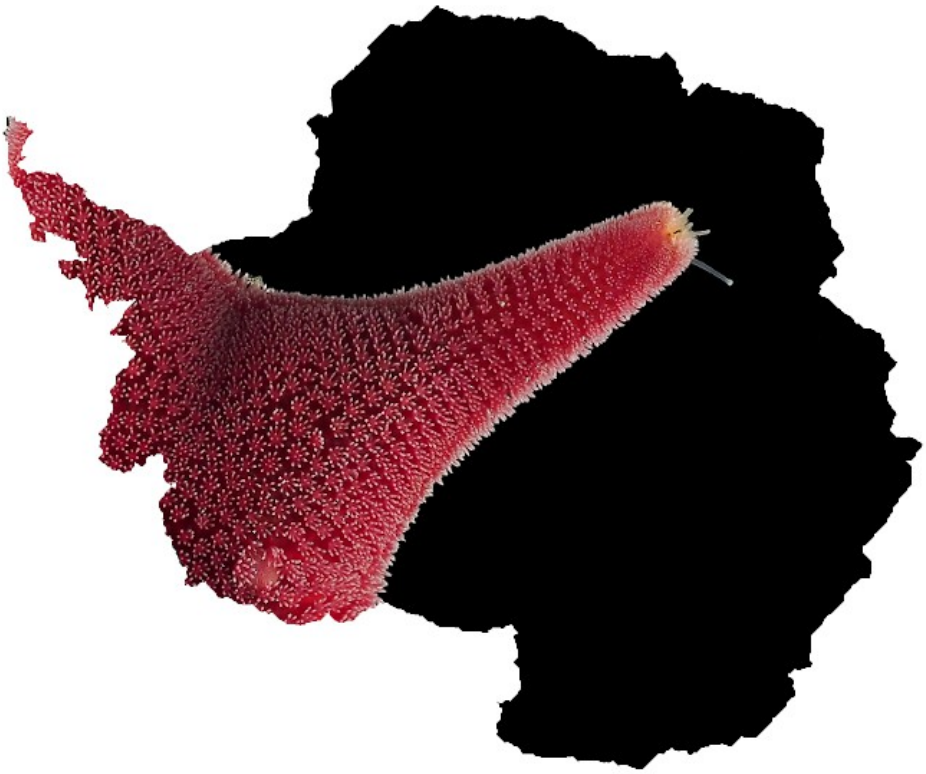

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Influence of environmental drivers on trophic diversity

Écologie trophique des étoiles de mer de l'Océan Austral :
Influence des facteurs environnementaux sur la diversité trophique

Baptiste Le Bourg

Thesis submitted for the degree of Doctor in Sciences

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Résumé

Comme le reste du monde, l'Océan Austral est impacté par le changement climatique. Néanmoins, ces changements varient en fonction des différentes régions de cet océan. Les modifications de la couverture par la glace de mer autour du continent Antarctique en sont une des manifestations les plus visibles. Ainsi, la couverture glaciaire a fortement diminué en Péninsule Antarctique Occidentale, tandis qu'elle tend à légèrement augmenter sur le reste de la façade du continent. Ces modifications des conditions environnementales influencent le fonctionnement des écosystèmes de cet océan. Notamment, la disparition ou la persistance de la couverture glaciaire dans une région où elle avait une présence saisonnière peut empêcher l'apparition des efflorescences estivales du phytoplancton, impactant ainsi la dynamique des populations de krill et de leurs prédateurs dans le milieu pélagique. Le milieu benthique sera lui aussi perturbé par les modifications environnementales résultant du changement climatique, puisque les flux de matière organique vers ce compartiment seront affectés.

Les étoiles de mer (Echinodermata : Asteroidea) sont un élément clé du benthos de l'Océan Austral, avec 12% des espèces d'étoiles de mer connues y vivant. En milieu tempéré, ce taxon peut, au travers d'interactions trophiques, jouer un rôle important dans le fonctionnement des écosystèmes en contrôlant les populations d'autres organismes qui ont eux-mêmes un effet conséquent sur les écosystèmes. Ce groupe est considéré comme assez résistant aux changements de température de l'eau de mer en milieu Antarctique. Il est cependant susceptible d'être affecté par les modifications des conditions environnementales et leur influence sur le fonctionnement des réseaux trophiques. En effet, la réduction de l'abondance ou la disparition de proies communes peut entraîner un risque accru compétition dans les assemblages d'étoiles de mer. Afin de déterminer le rôle écologique des étoiles de mer dans l'Océan Austral, et de comprendre comment elles pourraient être impactées par le changement climatique, une étude de leur écologie trophique et des facteurs qui la contrôlent est nécessaire. Par conséquent, les objectifs de cette thèse de doctorat étaient de déterminer quelle est la place des étoiles de mer dans l'Océan Austral, et comment des facteurs environnementaux comme la turbidité, la profondeur et la glace de mer impactent leur diversité trophique.

Pour ce faire, les rapports isotopiques du carbone ($\delta^{13}C$), de l'azote ($\delta^{15}N$) et du soufre ($\delta^{34}S$) ont été analysés dans des tissus d'étoiles de mer prélevées dans l'ensemble de l'Océan Austral (n = 2454 individus, auxquels s'ajoutent des données sur 204 individus issues de la littérature ou

partagées par des collègues). Une proportion importante des échantillons d'étoiles de mer est issue de collections archivées dans des institutions et/ou des muséums, ce qui a permis de significativement augmenter la couverture spatiale et temporelle de l'échantillonnage. Cependant, ces échantillons ont pour la plupart été conservés dans de l'éthanol, et certains ont été préalablement fixés avec du formaldéhyde. Or, les liquides de préservation peuvent altérer les rapports isotopiques des tissus biologiques. Par conséquent, l'impact de la méthode de préservation sur les rapports isotopiques dans les tissus d'étoiles de mer a été étudié (chapitre 3) lors d'une expérience à long terme (deux ans). Celle-ci a montré qu'il était possible de corriger mathématiquement l'effet des liquides de préservation sur les rapports isotopiques des étoiles de mer, et donc d'utiliser des échantillons archivés pour des études d'écologie trophique.

Afin de mieux connaître l'importance potentielle des étoiles de mer dans les écosystèmes de l'Océan Austral, le réseau trophique des forêts de *Macrocystis pyrifera* (Phaeophycées, Laminariales ; ou "kelp") subantarctiques a été reconstitué grâce à l'analyse des rapports isotopiques dans des tissus d'invertébrés (19 taxa, dont 6 d'étoiles de mer) et de producteurs primaires échantillonnés dans les îles Kerguelen (chapitre 4). L'utilisation de modèles de mélange isotopique a démontré qu'il n'y a pas de consommateur majeur de *Macrocystis pyrifera* dans ces forêts de kelp, et que le réseau trophique est alimenté par la matière organique pélagique et du micro/macrophytobenthos vivant (à l'exception du kelp) ou sous forme de détritus (incluant probablement des détritus de kelp). Ceci suggère que les étoiles de mer n'ont pas les mêmes fonctions écologiques dans les forêts à *Macrocystis pyrifera* des régions subantarctiques que dans celles des régions plus tempérées où elles contrôlent partiellement les populations d'herbivores. Nos résultats démontrent également que les étoiles de mer subantarctiques ne se limitent pas à être des prédateurs au sommet des chaînes alimentaires. D'une part, certaines espèces occupent d'autres positions trophiques plus basales. D'autre part, leurs niches trophiques ne se recouvrent pas nécessairement : certaines exploitent plus la partie du réseau trophique soutenu par la production pélagique et d'autres la partie du réseau trophique soutenue par la production benthique (y compris détritique).

Après cette analyse d'un réseau trophique entier, nous avons réalisé une comparaison des niches isotopiques d'étoiles de mer à une échelle locale, et étudié les liens possibles entre changements ontogénétiques, c'est-à-dire au cours de la vie et de la croissance, et écologie trophique (chapitre 5). L'analyse des rapports isotopiques dans des étoiles de mer prélevées dans l'anse d'Ezcurra (baie de l'Amirauté, île du Roi-George, îles Shetland du sud) a montré que la taille, et plus particulièrement

le rayon du disque central, peut être reliée aux rapports isotopiques chez certaines espèces, indiquant des changements ontogénétiques de l'alimentation chez ces dernières. Cette observation n'est cependant valable que pour certaines espèces, en particulier des espèces omnivores, où on observe une élévation de la position trophique en fonction de la taille de l'étoile de mer. La relation entre le rayon du disque et l'alimentation peut notamment s'expliquer par le fait que les étoiles de mer les plus grandes peuvent dévaginer leur estomac sur de plus grandes surfaces et donc consommer des proies plus grandes et/ou de niveau trophique plus élevé. Chez les étoiles de mer consommant du sédiment ou potentiellement suspensivores, cette relation entre la taille et les rapports isotopiques n'est généralement pas observée, ce qui suggère qu'il y a probablement moins de variabilité du régime alimentaire en fonction de la taille des individus chez ces espèces. L'analyse des rapports isotopiques dans les étoiles de mer prélevées dans l'anse d'Ezcurra indique également que certaines espèces d'étoiles de mer présentent une variabilité de régime alimentaire importante qui détermine en partie leurs interactions trophiques interspécifiques. La turbidité générée par l'apport de matière terrigène par les eaux de ruissellement issues de la fonte des glaciers terrestres crée un gradient environnemental important de l'intérieur vers l'extérieur de l'anse d'Ezcurra, qui détermine les conditions d'habitat et la nature des ressources disponibles pour les étoiles de mer. Certaines espèces adaptent leurs régimes alimentaires en fonction de ces conditions variables. Les interactions entre espèces sont également affectées. A l'intérieur de l'anse, sujet à une importante turbidité, les espèces *Diplasterias brandti* et *Odontaster validus* ont des valeurs de $\delta^{13}C$ plus différenciées (i.e. des sources de nourriture plus différentes) et des niches isotopiques se recouvrant moins, qu'à l'extérieur, sujet à une turbidité moindre. De même, la taille de la niche isotopique d'*Odontaster validus* est plus réduite vers l'intérieur de l'anse que vers l'extérieur. Ceci correspond probablement à une situation moins favorable en termes de disponibilité et de diversité des ressources à l'intérieur de l'anse. Ceci pourrait conduire à une constriction de la niche isotopique d'*Odontaster validus* ainsi qu'à une ségrégation des ressources accrue qui pourrait limiter la compétition interspécifique entre les quelques espèces capables de survivre à ces conditions défavorables.

Dans le chapitre 6, nous avons étudié l'impact du groupe trophique, de la profondeur, de la concentration de glace et de la durée de la saison glaciaire sur l'alimentation des étoiles de mer par l'intermédiaire d'une analyse globale de notre jeu de données à l'échelle de l'Océan Austral. De plus, l'Océan Austral a été subdivisé en différentes écorégions benthiques d'après des données environnementales (température au fond, glace de mer, bathymétrie) et biologique (distribution des

espèces) afin d'étudier les variations biogéographiques de l'alimentation des étoiles de mer. Cette subdivision a notamment mis en évidence la séparation des environnements antarctique et subantarctique, la différence des valeurs de $\delta^{13}C$ de la matière organique dans les eaux de surface entre les écorégions subantarctiques et antarctiques étant reflétée dans les tissus d'étoiles de mer benthiques. Dans ce chapitre, la compilation des informations disponibles sur leur régime alimentaire a permis de procéder à une classification des taxa d'étoiles de mer de l'Océan Austral en groupes trophiques, allant des suspensivores aux prédateurs de proies mobiles. Les différences de rapports isotopiques entre ces groupes trophiques et leur variabilité dans certains d'entre eux suggèrent une diversité des sources de nourriture et/ou des stratégies d'alimentation entre et au sein des groupes trophiques. Ces résultats confirment bien que, contrairement à ce qui est parfois dit dans la littérature, les étoiles de mer de l'Océan Austral font preuve d'une grande diversité trophique. La profondeur est apparue comme un facteur influençant fortement l'écologie trophique des étoiles de mer, aussi bien à l'échelle de tout l'Océan Austral que des écorégions. En effet, les étoiles de mer côtières semblent exploiter des réseaux trophiques soutenus par une diversité de producteurs primaires pélagiques et benthiques tandis que les étoiles de mer plus profondes paraissent dépendre de la sédimentation de la production primaire de surface. Ainsi, les étoiles de mer côtières sont caractérisées par l'exploitation d'un plus grand nombre de sources de matière organique. Par contre, il est également apparu que les étoiles de mer plus profondes ont une plus grande diversité de positions trophiques que les côtières. La plus faible diversité et la plus faible disponibilité des ressources trophiques en milieu profond pourraient favoriser la diversification des comportements alimentaires (e.g. omnivorie, prédation, consommation de sédiment) des étoiles de mer, ce qui pourrait permettre de réduire la compétition entre espèces. L'impact de la glace de mer sur l'alimentation des étoiles de mer antarctiques a également été étudié. En cas de forte concentration en glace de mer, les communautés sympagiques semblent être utilisées comme ressources trophiques par les étoiles de mer. De même, pour certains groupes trophiques, une dépendance croissante à l'égard de phytodetritus dégradés semble exister dans les stations où la durée de la saison glaciaire est la plus élevée. Ce mécanisme pourrait permettre d'atténuer les impacts de la glace de mer sur la disponibilité des ressources trophiques pendant les plus longues périodes de couverture de glace de mer. Nos résultats suggèrent aussi que les liens entre glace de mer et alimentation des consommateurs benthiques sont multiples mais complexes à interpréter. En outre, ils ne sont pas tous consistants d'une écorégion à l'autre, vraisemblablement en lien avec les caractéristiques océanographiques très variées que l'on peut y rencontrer. Enfin, les impacts des

différents paramètres environnementaux peuvent varier d'un groupe trophique à l'autre, illustrant la nécessité de prendre en compte la diversité trophique pour prédire la susceptibilité des étoiles de mer aux changements environnementaux futurs, qu'ils soient d'origine naturelle ou anthropique.

En résumé, les travaux présentés dans cette thèse montrent que l'écologie trophique des étoiles de mer de l'Océan Austral est influencée par un ensemble de facteurs intrinsèques (taille, groupe trophique) et extrinsèques (turbidité, profondeur, glace de mer). Les informations sur l'influence des facteurs environnementaux permettent d'établir des hypothèses sur les possibles impacts du changement climatique sur les étoiles de mer et leur rôle dans les réseaux trophiques benthiques de l'Océan Austral. En effet, les paramètres environnementaux influencent, au travers de la disponibilité en ressources, l'écologie trophique des étoiles de mer, et notamment les interactions entre espèces. Ainsi, la plus faible diversité et la plus faible disponibilité des ressources trophiques en milieu turbide et en milieu profond ont été considérées comme pouvant favoriser la diversification des comportements alimentaires pour éviter la compétition entre espèces. Au contraire, leur plus grande disponibilité en milieu peu turbide et côtier permet la consommation de proies similaires avec un risque limité de compétition. La glace de mer a des impacts plus variés sur la disponibilité en ressources trophiques, servant d'habitat aux communautés sympagiques et favorisant les efflorescences de phytoplancton lors de sa débâcle, mais les inhibant en cas de persistance. Par conséquent, les modifications de la couverture glaciaire et de sa dynamique à cause du changement climatique vont induire des changements dans la disponibilité des ressources trophiques pour le benthos de l'Océan Austral. De même, des modifications de la turbidité en milieu côtier suite à la modification de la dynamique des glaciers terrestres pourraient avoir des conséquences sur la disponibilité en ressources dans ce type d'environnement. Ces changements vont probablement modifier la nature des interactions trophiques entre les taxa d'étoiles de mer, avec une hausse ou une baisse de l'importance de la compétition, ce qui pourrait entraîner des modifications dans la structure des assemblages d'étoiles de mer dans l'Océan Austral.

Abstract

Like in the rest of the world, climate change impacts the Southern Ocean, but not in the same way in all regions of this ocean. Changes in sea ice cover around the Antarctic continent are one of the most visible manifestations. For example, sea ice cover has decreased significantly in the Western Antarctic Peninsula while it tends to increase slightly on the rest of the coastline of the continent. These changes in environmental conditions influence the functioning of the ecosystems of this ocean. In particular, the disappearance or persistence of sea ice in a region where it was seasonally present may prevent the appearance of summer phytoplankton blooms, thus impacting the dynamics of krill populations and their predators in the pelagic environment. The benthic environment will also be disturbed by environmental modifications resulting from climate change, as organic matter fluxes toward this compartment will be affected.

Sea stars (Echinodermata: Asteroidea) are a key component of Southern Ocean benthos, with 12% of the known sea star species living there. In temperate environments, this taxon may play an important role in the functioning of ecosystems with its trophic interactions controlling the populations of other organisms, which themselves have a large effect on the ecosystems. This group is considered to be quite resistant to changes of seawater temperature in the Antarctic environment. However, it will likely be affected by changes of environmental conditions and functioning of food webs. Indeed, a reduction in the abundance or disappearance of common prey can lead to an increased competition in sea star assemblages. In order to determine the ecological role of sea stars in the Southern Ocean and to understand how they might be impacted by climate change, a study of their trophic ecology and of the factors controlling it is necessary. Therefore, the objectives of this PhD thesis were to determine the trophic role of sea stars in the Southern Ocean, and how environmental factors such as turbidity, depth and sea ice impact their trophic diversity.

To do so, stable isotope values of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) were analysed in tissues of sea star sampled across the Southern Ocean (n = 2454 individuals, plus data on 204 individuals from the literature or shared by colleagues). A significant proportion of the sea star samples came from collections archived in institutions and/or museums, which significantly increased the spatial and temporal coverage of the study. However, most of these samples were preserved in ethanol, and some have been previously fixed with formaldehyde. Preservative fluids may alter the stable isotope values of biological tissues. Therefore, the impact of the preservation method on the stable isotope values in sea star tissues was studied (chapter 3). A two year-long

experiment showed that it was possible to mathematically correct the effect of preservative fluids on stable isotope values in sea stars, making it possible to use archived samples for trophic ecology studies.

In order to better understand the potential importance of sea stars in the ecosystems of the Southern Ocean, the food web of subantarctic *Macrocystis pyrifera* (Phaeophyceae, Laminariales; or "kelp") forests was reconstructed by analysing stable isotope values in invertebrate (19 taxa, including 6 sea star taxa) and primary producer tissues sampled in the Kerguelen Islands (chapter 4). Mixing models did not highlight major *Macrocystis pyrifera* consumers and showed that the food web is supported by pelagic organic matter and live (with the exception of kelp) or detrital micro/macrophytobenthos. This suggests that sea stars do not have the same ecological function in *Macrocystis pyrifera* forests from subantarctic regions than in those from more temperate regions, where they control grazer populations. The results also show that sea stars are not only top predators in the food chain. On the one hand, some species may occupy lower trophic positions. On the other hand, their trophic niches may not overlap: some species rely more on the food chain supported by pelagic production and others on the food chain supported by benthic (including detrital) production.

Following this analysis of an entire food web, isotopic niches of sea stars were compared at a local scale, and the possible relationship between ontogenetic changes, i.e. changes during growth, and trophic ecology were studied (chapter 5). The analysis of stable isotope values in sea stars sampled in Ezcurra Inlet (Admiralty Bay, King George Island, South Shetland Islands, chapter 5) showed that the size, and especially the central disc radius, can be linked to stable isotope values in some species, indicating the occurrence of ontogenetic changes in the diet of these species. This was observed only in some species, and notably omnivore species, for which the trophic position increased with body size. The relationship between the disc radius and the trophic ecology may be explained by larger sea stars being able to evert their stomach over larger areas and thus consume larger prey and/or prey with higher trophic level. For sediment feeding and potentially suspension feeding species, the relationship between size and stable isotope values was usually not observed, suggesting lower variability of the trophic ecology between size classes in these species. The analysis of stable isotope values in sea stars sampled in Ezcurra Inlet also indicates that the diet variability of some sea star species may be important, which in part determines their interspecific trophic interactions. The turbidity generated by the terrestrial inputs provided by meltwater run-off from terrestrial glaciers results in an important environmental gradient from the inner to the outer

Ezcurra Inlet, which determines the habitat conditions and the characteristics of the resources available for sea stars. Some species may adapt their diet depending on those variable conditions. Interspecific interactions are also impacted. Indeed, the *Diplasterias brandti* and *Odontaster validus* species have more different $\delta^{13}C$ values (i.e. more different food sources) and lower isotopic niche overlap in the inner inlet, where high turbidity occurs, than in the outer, where turbidity is lower. Similarly, the size of the isotopic niche of *Odontaster validus* is smaller in the inner Ezcurra Inlet than in the outer. This is probably the result of a more limited availability and diversity of resources in the inner inlet. This may lead to the constriction of *Odontaster validus* isotopic niche and to resource segregation that may limit interspecific competition between the few species able to survive in these unfavourable conditions.

In the chapter 6, the impact of trophic group, depth, sea ice concentration and sea ice season duration on the trophic ecology of sea stars was assessed thanks to a global analysis of the dataset at the scale of the whole Southern Ocean. The Southern Ocean was subdivided into different benthic ecoregions according to environmental (seabed temperature, sea ice, bathymetry) and biotic data (species distribution), to study biogeographic variations in the trophic ecology of sea stars. This subdivision notably highlighted the separation between Antarctic and Subantarctic environments, with the different $\delta^{13}C$ values in organic matter from the surface in Subantarctic and Antarctic waters being reflected in tissues from benthic sea stars. In this chapter, the compilation of the available information on their diet allowed to make a classification of sea star taxa from the Southern Ocean into trophic groups, ranging from suspension feeders to predators of active prey. The differences of stable isotope values between trophic groups and their variability in some of them suggested a diversity of food sources and/or of feeding strategies between and within trophic groups. These results confirm that, contrary to what is sometimes stated in the literature, sea stars in the Southern Ocean show a great trophic diversity. Depth has important effects on the trophic ecology of sea stars, both across the entire Southern Ocean and within ecoregions. Indeed, coastal sea stars may exploit food webs supported by a variety of pelagic and benthic primary producers while deeper sea stars may depend on the sedimentation of the surface primary production. Coastal sea stars are then characterised by a high diversity of food sources, while deeper sea stars have a higher diversity of trophic positions than coastal ones. The lower diversity and availability of food sources in deep waters may induce the diversification of sea star feeding behaviours (e.g. omnivory, predation, sediment feeding), which would reduce competition between species. The impact of sea ice on the trophic ecology of sea stars was also investigated. The sympagic communities may be

used as a food source by sea stars in case high sea ice concentrations. Furthermore, increasing reliance on degraded phytodetritus during longer periods of sea ice cover may occur in several trophic groups. This may dampen the impacts of sea ice presence on resource availability during long periods of sea ice cover. Our results also suggest that multiple relationships do exist between sea ice and the diet of benthic consumers, but they are not easy to interpret. Finally, not all of them are consistent across ecoregions, probably as a result of their contrasted oceanographic features. In addition, the impacts of the environmental parameters may differ between trophic groups, highlighting the importance of trophic diversity to predict the sensitivity of sea stars to future environmental changes, whether natural or anthropogenic.

To summarise, the studies of this thesis show that the trophic ecology of sea stars from the Southern Ocean is impacted by a combination of intrinsic (body size, trophic group) and extrinsic features (turbidity, depth, sea ice). Information on the influence of environmental parameters may provide hypotheses regarding the possible impacts of climate change on sea stars and on their role in benthic food webs of the Southern Ocean.

Indeed, the environmental parameters may influence the trophic ecology of sea stars and the trophic interactions between taxa thanks to their impact on resource availability. The lower diversity and availability of food sources in turbid and deep waters have been considered as potential sources of diversification of feeding behaviours to avoid competition between species. By contrast, their greater availability in less turbid and coastal environments allows the consumption of similar prey with limited risks of competition. Sea ice has more variable impacts on resource availability, being an habitat for sympagic communities and inducing phytoplankton blooms after its break up, but inhibiting them in case of persistence. Consequently, changes in the ice cover and its dynamics because of climate change will induce changes in the resource availability for the Southern Ocean benthos. Similarly, changes in turbidity in coastal areas as a result of modifications in the dynamics of terrestrial glaciers could have consequences on resource availability in this type of environment. These changes are likely to modify the trophic interactions between sea star taxa, with an increase or decrease of the importance of competition, which may result in modifications of the structure of sea star assemblages in the Southern Ocean.

Abbreviations

$\delta^{13}C$: stable isotope ratios of carbon

$\delta^{15}N$: stable isotope ratios of nitrogen

$\delta^{34}S$: stable isotope ratios of sulfur

ACC: Antarctic Circumpolar Current

ACoC: Antarctic Coastal Current

CD: mean distance to centroid

GIS: Geographic Information System

HBI: highly branched isoprenoid

HNLC: High Nutrient, Low Chlorophyll

IP_{25}: Ice Proxy with 25 carbon atoms

$IPSO_{25}$: Ice Proxy for the Southern Ocean with 25 carbon atoms

MNND: mean of the nearest neighbour distance

PCA: principal component analysis

POM: particulate organic matter

PSD: pseudo-standard deviation

PSD_C: pseudo-standard deviation of $\delta^{13}C$ values

PSD_{CB}: Bayesian estimation of the pseudo-standard deviation of $\delta^{13}C$ values

PSD_{CC}: sample-size corrected pseudo-standard deviation of $\delta^{13}C$ values

PSD_N: pseudo-standard deviation of $\delta^{15}N$ values

PSD_{NB}: Bayesian estimation of the pseudo-standard deviation of $\delta^{15}N$ values

PSD_{NC}: sample-size corrected pseudo-standard deviation of $\delta^{15}N$ values

PSD_S: pseudo-standard deviation of $\delta^{34}S$ values

PSD_X: pseudo-standard deviation on the x-axis

PSD_{XB}: Bayesian estimation of the pseudo-standard deviation on the x-axis

PSD_{XC}: sample-size corrected pseudo-standard deviation on the x-axis

PSD_Y: pseudo-standard deviation on the y-axis

PSD_{YB}: Bayesian estimation of the pseudo-standard deviation on the y-axis

PSD_{YC}: sample-size corrected pseudo-standard deviation on the y-axis

SD: standard deviation

SDNND: standard deviation of the distances between each point and its closest neighbour in the

convex hull

SEA: standard ellipse area

SEA_B: Bayesian estimation of the standard ellipse area

$SEA_{B.CN}$: Bayesian estimation of the standard ellipse area computed with $\delta^{13}C$ and $\delta^{15}N$ values

$SEA_{B.CS}$: Bayesian estimation of the standard ellipse area computed with $\delta^{13}C$ and $\delta^{34}S$ values

SEA_C: sample-size corrected standard ellipse area

$SEA_{C.CN}$: sample-size corrected standard ellipse area computed with $\delta^{13}C$ and $\delta^{15}N$ values

$SEA_{C.CS}$: sample-size corrected standard ellipse area computed with $\delta^{13}C$ and $\delta^{34}S$ values

SIA: stable isotope analysis

SIBER: stable isotope Bayesian ellipses in R

simmr: stable isotope mixing models in R

SST: sea surface temperature

TA: total area of the convex hull

WAP: Western Antarctic Peninsula

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Foreword

The Southern Ocean is affected by the current global climate change, with increasing air and ocean temperatures occurring in the area. However, the impacts of climate change differ between areas, as highlighted by the variations of the evolution of air temperature, sea ice extent, and ice season duration among Antarctic regions. Benthic communities of the Southern Ocean will also be affected by climate change. In particular, changes in the food web functioning are expected.

Echinoderms are an important group of the Southern Ocean benthos. 624 species were recorded in the Southern Ocean, i.e. around 8 % of all known echinoderm species. They are important contributors to the abundance and biomass of the Southern Ocean benthos, and can be the dominant benthic taxon in some areas.

This thesis reports the results of a five year-long study on the trophic ecology of sea stars from the Southern Ocean, using stable isotope markers. In particular, the objectives were to determine the trophic role of sea stars in the Southern Ocean, and how environmental factors such as turbidity, depth and sea ice influence their trophic ecology and diversity. Ultimately, these results may help to determine how sea stars might be impacted by climate change.

This work was carried out as part of the vERSO (Ecosystem Responses to global change: a multiscale approach in the Southern Ocean; BR/132/A1/vERSO) and RECTO (Refugia and Ecosystem Tolerance in the Southern Ocean; BR/154/A1/RECTO) projects, funded by the Belgian Science Policy Office (BELSPO). The goals of these research projects were to assess the impact of environmental modifications induced by climate change on benthic Antarctic ecosystems by using interdisciplinary approaches (e.g. populations history, trophic ecology, taxa sensitivity, mathematical modeling).

Chapter 1 : General introduction

The Admiral, by Giuseppe Arcimboldo.

“ Dis-moi ce que tu manges, je te dirai ce que tu es. ”

Jean Anthelme Brillat-Savarin, 1825, Physiologie du goût

1.1 Trophic ecology

1.1.1 Concepts and definitions

In order to survive, all organisms require organic matter. While autotrophic organisms are able to produce their own organic matter from inorganic molecules, heterotrophic organisms must consume preformed organic matter, which is provided by other organisms. As a result, organisms can be related with each other by their trophic relationships, i.e. relationships between organisms that "eat" and organisms that "are eaten". The succession of trophic relationships (from nutrients to predators) between organisms thus forms a food chain, with each trophic level being the position of each organism in the food chain. Yet, organisms usually need to consume more than one type of prey to meet their energy requirements, and therefore are not restricted to a single food chain nor a discrete trophic level. Consequently, food webs provide a more realistic model than food chain to understand the pathway of matter and energy in ecosystems (Fig. 1.1).

Food webs encompass various interconnected food chains which structure natural communities. Variations in the relative importance of one component of a food web may change abundances of the different species being part of the food web and/or may result in modifications of its composition and functioning. Changes in carbon sources abundance and/or composition may induce trophic cascades by affecting both primary and higher trophic level consumer populations (bottom-up control; e.g. Frederiksen et al., 2006; Kagata and Ohgushi, 2006; Tulloch et al., 2019). Conversely, changes in predator abundances can also induce trophic cascades by modifying the abundance of prey (top-down control), which will then impact the abundance of other components of the food web by predation (e.g. Mumby et al., 2007; Szpak et al., 2013; Morris and Letnic, 2017). Similarly, modifications of predator abundance may also influence horizontal interactions between prey of similar trophic level, as predators can mediate horizontal relationships. For example, the abundance of an organism may be modified by the competition with another organism whose abundance was previously reduced by a predator (e.g. Paine, 1966; Frid and Marliave, 2010). Consequently, trophic interactions, and in particular top-down control, are important drivers of species diversity (Terborgh, 2015) and adequate knowledge of organisms' trophic ecology is necessary to better understand their importance in the community and the ecosystem functioning.

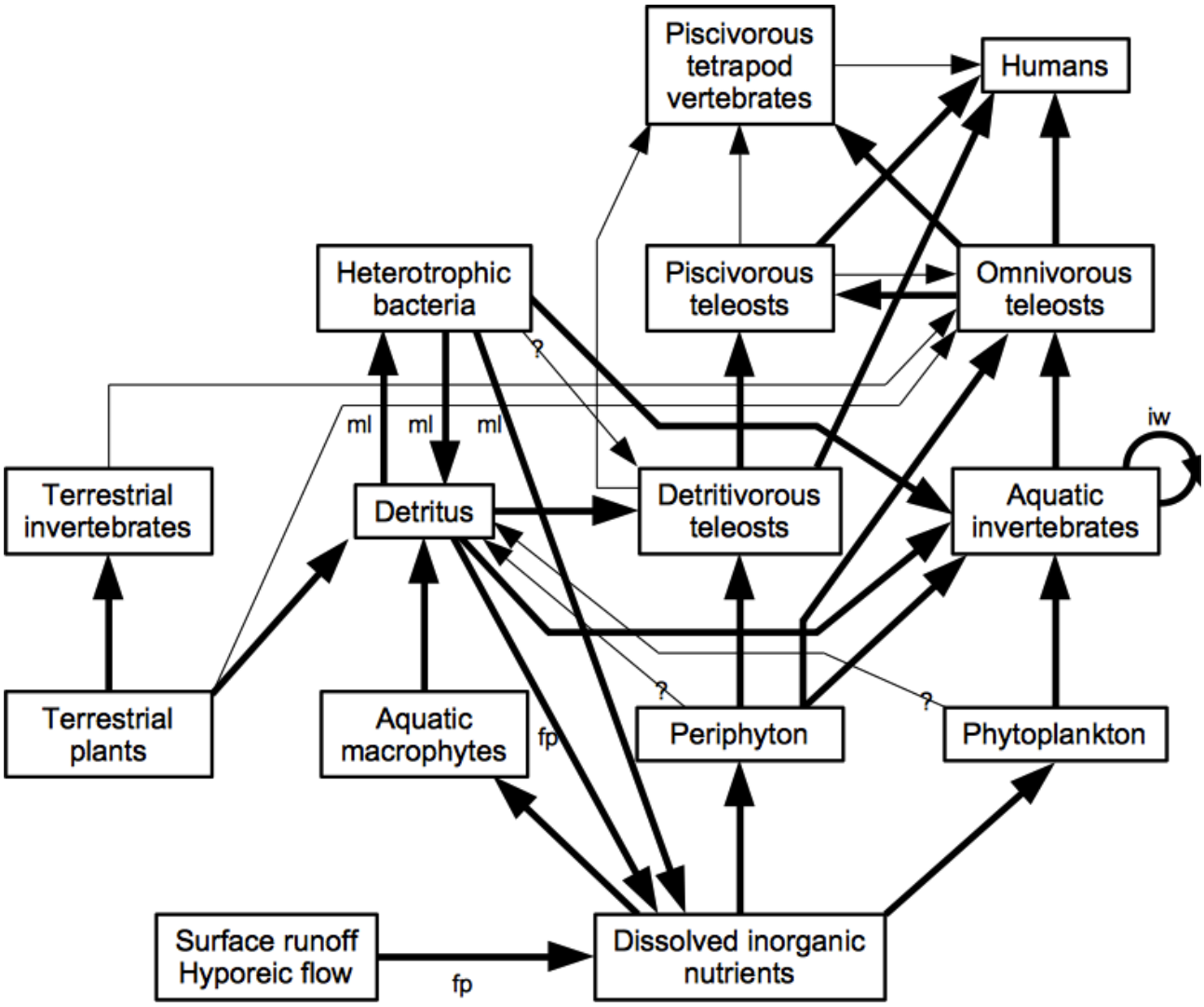

Fig. 1.1. Example of generalised food web in floodplain/river ecosystems showing interconnected food chains. Boxes are carbon sources and organism groups and vectors are consumer/resource interactions with thick arrows representing dominant pathways. Several organism groups constitute their own food web such as the invertebrates (iw: invertebrate food web) or the bacteria (ml: microbial loop path). Furthermore, carbon source availability may be improved by physical phenomenons (fp: nutrient pathways enhanced by flood pulses). ?: poorly quantified pathways. Figure adapted from Winemiller, 2004.

While ecology describes the various relationships between organisms and their environment and between organisms, trophic ecology refers more specifically to how heterotrophic organisms meet their energy requirements. Similarly, where the ecological niche describes the use of biotic and abiotic resources by individuals or species for their survival, the trophic niche is the component of the ecological niche which focuses on the use of these resources to meet their energy requirements. In both cases, the niches are models of the relationships between the organisms and their environment, which define a sustainability area for organisms and/or highlight the impacts of environmental factors on the organisms and *vice versa* (Pocheville, 2015).

Trophic ecology encompasses various parameters of an organism's biological traits in order to describe its feeding behaviour, and various concepts can be used to describe its trophic niche. Various parameters are used to estimate the ecological and/or trophic niche width of an organism or a species. They include the range of prey consumed by an organism, a population or a species, the evenness of prey components in the diet over time, the range of prey trophic levels and the foraging locations (Bearhop et al., 2004). These parameters and thus the ecological and trophic niche widths depend of both environmental factors and factors intrinsic to an organism. Examples of environmental factors include prey availability but also the presence of other organisms with similar trophic ecology. Indeed, in environments where organisms with redundant niches coexist, the interactions between these organisms may have variable results. A group of organisms may exploit a same resource without competing if the abundance of this resource is sufficient to provide the needs for all organisms (Costa-Pereira et al., 2019). However, as notably highlighted by the interactions between native and introduced organisms, organisms with similar ecology impact each other's niche if the abundance of this resource is limited. Some organisms may specialise on supplementary resources that are not, or less, used by the others (niche partitioning; Schoener, 1974; e.g. Mason et al., 2008; Juncos et al., 2015). They could also increase their niche width to continue to satisfy their energy requirements (optimal foraging; Stephen and Krebs, 1986; e.g. Svanbäck and Bolnick, 2007; Costa-Pereira et al., 2019), which would result in a reduction of competitive interactions between these organisms and the others. By contrast, in situations where all resources are exploited, competitive interactions will result in reduction of the niche width (niche partitioning; Schoener, 1974; e.g. Tran et al., 2015; Jackson et al., 2016; Costa-Pereira et al., 2019) or exclusion of several organisms from the food web (competitive exclusion; Hardin, 1960; e.g. Bøhn et al., 2008). Examples of intrinsic factors include morphological features (Motta, 1989; Wainwright, 1996; Cucherousset et al., 2011) and the foraging and feeding behaviours

(Beddingfield and McClintock, 1993; Pichegru et al., 2007), which determine if the food is efficiently acquired and consumed in order to cover the energy requirements. The resulting estimation of the ecological and trophic niche widths allows to classify organisms into specialists or generalists.

At the scale of species, uneven consumption of a restricted range of prey indicates that a species is a specialist species which thrives on a limited diet, and thus presumably on a narrow range of environmental conditions. Specialist species survive in mostly restricted (Charrette et al., 2006) and homogenous environments in space and time and are dependent on the availability and quality of their preferred food (Harvey and MacDougall, 2014; Curtis et al., 2015). They are vulnerable and less likely to recover from the fragmentation or the disturbance of their environment (Charrette et al., 2006; Devictor et al., 2008; Edwards et al., 2013).

By contrast, species known to feed on a wide range of prey and able to live in various environmental conditions are labelled as generalist species. These species benefit from more heterogenous environmental conditions and may display more trophic plasticity, i.e. a capacity to modify their diet and feeding behaviour, under spatially (Abbas et al., 2011; Gosch et al., 2019) and temporally (Kirkwood et al., 1997; McMeans et al., 2019) variable environmental conditions. As a result, they are less severely affected by the fragmentation or the disturbance of their habitat (Devictor et al., 2008; Abbas et al., 2011) and are thus prone to persist when facing variable or changing environmental conditions (Evans and Moustakas, 2018). However, some caution is necessary when labelling a species as generalist. Indeed, a generalist species would be a species whose individuals feed on a wide range of prey, but it is possible that individual variations within a species' diet occur, resulting in a generalist species made of specialist individuals and/or organism groups (Vander Zanden et al., 2010; Cucherousset et al., 2011; Powell and Taylor, 2017). Furthermore, ontogenetic changes of dietary habits, and thus of the trophic niche width, frequently occur during the life history of organisms in conjunction to ontogenetic changes of morphological features (Luczkovich et al., 1995; Scharf et al., 2000) or of habitat (Sánchez-Hernández et al., 2019).

1.1.2 Stable isotopes as a tool to investigate the trophic ecology of organisms

Stomach content analysis is a well-known and intuitive method to study the trophic ecology of organisms and provides a qualitative and quantitative view of the diet (Hyslop, 1980). Yet, this is only a snapshot of the diet, because prey found intact in stomachs were ingested recently. By

contrast, longer term analysis of the diet with stomach contents is harder to achieve because it is difficult to identify partially digested prey items. Consequently, a large number of samples is necessary to assess the trophic ecology of a group of organisms with this method. Conversely, it is easy to overestimate the contribution of organisms with hard body parts that are not digested. Finally, stomach content analyses do not provide information about effective assimilation of the ingested prey and several items found in stomach contents may actually not contribute to the energy requirements of the organism. As a result, using an alternative method to stomach content analysis is frequently necessary to assess the trophic ecology of organisms and/or the functioning of food webs.

Stable isotope analysis (SIA) is now a common tool for food web studies. It allows quantitative investigation of food webs and it provides longer term information on the diet of organisms than stomach content analyses. Furthermore, stable isotope ratios can be analysed in most organisms, including photosynthetic ones, and in any tissues, but also in organic particles in water and sediment, and thus provide information on the baseline items of food webs. Stable isotope ratios are analysed with mass spectrometry and are expressed in δ notation and in ‰ relative to international references.

The investigation of trophic ecology with the SIA method works on the principle that there is a relationship between the stable isotope ratios in the tissues of an organism and those of its diet as it is assimilated (DeNiro and Epstein, 1978; 1981). As a result, the combination of the stable isotope ratios of the various food items assimilated by an organisms produces, as the weighted average, the stable isotope ratios in the tissues of this organism. However, stable isotope composition in the organism is generally a little different than this weighted average as isotopic fractionation (i.e. small change in isotopic composition) occurs during the multiple chemical and physical processes link to animal metabolism (DeNiro and Epstein, 1978; Vander Zanden and Rasmussen, 2001; Mill et al., 2007). The combination of these two phenomenons could be summarised into the famous quote “you are what you eat, plus a few per mil” (DeNiro and Epstein, 1976). Consequently, the common conception about stable isotopes is that the proportion of heavy isotopes increase for each trophic level, although the extent of this increase is subject to variation (Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003; Caut et al., 2009; Wyatt et al., 2010). This increase is referred as trophic fractionation. Stable isotopes of carbon and nitrogen are the most frequently investigated in trophic ecology studies. Carbon isotopic compositions (^{13}C:^{12}C; $\delta^{13}C$) are generally used to determine the origin of primary sources of carbon in food webs or feeding areas because of the

differences of stable isotope composition between the different types of primary producers (i.e. phytoplankton, phytobenthos, terrestrial organic matter…) and of the low ^{13}C enrichment in organisms relative to their diet (DeNiro and Epstein, 1978; France, 1995; Hobson, 1999; Michener and Kauffman, 2007). For example, a typical pattern in the Southern Ocean is that $\delta^{13}C$ is usually low in phytoplankton and much higher in sea ice materials (Rau et al., 1991a; Leventer, 2003; Mincks et al., 2008; Wing et al., 2018). Nitrogen isotopic compositions (^{15}N:^{14}N; $\delta^{15}N$) are used to assess nitrogen sources and to estimate the trophic position of consumers, as organisms are generally more enriched in ^{15}N relative to their diet, resulting in sharper increase of $\delta^{15}N$ values with trophic level than of $\delta^{13}C$ values (DeNiro and Epstein, 1981; Michener and Kauffman, 2007). Stable isotopes of sulfur are also investigated to study the trophic ecology of organisms, although to a lesser extent than carbon and nitrogen. Similarly to $\delta^{13}C$ values, sulfur isotopic compositions (^{34}S:^{32}S; $\delta^{34}S$) are used in studies on marine food webs to refine the discrimination between primary producers or between benthic and pelagic sources, thanks to the differences of $\delta^{34}S$ values between seawater sulfates, sediment porewater sulfates and sediment sulfides (Fry et al., 1982; Machás and Santos, 1999; Connolly et al., 2004).

The increasing use of SIA also led to the development of ecological metrics and models to ease the interpretation of data. The metrics measure the differences of stable isotope values between individuals or organism groups and thus provide informations on the isotopic and thus trophic diversity. Some metrics are preferentially used to investigate the isotopic diversity within a community or an organism assemblage (Layman et al., 2007; Cucherousset and Villéger, 2015) while other metrics are mostly used to assess the isotopic diversity between individuals of a same group of organisms (Jackson et al., 2011; Reid et al., 2016). SIA also allows both quantitative and qualitative investigations of the diet of organisms, as well as reconstructing the trophic pathways within communities or assemblages, thanks to the development of mixing models that assess the relative contribution of prey or carbon sources to the diet of organisms when SIA are done on various organism groups in a same community (Parnell et al., 2010; 2013). Finally, comparison of the stable isotope values of an organism with those of the basal carbon sources allow trophic level estimation (Quezada-Romegialli et al., 2018). All these approaches provide different information on the trophic ecology of organisms or on the food web functioning and ultimately contribute to the estimation of the trophic and ecological niche widths of organisms. The diversity of these approaches also demonstrates the usefulness of SIA in studying ecosystem functioning.

1.2 The Southern Ocean: oceanography and biology

The Southern Ocean, a.k.a Antarctic Ocean or Austral Ocean, is the oceanic region surrounding the whole Antarctic continent, the coldest landmass on earth. Indeed, while the Arctic Ocean may be considered as an ocean surrounded by continents, its polar opposite, the Antarctic, may be considered as a continent surrounded by the ocean. These features result in peculiar oceanographic conditions.

1.2.1 Physical oceanography and regionalisation of the Southern Ocean

The Southern Ocean is the continuation of the deep Atlantic, Pacific and Indian Oceans basins. The continental shelf of the Antarctic itself is unusually deep as a result of continuous glacial erosion (Post et al., 2014).

The Southern Ocean lacks any major continental barriers from west to east. As a result, it is encompassed by the Antarctic Circumpolar Current (ACC), a strong eastward current, itself forced by strong cyclonic eastward winds that do not encounter any continental obstacle either. This current effectively isolates the Southern Ocean cold water masses from the northern warmer ones. The ACC itself can be divided into boundaries that separate regions with distinct water mass properties. Those borders are called fronts. While the lack of continental barrier allows the ACC to flow continuously eastward, the pathway of these fronts is nevertheless influenced by topographic constraints, with diversions in the flow occurring around continental shelves of islands of the Southern Ocean and, to a lesser extent, the mid-ocean ridges in the Pacific and Indian Oceans. Similarly, westward katabatic winds originating from the Antarctic continent result in the generation of the Antarctic Coastal Current (ACoC), which encompasses the continent and is bordered by the Antarctic Slope Front (Baines, 2006).

Sea ice is another major component of the Southern Ocean with the sea ice zone reaching the southern front bordering the ACC in winter, and sea ice still having perennial presence during summer in several areas (Post et al., 2014). While sea ice in the Arctic Ocean is multi-year, sea ice of the Southern Ocean is mostly a seasonal phenomenon (Dieckmann and Hellmer, 2003). Sea ice in the Southern Ocean can be classified into two major types. Pack ice refers to the ice moving across the oceanic regions. It is usually characterised by low mean thickness and an annual presence but perennial pack ice with high thickness also exists, such as in the Weddell Sea (Worby et al., 2008). Fast ice is sea ice that is locked to the coast, to the sea floor or to grounded icebergs. On the Antarctic continent-Southern Ocean interface, sea ice can be driven away from the coast in areas

where strong katabatic winds occur, leaving open water that produces new ice which is itself driven away from the coast. As a result, these areas, named polynyas, always contain open water surrounded by sea ice (Williams et al., 2007).

The Southern Ocean can be divided into separate regions with distinct environmental properties. Raymond (2014) classified 20 regional clusters according to three main properties: the sea surface temperature (SST), the depth, and the sea ice season duration. The results of this study showed a latitudinal regionalisation of the open ocean areas, consistent with the oceanic fronts (Fig. 1.2). According to this classification, the Southern Ocean contains a continental shelf surrounded by continuously deep waters occasionally interrupted by continental shelves of islands located within the ACC. The general characteristics of the Southern Ocean also include a North-South gradient of SST decrease throughout the waters included within the ACC and a North-South gradient of sea ice cover below the southern border of the ACC.

1.2.2 Southern Ocean biology

1.2.2.1 Pelagic ecosystems

The Southern Ocean is mostly an oligotrophic ocean with a patchy distribution of phytoplankton blooms (Sullivan et al., 1993) despite high concentrations of nutrients (Levitus et al., 1993), making it a High Nutrient, Low Chlorophyll (HNLC) ocean. In open water and water masses included in the ACC, low primary production and a phytoplankton community dominated by picoplankton is usually observed (e.g. Ehnert and McRoy, 2007; Arrigo et al., 2008; Shramik et al., 2013) although local diatom blooms regularly occur around South Georgia (Borrione and Schlitzer, 2013), Kerguelen (Mongin et al., 2008) and Crozet archipelagos (Seeyave et al., 2007). Similarly, on the Antarctic continental shelf, sea ice and terrestrial glacier melting induces blooms of large diatoms in the early summer (Dierssen et al., 2002; Garibotti et al., 2005; Rozema et al., 2017). Otherwise, the lack of sea ice during winter (Montes-Hugo et al., 2009; Rozema et al., 2017), or the lack of sea ice melting during summer (Mendes et al., 2013), result in lower chlorophyll concentration and a phytoplankton community dominated by smaller photosynthetic organisms such as cryptophytes (Garibotti et al., 2005; Mendes et al., 2013; Rozema et al., 2017). Low iron levels and minimal inputs by melting sea ice in HNLC waters (Honjo et al., 2000; Leventer, 2003) and high local iron inputs originating from islands and melting of both terrestrial and sea ice on the Subantarctic and Antarctic continental shelves are currently the main hypotheses to explain this pattern (Martin et al., 1990; Sedwick and DiTullio, 1997; Death et al., 2014; Robinson et al., 2016).

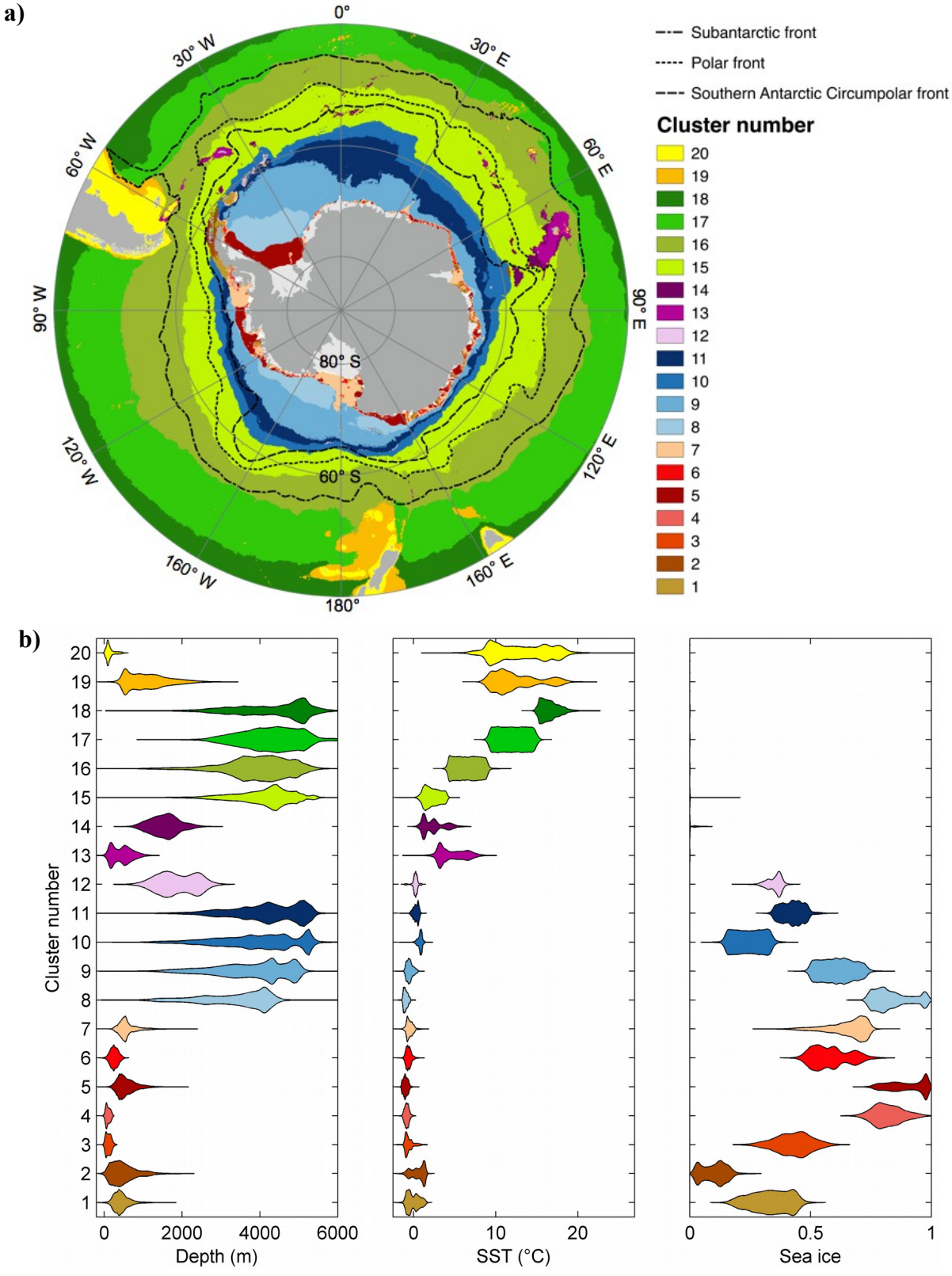

Fig 1.2. a) Pelagic regionalisation of the Southern Ocean with lines being oceanic fronts and each colour being a cluster with distinct water mass properties. b) Depth, summer sea surface temperature (SST) and sea ice season duration (proportion of time for which at least 85 % of the ocean is covered by sea ice) in each cluster. Figures adapted from Raymond, 2014.

Two other factors may explain the impact of sea ice melting on primary production in the sea ice zone and on the continental shelf. First, stratification induced by freshwater inputs decreases the mixed layer depth (Smith and Nelson, 1985). Second, release of ice-associated photosynthetic organisms may serve as a "seeding" for the phytoplankton bloom associated with sea ice melting (Smith and Nelson, 1985; Lizotte, 2001). Indeed, sea ice itself is also a habitat for specific microbial communities, including photosynthetic organisms (i.e. sympagic communities; Arrigo, 2017). These communities are vertically distributed along the sea ice thickness (Horner et al., 1992; Arrigo and Thomas, 2004; Arrigo, 2017). Higher biomass is present in fast ice than in pack ice (Archer et al., 1996), with peak of biomass at the surface during fast ice formation and at the bottom before sea ice breakup (Fiala et al., 2006). In pack ice, higher biomasses were reported at the surface (Garrison and Buck, 1989; Archer et al., 1996). Diatoms are usually the dominant autotrophic taxon in sea ice (Garrison and Buck, 1989; Archer et al., 1996; Fiala et al., 2006). Nevertheless, the importance of this factor for the summer phytoplankton bloom is variable. Indeed, the "seeding" of the summer phytoplankton bloom is more likely induced by the marginal ice zone communities (Lizotte, 2001) while fast ice communities are unlikely to "seed" the bloom (McMinn, 1996; Riaux-Gobin et al., 2003). Contribution of the sea ice photosynthetic community to the whole Southern Ocean primary production is low (1-3 %; Arrigo and Thomas, 2004; Arrigo, 2017). However, the production is locally concentrated, and thus constitutes an important source of matter for higher trophic levels in the sea ice zone (Brierley and Thomas, 2002; Leventer, 2003; Kohlbach et al., 2017; 2019).

Anyway, summer phytoplankton blooms associated with sea ice melting are of considerable importance for the Antarctic pelagic food web functioning. Indeed, the seasonally abundant Antarctic krill *Euphausia superba* is an important diatom consumer (Haberman et al., 2003; Kohlbach et al., 2019) and is thus frequently associated with sea ice melting areas (Loeb et al., 1997; Nicol et al., 2000). As a result, krill predators (baleen whales, sea birds) are also associated with sea ice melting areas as they provide a feeding ground (Nicol et al., 2000).

1.2.2.2 Benthic ecosystems and their relationships with the surface primary production

The benthic ecosystem of the Southern Ocean is atypical when compared to other ecosystems. Its current composition can be considered as the result of evolutionary processes. Indeed, climatological and oceanographic changes (e.g. sea water cooling, glaciation) during the Cenozoic era resulted in both extinction of several taxa and functional groups, and evolutive radiations of others (Clarke et al., 2004). In particular, durophagous predators were eliminated from the Southern

Ocean benthos, allowing the development of an important suspension feeding community (Clarke et al., 2004; Aronson et al., 2009).

Parameters influencing the structure of benthic communities include the type of bottom, ice dynamics and the depth. Benthic ecosystems from the Antarctic continental shelf can be roughly separated into two types of communities according to the type of bottom (Gutt and Starmans, 1998; Gutt, 2007). The first ones are dominated by deposit feeders living on or within muddy sediments (Gerdes et al., 1992; Arnaud et al., 1998; Barry et al., 2003; Gutt, 2007). Examples of important taxa associated with these communities include echinoderms and polychaetes (Gerdes et al., 1992; Gutt and Starmans, 1998). These communities are supported by particle fluxes from the surface, and in particular particles derived from the summer phytoplankton bloom that sink fast, and thus are usually associated with areas of low current speed (Gutt et al., 1998; Mincks et al., 2008) although some were observed in waters with strong current (Gerdes et al., 1992). The second community types are dominated by sessile suspension feeders (Barry et al., 2003; Gutt, 2007). Important suspension feeder taxa include sponges, hydrozoans, ascidians and bryozoans (Arnaud et al., 1998; Gutt and Starmans, 1998; Barry et al., 2003). These types of communities are associated with hard or coarse sediment bottoms (Barry et al., 2003), although they can also appear on muddy bottoms (Arnaud et al., 1998). The heterogenous nature of the sediments associated with this type of communities indicates that they are also associated with zones of strong bottom current, suggesting that these communities are mostly supported by the resuspension of sediment in the water column (Arnaud et al., 1998; Gili et al., 2001; Barry et al., 2003; Isla et al., 2006; Gutt, 2007). An alternative hypothesis on the functioning of these communities is that they rely on small and slowly sinking particles from the surface (Mintenbeck et al., 2007).

Ice dynamics also impacts benthic community structure. On the one hand, iceberg scouring, i.e. events when the keel of floating ice is coming into contact with the seabed, has considerable impact on benthic communities. The frequency of iceberg scouring is linked to the duration of the fast ice season, with more iceberg scouring events occurring during shorter fast ice seasons (Smale et al., 2007a, Barnes and Souster, 2011) as iceberg are retained by fast ice during winter but released during summer. Iceberg scouring may occur up to a depth of 600 m (Dowdeswell and Bamber, 2007) but its frequency tends to decrease with depth in shallow environments (Smale et al., 2007a). Iceberg scouring is a significant source of mortality for benthic organisms (Barnes and Souster, 2011) and induces significant reduction of abundance, biomass and diversity at local scales (Peck et al., 1999; Gerdes et al., 2003; Smale et al., 2007b; 2008). However, sites impacted by iceberg

scouring are progressively recolonised (Peck et al., 1999; Smale et al., 2008) and species that are usually excluded from undisturbed sites may develop more successfully in the recolonisation stages (Gutt and Piepenburg, 2003). Consequently, while iceberg scouring is a source of reduced species richness at local scale, it is a source of higher species richness at regional scale (Smale and Barnes, 2008). On the other hand, the dynamic of terrestrial glaciers, including glaciers terminating on land and tidewater glaciers, i.e. glaciers terminating in the sea, may also locally impact shallow water communities through its influence on sedimentation rates. Indeed, terrestrial ice run-off provided by melting tidewater glaciers may provide important quantities of terrestrial inorganic matter to the adjacent waters, resulting in spatial gradients of turbidity (Pęcherzewski et al., 1980; Isla et al., 2001; Khim et al., 2007). Turbidity is a chronic disturbance for aquatic organisms as elevated particle concentration may reduce primary production by restricting light transmission or directly affect aquatic organisms respiration, feeding, growth and reproduction (Wilber and Clarke, 2001; Thrush et al., 2004; Donohue and Garcia Molinos, 2009; Bell et al., 2015). More turbid areas can give rise to more limited benthic diversity, as notably observed in South Shetland Island fjords (Pabis et al., 2011; Pasotti et al., 2015a; Sahade et al., 2015), while more limited terrestrial inputs in other Antarctic fjords from the Western Antarctic Peninsula (WAP; Eidam et al., 2019) may explain the higher diversity recorded in these areas (Grange and Smith, 2013).

Eurybathy, i.e. the ability to live at a wide range of depth, is a common feature of Antarctic benthic organisms (Brey et al., 1996). However, depth may be an important factor in structuring benthic communities. Indeed, the communities dominated by suspension feeders are more prevalent in shallower waters while the communities dominated by deposit feeders characterise the deeper waters (Barry et al., 2003). Similarly, changes in species composition and diversity with depth occur within taxa (Brandt et al., 2009; Barnes and Kuklinski, 2010; Moles et al., 2015; Neal et al., 2018). Variation of the intensity of physical processes with depth may shape the depth zonation of benthic communities. For example, phytobenthos would not grow beyond the euphotic zone. Similarly, lower current speed in deeper areas would prevent the development of suspension feeders relying on resuspended sediment and explain the prevalence of deposit feeders in deeper areas (Barry et al., 2003). Finally, deeper zones would not be impacted by the disturbances occurring in shallower zones such as iceberg scouring.

As a result of the various environmental parameters influencing them, benthic ecosystems are spatially heterogenous. Similarly to Raymond (2014), Douglass et al. (2014b; 2014c) classified benthic ecoregions according to their depth, the seabed temperature and the sea ice season duration.

However, biotic parameters were also used in this classification such as the surface chlorophyll a concentration or the spatial and bathymetric distribution of benthic organisms. As a result, Douglass et al. (2014b; 2014c) identified 23 benthic ecoregions (Fig. 1.3). Furthermore, 9 bathomes, i.e. depth classes whose boundaries are defined by rapid transitions in the species composition, and 28 geomorphic features, i.e. a classification of the seabed according its surface morphology, were identified. By combing the ecoregion, the bathomes and the geomorphic features, 562 unique types of benthic environments were identified in the Southern Ocean.

Benthic communities appear to be supported, through benthic-pelagic coupling, by particulate organic matter originating from the surface layers. Various components constitute the surface particles exported to the bottom (see Turner, 2015 for a review) but they mostly include phytoplankton detritus and zooplankton faecal pellets. Export of oceanic surface production to the bottom is generally low worldwide (< 5-10 %) but can be higher than 10 % in polar waters (Buesseler, 1998). The importance of particle fluxes in the Southern Ocean is seasonally driven with highest fluxes in the austral summer, when sea ice concentration is low and primary production is high, and minimal fluxes in the winter, when sea ice concentrations are the highest (Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015). Furthermore, summer particle fluxes are southernly delayed in relation with the receding sea ice edge (Honjo et al., 2000). Diatom phytodetritus from the phytoplankton blooms are the main components of the particles exported to the bottom during summer (Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015) while zooplankton dominates particle fluxes during winter (Kim et al., 2015). It should also be noted that lithogenic fluxes in the open Southern Ocean are low, further highlighting iron limitation in HNLC waters (Honjo et al., 2000). Sea ice may also be an important contributor to the particle fluxes to the benthic ecosystems of the Southern Ocean, with sea ice materials being exported to the sea floor (Abelmann and Gersonde, 1991; Kim et al., 2019). However, most of the sea ice materials are likely exported as faecal pellets (Thomas et al., 2001; Leventer, 2003), although they may also be exported as cell aggregates (Riebesell et al., 1991) like in the Arctic Ocean (Leventer, 2003).

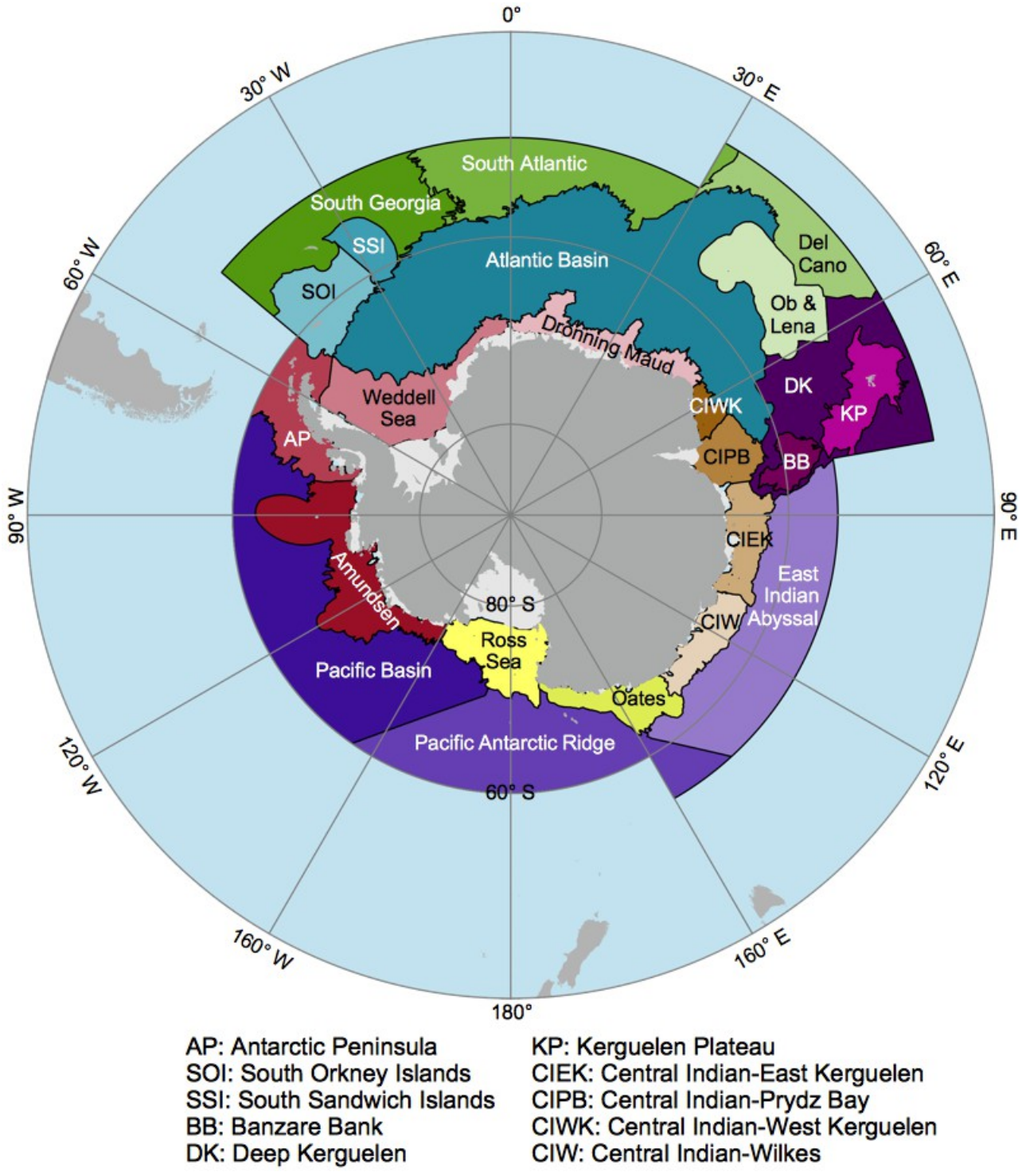

Fig. 1.3. Benthic ecoregions identified within the Southern Ocean by Douglass et al. (2014b; 2014c).

Knowing that sea ice melting, phytoplankton blooms and subsequent particle fluxes in Antarctic are seasonally driven, strong particle fluxes from the surface are discrete events and thus, reliance on surface production may suggest increased activity in the benthic communities during a summer bloom but limited activity or starvation during winter, especially for the deposit feeder communities. Yet, seasonality in the deposit feeder communities appeared to be muted with no increase of abundance after phytoplankton bloom (Veit-Köhler et al., 2011) or no seasonal changes of feeding rates occurring (Smith et al., 2012). Actually, an important part of the sinking particles accumulate on the sea floor where they are poorly degraded by microbial activity thanks to low temperature. As a result, they provide an abundant food source for the communities over longer periods. This abundant food source could thus be considered as a "food bank" for the benthic communities (Smith et al., 2012). Similarly, relatively constant resuspension of particles supports the suspension feeder communities throughout the year (Isla et al., 2006). In Coastal Antarctic, the separation between deposit and suspension feeder communities also occurs. Indeed, several organisms from these communities are still supported by pelagic production (Zenteno et al., 2019) and detritus (Dunton, 2001). However, other carbon sources also contribute to the benthos functioning such as micro (Gillies et al., 2012) and macrophytobenthos (Dunton, 2001; Gillies et al., 2012; Zenteno et al., 2019). The sea ice microbial community can also be an important carbon source if sea ice persists over time (Wing et al., 2012; 2018; Michel et al., 2019; Rossi et al., 2019). Furthermore, although the food sources are consumed by specific feeding guilds, higher trophic level organisms are feeding on a mix of those feeding guilds (Gillies et al., 2012; 2013) and thus further reduce the separation between food chains in Antarctic coastal areas.

1.3 Climate change in Southern Ocean

1.3.1 Physical phenomenons

The Southern Ocean is affected by the current global climate change, with increasing air and ocean temperatures occurring in the area (Gille, 2002; Chapman and Walsh, 2007; Zhang, 2007). However, the impacts of climate change differ between areas, as highlighted by the variations of the evolution of air temperature (Chapman and Walsh, 2007), sea ice extent, and ice season duration among Antarctic regions (Stammerjohn et al., 2008b).

In the WAP, i.e. the Amundsen and Bellingshausen seas, mean atmospheric temperatures have increased by 2.5-3°C since the 1950s (Chapman and Walsh, 2007), making of WAP one of the most rapidly warming regions in the world. Furthermore, an increase of water temperature occurred in

the last 50 years (Meredith and King, 2005; Schmidtko et al., 2014) and sea ice extent is decreasing (Stammerjohn et al., 2008a). The increase of water temperature is surface intensified, with a 1°C increase in surface waters of several areas (Meredith and King, 2005). Ice season duration in WAP is also becoming shorter, with later sea ice advance during the autumn and, to a lesser extent, earlier sea ice retreat during spring (Stammerjohn et al., 2008a). Increased northwesterly winds originating from the also warming subtropical Pacific during the autumn have been proposed as causes of the rapid surface temperature increase and sea-ice extent decrease in this region. These winds bring warmer temperatures that melt sea ice and displace sea ice towards the WAP coasts (Orr et al., 2004; Stammerjohn et al., 2008a; Ding and Steig, 2013, Fig. 1.4.a). Furthermore, the largest anomalies towards a shorter ice season appeared to occur during La Niña and/or positive Southern Annular Mode events, which both generate persistent northerly winds over the region (Stammerjohn et al., 2008a).

While being intensified at the surface, the increase of water temperatures also occurs in deep waters of the WAP continental shelf because of increasing temperatures of waters surrounding the Antarctic shelf (Gille, 2002; Schmidtko et al., 2014). Indeed, the deep water of the Antarctic shelf contains water originating from circumpolar deep water, which is also subject to warming. Cyclonic wind patterns are present over the Amundsen and Bellingshausen seas, but with the low-pressure centre being on the continental shelf. As a result, the lack of easterly winds and the sufficiently weak westerly winds over the shelf break allow warmer deep waters from circumpolar origin to rise up to the shelf break, giving it access to the continental shelf where it may enhance basal melt of ice shelves (Schmidtko et al., 2014, Fig. 1.4.a).

In the rest of the Southern ocean, air temperatures also increased since the 1950s, although at a lower rate than in WAP (Chapman and Walsh, 2007; Zhang, 2007). However, increasing sea ice cover and ice season duration were observed in these regions (Stammerjohn et al., 2008b; Parkinson and Cavalieri, 2012). A first factor to explain this apparently paradoxical phenomenon is that the ozone depletion in the stratosphere contributed to the strengthening of the circumpolar cyclonic westerly winds (Thompson and Solomon, 2002; Gillett and Thompson, 2003). The wind then contributes to increase sea ice export from ice producing areas where more sea ice is then produced (Zhang, 2007; Turner et al., 2009). A second factor is the ocean stratification and the prevention of oceanic upward heat transport, either because of a freshening of surface water due to both sea ice and continental ice sheets melting (Zhang, 2007; Britanja et al., 2013), or because of cyclonic wind generating strong easterly winds over the shelf break in Ross and Weddell gyres (Schmidtko et al.,

2014, Fig. 1.4.b). Finally, increasing precipitations may be a supplementary contributor to the increasing of sea ice extent by further freshening surface waters (Zhang, 2007).

It should be noted that variations of sea ice extent are not a linear phenomenon, as highlighted by the recent and sharp increase of sea ice extent in the WAP and the recent and sharp decrease of sea ice extent in areas usually characterised by increasing sea ice extent (Parkinson, 2019).

The ocean acidification phenomenon also occur in the Southern Ocean. The increasing carbon dioxide (CO_2) atmospheric levels from anthropogenic origin induce a higher CO_2 uptake in water, particularly in the polar oceans because cold temperatures enhance gas solubility (DeJong et al., 2015; Negrete-García et al., 2019). As CO_2 uptakes increase, the successive chemical reactions induced by its dissolution induce a pH decrease by producing hydrogen (H^+) and carbonate ions (CO_3^{2-}, Feely et al., 2009). However, H^+ react with CO_3^{2-} to produce HCO_3^-, leading to a reduction of CO_3^{2-} concentration. The dissolution of CO_2 also occurs by its reaction with the calcium carbonate ($CaCO_3$) present in water (Feely et al., 2004; 2009; Orr et al., 2005; Jiang et al., 2015) and in organisms' calcified skeletal structures (Feely et al., 2004). As a result of these reactions, pH, CO_3^{2-} concentration, and the saturation state of $CaCO_3$ in the global ocean are thus decreasing (Feely et al., 2009; Orr et al., 2005; Jiang et al., 2015), especially in the Southern Ocean, because of the higher uptake of CO_2 in cold waters, of the upwelling bringing carbon rich waters to the surface (Orr et al., 2005; Negrete-García et al., 2019), and of the already low saturation state in these regions (Orr et al., 2005; DeJong et al., 2015; Jiang et al., 2015).

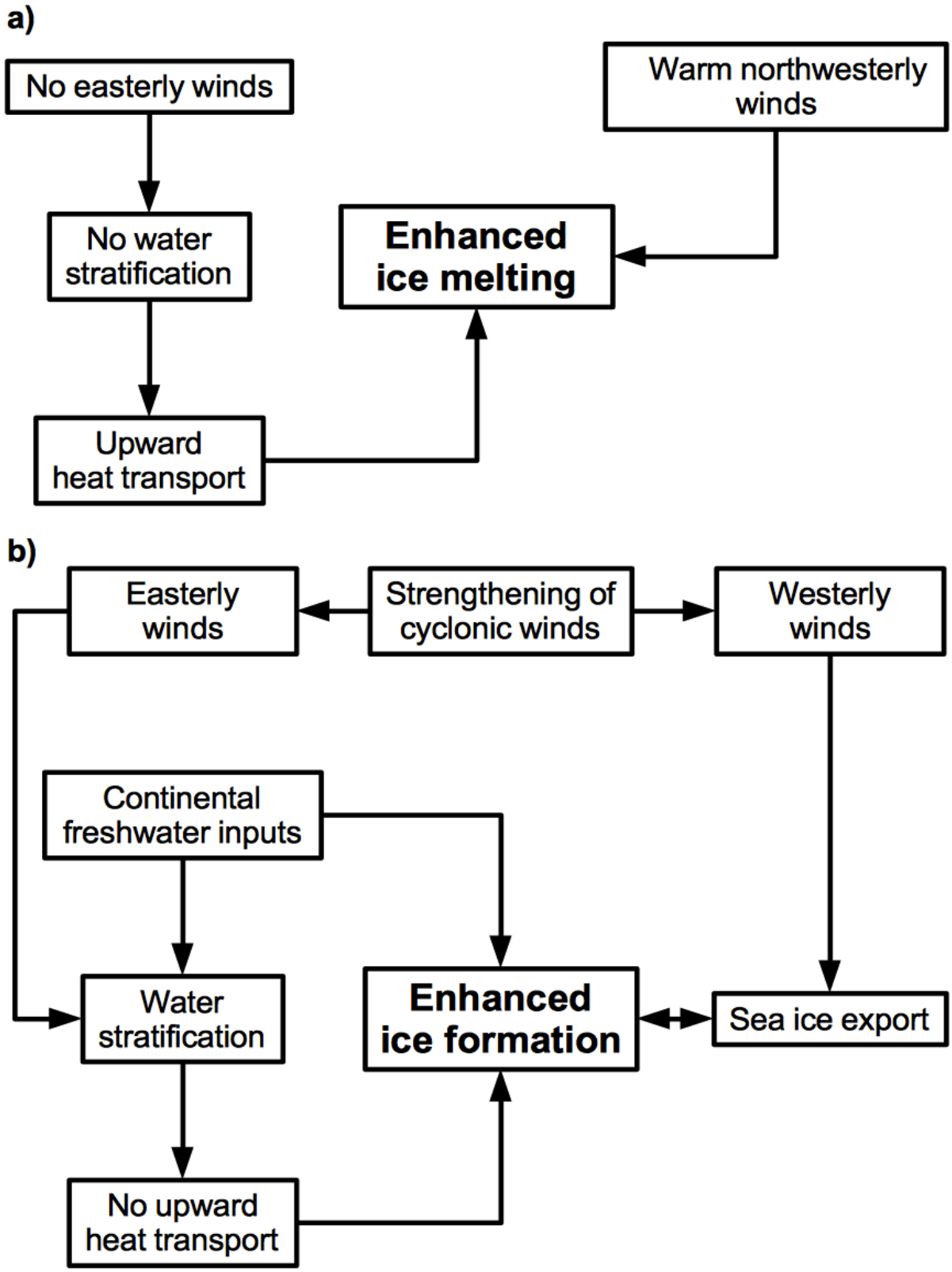

Fig. 1.4. Schematic summary of the mechanisms inducing a) the reduction (Orr et al., 2004; Stammerjohn et al., 2008a; Ding and Steig, 2013; Schmidtko et al., 2014) and b) the extension (Thompson and Solomon, 2002; Gillett and Thompson, 2003; Zhang, 2007; Turner et al., 2009; Britanja et al., 2013; Schmidtko et al., 2014) of the sea ice cover in Antarctic.

1.3.2 Impacts of climate change on the Southern Ocean biota

The modifications of sea ice cover in the Southern Ocean will have an impact on communities. For example, in pelagic ecosystems, sea ice has an indirect influence on the dynamic of summer phytoplankton communities, as its melting may influence oceanic stratification (i.e. vertical differentiation of water masses) that impacts the Southern Ocean phytoplankton community succession (Garibotti et al., 2005; Rozema et al., 2017; Schofield et al., 2017). As previously explained, sea ice retreat induces blooms of large diatoms in the early summer (Garibotti et al., 2005; Rozema et al., 2017) and the lack of sea ice during winter (Montes-Hugo et al., 2009; Rozema et al., 2017), or the lack of sea ice melting during summer (Mendes et al., 2013), may result in less important diatom blooms and/or lower chlorophyll concentrations in summer. Otherwise, when diatom blooms do not occur (Mendes et al., 2013; Rozema et al., 2017) or are over (Garibotti et al., 2005), the phytoplankton community is dominated by smaller photosynthetic organisms such as cryptophytes. The taxonomic composition of the phytoplankton community thus influences the consumer composition, with krill (and thus its predators) thriving in regions where sea ice presence is sufficient to induce the bloom of diatoms they consume (Haberman et al., 2003), and salps dominating regions where sea ice is absent as no diatom blooms occur (Loeb et al., 1997; Nicol et al., 2000). Higher trophic levels will then be affected by the primary consumer composition, with baleen whale populations likely being negatively affected by the reduction of krill populations in case of sea ice retreat (Braithwaite et al., 2015; Tulloch et al., 2019).

Benthic communities of the Southern Ocean will also be affected by climate change (Ingels et al., 2012). In particular, changes in the food web functioning have to be expected. Indeed, as the sinking pelagic phytoplankton is one of the main basal food sources for the benthic food webs (Mincks et al., 2008; Smith et al., 2012), the changes currently observed in phytoplankton communities will likely impact the benthic communities in the long term, even if the “food banks” may temporary delay this change. Yet, degradation rates of the “food banks” themselves may also increase as a result of the increasing temperatures of the Southern Ocean bottom waters that may enhance bacterial degradation rates (Arnotsi et al., 1998; Smith et al., 2012). Furthermore, particles derived from the sea ice microbial community may also be an important source of carbon for benthic communities (Norkko et al., 2007; Wing et al., 2012; 2018). Finally, reduction of fast ice season duration may induce more frequent iceberg scouring events (Smale et al., 2007a; Barnes and Souster, 2011) that would lead to immediate reduction of diversity, abundance and biomass of the benthos in the impacted sites (Peck et al., 1999; Gerdes et al., 2003; Smale et al., 2007b; 2008).

Conversely, while most of the studies focus on the ecological consequences of the loss of sea ice, recent results show that sea ice persistence in some regions may also impact coastal benthic communities by reducing light transmission to the bottom, resulting in decline of phytobenthos and transition to invertebrate-dominated communities (Clark et al., 2015) or by inducing trophic shifts in the communities, with benthic consumers relying less on predation and/or scavenging and feeding more directly on sympagic organic materials as high quantities become available (Michel et al., 2019).

Sea ice cover modification is not the only phenomenon induced by climate change that may impact benthic communities. Similarly to sea ice, recession of terrestrial ice sheet and tidewater glaciers will also impact communities of the Southern Ocean. Indeed, loss of terrestrial ice sheet may initially cause increases of iceberg scouring (Pasotti et al., 2015a; Sahade et al., 2015) but also of freshwater and terresrtial inputs in the ocean (Dierssen et al., 2002). Higher terrestrial inputs would induce higher turbidity in coastal areas (Boldt et al., 2013; Sahade et al., 2015; Munoz and Wellner, 2016). The increased freshwater inputs would contribute to summer phytoplankton blooms (Dierssen et al., 2002) but the increased turbidity will have strong impacts on the coastal benthos, and thus on the food web functioning (Pasotti et al., 2015a; 2015b; Sahade et al., 2015). Conversely, recession of tidewater glaciers may open new areas for colonisation for benthic organisms (Pasotti et al., 2015a).

Higher ocean temperatures will also directly affect organisms' survival (Peck et al., 2004; 2009; 2010). Similarly, the effects of ocean acidification have been investigated in various marine organisms and include enhanced or reduced growth rates and photosynthesis, reduced survival and altered larval development (Kroeker et al., 2013). In particular, reduction of calcification rates occur in organisms with calcified skeletal structures (e.g. mollusks and corals; Kroeker et al., 2013) as waters with a low saturation state induce dissolution of $CaCO_3$ (Jiang et al., 2015) and mollusk specimens with dissolved shells have been observed in the Southern Ocean (Bednaržek et al., 2012). Conversely, higher ocean temperatures will ease the arrival of exotic species (Aronson et al., 2009). In particular, litholid crabs, i.e. durophagous predators, were observed in the waters of the WAP (Thatje et al., 2008; Aronson et al., 2015), indicating that exotic functional groups such as durophagous predators that were previously excluded from the Southern Ocean are returning in the region. The arrival of those exotic organisms will likely increase both predation and competition pressure on native organisms.

However, these effects are taxon-specific, as shown by the examples of active organisms

surviving to higher temperatures than sessile organisms (Peck et al., 2009) or the lack of significant effects of acidification on the calcification rates of echinoderms and crustaceans contrary to mollusks and corals (Kroeker et al., 2013). They may also depend of the development stage of the organisms, as shown by by the better tolerance of juvenile organisms than adult to temperature changes (Peck et al., 2009; 2013) or the higher sensitivity to ocean acidification in mollusk and/or echinoderm larval stages than in adults (Kroeker et al., 2013).

The combination of all these phenomena and their impacts will likely impact the structure of the benthic food webs of the Southern Ocean.

1.4 Antarctic asteroids

Echinoderms are an important group of the Southern Ocean benthos. 624 species were recorded in the Southern Ocean, i.e. around 8 % of all known echinoderm species (De Broyer et al., 2019). They are important contributors to the abundance and biomass of the Southern Ocean benthos and were reported as the dominant benthic taxon in some areas (e.g. Gerdes et al., 1992; Piepenburg et al., 2002; Linse et al., 2013). Among echinoderms, sea stars (Fig. 1.5), or asteroids, are a key group of the Southern Ocean benthos. Indeed, 235 species, i.e. around 12 % of the known sea star species, are living in the Southern Ocean (Danis et al., 2014).

Worldwide, sea stars play a key role in ecosystem functioning. The term “keystone predator” was actually first coined for the species *Pisaster ochraceus* (Paine, 1969), after experiments showed that its absence led to significant decreases in intertidal biodiversity (Paine, 1966) and their decline (Schultz et al., 2016) or their outbreak (Kayal et al., 2012) may lead to trophic cascades. Sea stars are usually considered as generalist predators and facultative scavengers. However, some levels of trophic specialisation exist in this group (Jangoux, 1982). For example, three trophic groups were reported in sea star assemblages from the deep Northern Atlantic (Howell et al., 2003; Gale et al., 2013): predators/scavengers, mud ingesters/infaunal predators and suspensivores. Furthermore, the trophic ecology of sea stars may be influenced by environmental parameters and habitat characteristics. For example, increasing occurrence of omnivores and decreasing occurrence of predators appears to occur as depth increase (Carey, 1972).

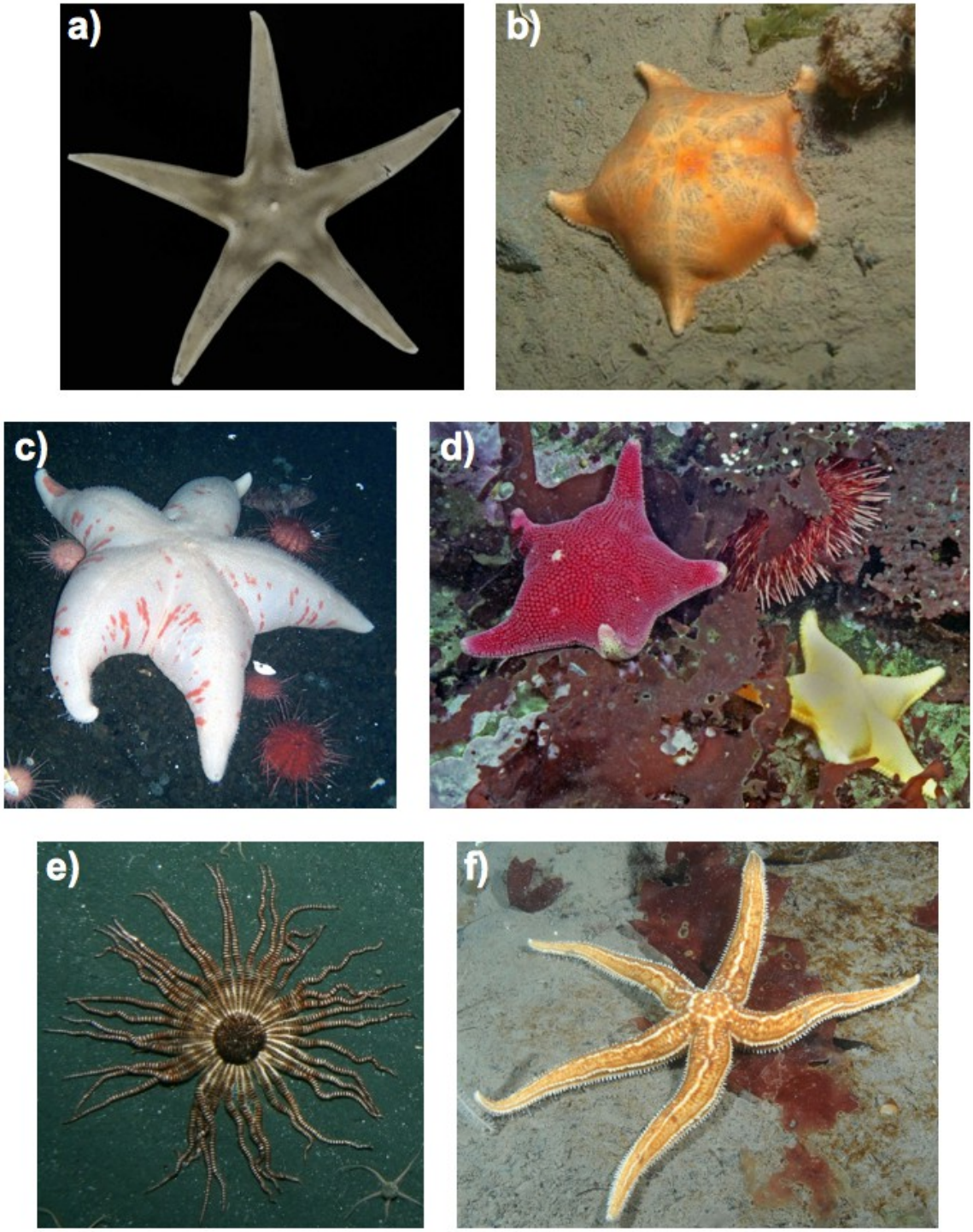

Fig. 1.5. Examples of common sea star species from the Southern Ocean. a) *Bathybiaster loripes* (credit: Université libre de Bruxelles; picture by Pernet P); b) *Glabraster antarctica* (picture by Schories D); c) *Perknaster* sp. (credit: National Science Foundation; picture by Kaiser H); d) *Odontaster validus* (left) and *Odontaster meridionalis* (right; picture by Rauschert M); e) *Labidiaster annulatus* (credit: National Institute of Water and Atmospheric Research); f) *Diplasterias brucei* (picture by Schories D).

Similarly to other oceanic regions, sea stars from the Southern Ocean were mostly reported as generalist predators with some level of specialisation (Dearborn, 1977; McClintock, 1994). Their potential importance in the functioning of the benthic food webs of the Southern Ocean was highlighted by Dayton et al. (1974) who observed that their predation contributes to structure sponge assemblages in coastal Antarctic. Indeed, predation by sea stars on a fast growing sponge species may prevent its dominance of the space resource, and consumption of predators of slow growing sponge species may contribute to the maintenance of these sponge species, resulting in the presence of a diverse sponge community, with both slow and fast growing species. Detailed investigations of the diet with stomach content analysis have been done for several species (Dayton et al., 1974), notably *Labidiaster annulatus* (Dearborn, 1977; Dearborn et al., 1991) and the common *Odontaster validus* (Pearse, 1965; Dayton et al., 1974). Subsequent investigations of the food web functioning of the Southern Ocean using stable isotope ratios included several sea star species, notably *Odontaster validus* and *Diplasterias brucei*, as a component of the food web (e.g. Mincks et al., 2008; Gillies et al., 2012; 2013; Zenteno et al., 2019). In these studies, sea stars were usually preliminarily classified as predators, scavengers and/or omnivores, although *Odontaster validus* was also classified as a deposit feeder. However, broader and long-term investigation of the trophic ecology of sea stars of the Southern Ocean is still lacking after McClintock's (1994) last review on the topic.

Studies to assess the impacts of climate change on sea stars from the Southern Ocean have been mostly limited to the species *Odontaster validus*. *Odontaster validus* is sensitive to acute temperature increase (Kidawa et al., 2010) as it can be inferred from the apparent lack of heat shock response (Clark et al., 2008). Similarly, an outbreak of ulcerative epidermal disease affecting the *Odontaster validus* population in Deception Island and coinciding with high temperatures (and increased seismicity; Núñez-Pons et al., 2018) may also indicate that sea stars from the Southern Ocean are sensitive to increasing seawater temperatures. Nevertheless, adult *Odontaster validus* appear to be able to perform biological activities normally when facing progressive increase of water temperature up to 9°C and still survive in medium-term warming experiments to at least 12°C, making this species one of the most eurythermal invertebrates from the Southern Ocean (Peck et al., 2008; Morley et al., 2012). Lower muscle mass relative to whole animal mass than in taxa such as mollusks and teleosts, and thus lower oxygen demand, was proposed as the explanation of *Odontaster validus*' thermal tolerance (Peck et al., 2008). Similarly, early development stages (fertilisation, embryo and larval development, larval morphology) of *Odontaster validus* do not

seem to be affected by increasing temperatures up to 6°C (Stanwell-Smith and Peck, 1998; Karelitz et al., 2017) but it should be noted that decreasing viability of embryos was observed at increasing temperatures (up to 3°C) for its congener *Odontaster meridionalis* (Stanwell-Smith and Peck, 1998). Studies on the effects of ocean acidification on *Odontaster validus* have been more limited. Yet, the absence of effect of reduced pH on the gonads (Dell'Acqua et al., 2019) is a first indicator of good acidification resistance/tolerance in adult *Odontaster validus*. However, for the early development stages, lower fertilisation, lower larval survival, slowed development and altered morphology may occur in low pH waters (Gonzalez-Bernat et al., 2013; Karelitz et al., 2017).

Nevertheless, the results obtained for *Odontaster validus* suggest that sea stars from the Southern Ocean may be able to adapt to future environmental parameter changes. However, it is still unlikely that this group undergoes the climate change without being impacted. Indeed, other taxa that may be potential prey for sea stars showed more sensitivity to increasing temperature (Peck et al., 2004; 2009; 2010) or to modifications of environmental conditions and their populations are thus more vulnerable to the current climate change. Consequently, sea stars of the Southern Ocean would have to change their diet in order to adapt the the potential rarefaction, or even extinction, of their current prey. Furthermore, it is still possible that the results regarding *Odontaster validus*' resistance to climate change are not applicable to other sea star species. In that case, if sea stars are actually the "keystone organisms" of the Southern Ocean benthos like they are in the Pacific coast of America (Paine, 1966, 1969), effects of their potential rarefaction, or even extinction, on the ecosystems of the Southern Ocean have to be expected.

Because of the various points discussed above, a general study is necessary to understand the trophic role of sea stars in the Southern Ocean.

With the exception of species from the Paxillosida and Notomyotida orders, sea stars are known to revert their stomach in order to preliminary digest their prey externally (Jangoux, 1982). As a result, stomach content analyses may be more complicated for this taxonomic group than for other taxa, and are more frequently conducted on species from the Paxillosida and Notomyotida orders (e.g. Ribi et al., 1977; Ganmanee et al., 2003; Baeta and Ramón, 2013; Fernandez et al., 2017) although some authors were able to use this method on other sea star groups (e.g. Dearborn et al., 1991; Gale et al., 2013). Consequently, using an alternative method to stomach content analysis is necessary to assess the trophic ecology of sea stars. As a result, stable isotopes are an interesting tool to investigate the trophic role of sea stars in ecosystems and thus will be the main methodology used in this study to investigate the trophic ecology of sea stars in the ecosystems of the Southern

Ocean.

1.5 Objectives and structure of the thesis

This PhD thesis proposed to assess the trophic ecology of sea stars from the Southern Ocean by using stable isotopes analysis approach. More specifically, the relationship between environmental conditions and trophic diversity and plasticity of sea stars was investigated. The general methods used in this thesis are described in the chapter 2.

Firstly, we have questioned the possibility of analysing stable isotope ratios in sea star tissues preserved in preservative fluids (chapter 3). Indeed, using sea stars from archived collections would allow to increase the spatial and temporal cover of the sampling effort but preservative fluids are known to alter stable isotope values. Secondly, the food web structure of a Subantarctic nearshore community was investigated, in order to assess the role of sea stars in the food web functioning (chapter 4). Thirdly, the influence of morphologic, ontogenetic and environmental features on the trophic ecology of sea stars was assessed by using the stable isotope data of sea stars from an Antarctic fjord (chapter 5). Finally, the relationship between environmental parameters and stable isotope values of sea stars were assessed to determine how environmental conditions globally affect the trophic ecology of sea star in the Southern Ocean (chapter 6). These different axes were integrated in a general discussion, a conclusion and perspective for future researches (chapter 7).

Chapter 2: General material and methods

FS Polarstern at the Ronne ice shelf (Weddell Sea) during the PS96 sampling campaign (credit: Alfred-Wegener-Institut; picture by Schröder M).

This chapter describes the common methods that were applied to study trophic ecology of sea stars of the Southern Ocean with a particular focus on stable isotopes data handling. Detailed methodology for each study is given in the corresponding chapters.

2.1 Sampling

To maximise the scope of this thesis, a double sampling strategy was set up. First, sea stars from the Southern Ocean were collected by colleagues during campaigns taking place in the framework of the vERSO and RECTO projects from December 2015 to March 2017. Second, suitable samples originating from multiple oceanographic campaigns and surveys during austral springs or summers from January 1985 to January 2015 were retrieved from collections stored in museums or partner institutions. Depending of the campaign, sea stars were frozen, dried, stored in ethanol or fixed with formaldehyde and then stored in ethanol. Details on the sampling campaigns, the storage methods and the number of samples used for SIA are provided in the figure 2.1 and the table 2.1. Furthermore, stable isotope data from sea stars sampled from December 2006 to January 2018 and found in the literature (Gillies and Stark, 2008; Michel et al., 2019; Zenteno et al., 2019) or shared by colleagues were also included in this study. Overall, 2454 sea star specimens were used for stable isotope analyses (SIA) and stable isotope data from 204 specimens were retrieved from the literature or shared by colleagues, resulting in stable isotope data from a total of 2658 sea star specimens.

2.2 Stable isotope analysis

In the laboratory, each sea star was identified to the lowest taxonomic level possible (i.e. species, genus or family) either visually or by genetic analysis: genomic DNA was extracted and 612 nucleotides sequences of the mitochondrial gene cytochrome c oxidase subunit I (COI) were then amplified. Sequences were analysed using species delineation methods and compared to a barcode library in order to separate analysed sea stars into clades (Moreau, 2019; Moreau et al., 2019). For each individual sea star, the arm length (distance from the mouth to the tip of the longest arm) and the disc radius (distance from the mouth to the interradial margin, i.e. the point separating two arms) were recorded (Fig. 2.2). Tegument was selected as target tissue for SIA, but in some instances (data found in the literature or provided by other institutions), podia were used (Table 2.1). For each sea star, one or several arms were separated from the central disc. Internal organs and podia were removed in each arm. With the exception of the already dried samples, the tegument of

each arm was then washed with demineralised water and oven-dried at 50°C during 48 hours. All samples were then homogenised into powder prior to SIA using a mortar and a pestle or a mixer mill (MM301, Retsch, Haan, Germany) depending on their toughness.

Table 2.1. Summary of the sampling campaigns, including the number of sampled sea star taxa and individuals used for stable isotope analyses and the preservation methodology.

Sampling campaign	Start date	End date	Preservation	n species	n samples
Second International Biomass Expedition (MD 42)	11/01/1985	10/02/1985	Ethanol	28	133
EPOS leg 3	13/01/1989	10/03/1989	Formaldehyde and ethanol	24	421
ANT-XXII/3 (ANDEEP-III)	02/01/2005	06/04/2005	Ethanol	23	91
JR144	26/02/2006	17/04/2006	Frozen	24	133
Sue-Ann Watson Expedition	08/03/2006	08/03/2006	Frozen	1	22
TRENZ program 2006-2007 (1)	01/12/2006	01/01/2007	Frozen	5	23
ANT-XXIV/2 (ANDEEP-SYSTCO)	28/11/2007	04/02/2008	Ethanol	27	113
CEAMARC	01/01/2008	27/01/2008	Ethanol	22	103
JR179	18/02/2008	11/04/2008	Frozen	5	8
TRENZ program 2009 (2)	01/01/2009	01/01/2009	Frozen	1	2
ARGOS	07/03/2009	20/03/2009	Frozen	12	27
JR230	01/12/2009	11/12/2009	Frozen or ethanol	18	72
TRENZ program 2009-2010 (3)	01/12/2009	20/03/2010	Frozen	7	40
ZA	06/12/2010	23/12/2010	Formaldehyde and ethanol	8	286
REVOLTA II 2010-2011	29/12/2010	04/02/2011	Ethanol	12	60
JR262	21/10/2011	22/11/2011	Frozen	17	77
REVOLTA IV 2012-2013	27/11/2012	04/02/2013	Ethanol	10	39
JR287	28/04/2013	07/06/2013	Frozen	8	23
JR308	31/12/2014	07/01/2015	Frozen or ethanol	15	38
REVOLTA V 2013-2014 (4)	22/01/2014	26/01/2014	Frozen	1	5
REVOLTA VI 2014-2015 (4)	17/12/2014	12/01/2015	Frozen	4	68
Prince Edward Islands 2015 (5)	19/04/2015	24/04/2015	Frozen	3	11
PS96	06/12/2015	14/02/2016	Frozen	31	241
Fildes Bay 2016 (6)	15/02/2016	19/02/2016	Frozen	1	5
JR15005	22/02/2016	28/03/2016	Frozen	26	142
Prince Edward Islands 2016 (7)	14/04/2016	21/04/2016	Frozen	2	3
Proteker 5	03/11/2016	31/12/2016	Frozen	9	124
REVOLTA VIII 2016-2017	24/01/2017	26/01/2017	Frozen	3	23
Antarctic Circumnavigation Expedition (ACE)	20/12/2016	19/03/2017	Ethanol	29	207
South Bay 2017 (8)	10/02/2017	10/02/2017	Frozen	1	26
Uni_Magellan	08/03/2017	08/03/2017	Dried	11	71
Prince Edward Islands 2017 (7)	13/04/2017	23/04/2017	Frozen	1	3
Marian Cove 2017-2018 (9)	23/12/2017	14/01/2018	Frozen	1	18
Total	**11/01/1985**	**14/01/2018**		**142**	**2658**

(1) Gillies and Stark, 2008. Lipid extraction for *Diplasterias brucei*. Stable isotope analysis on podia for 3 *Diplasterias brucei*.
(2) Gillies and Stark, 2008
(3) Gillies and Stark, 2008. 4 individuals from this dataset were not included in this study because carbonates were not extracted.
(4) Michel, 2019. Stable isotope analysis on podia.
(5) Puccinelli et al., 2018. Stable isotope analysis on tegument and podia together.
(6) Zenteno et al., 2019. Lipid extraction.
(7) Data provided by Eleonora Puccinelli. Stable isotope analysis on tegument and podia together.
(8) Data provided by Lisette Zenteno. Lipid extraction.
(9) Data provided by Claudia Andrade. Stable isotope analysis on podia. Lipid extraction.

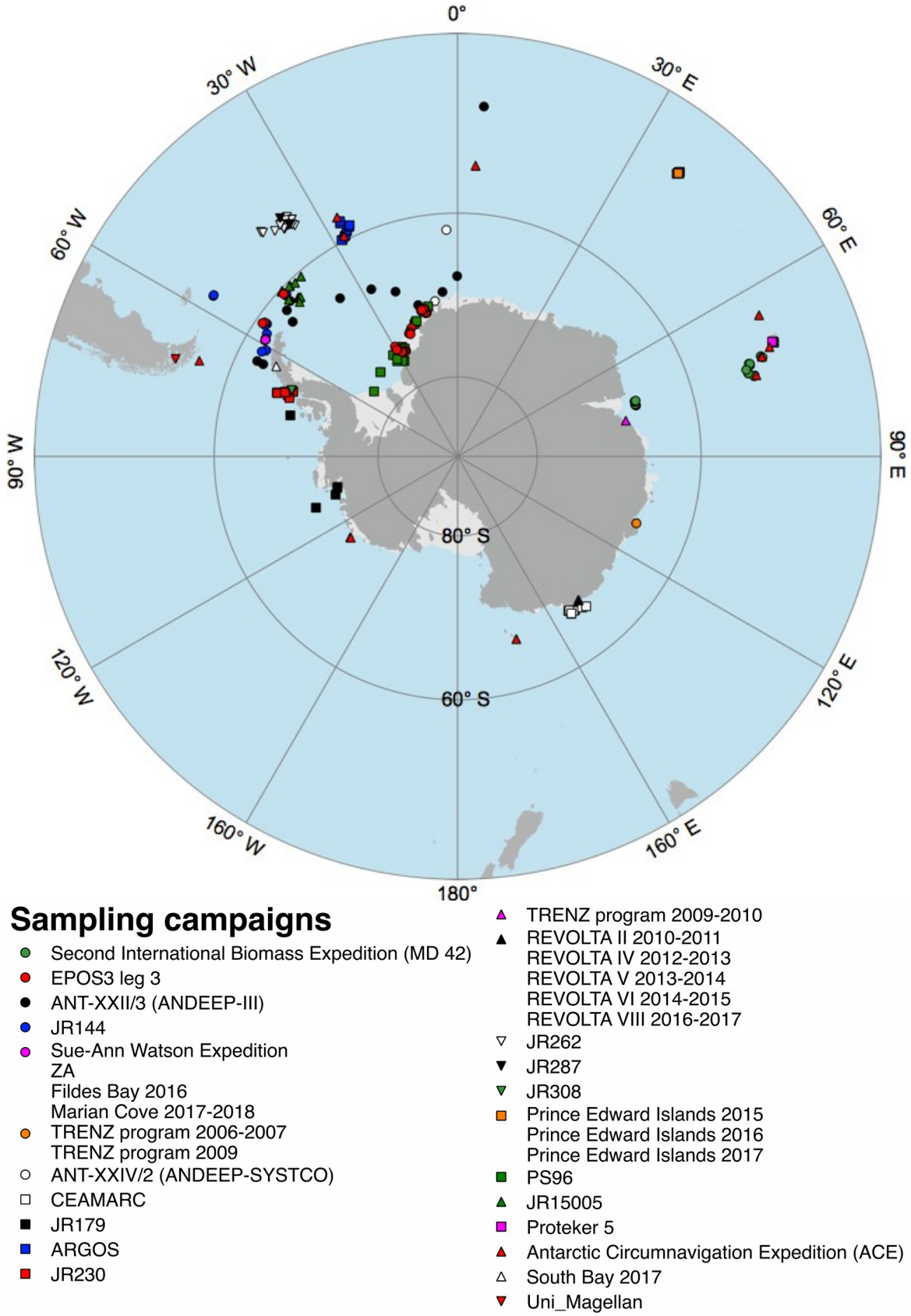

Fig. 2.1. Location of the sampling stations. Sampling campaigns occurring on close vicinity of each other (e.g. successive sampling in coastal Terre Adélie) are shown with the same symbol.

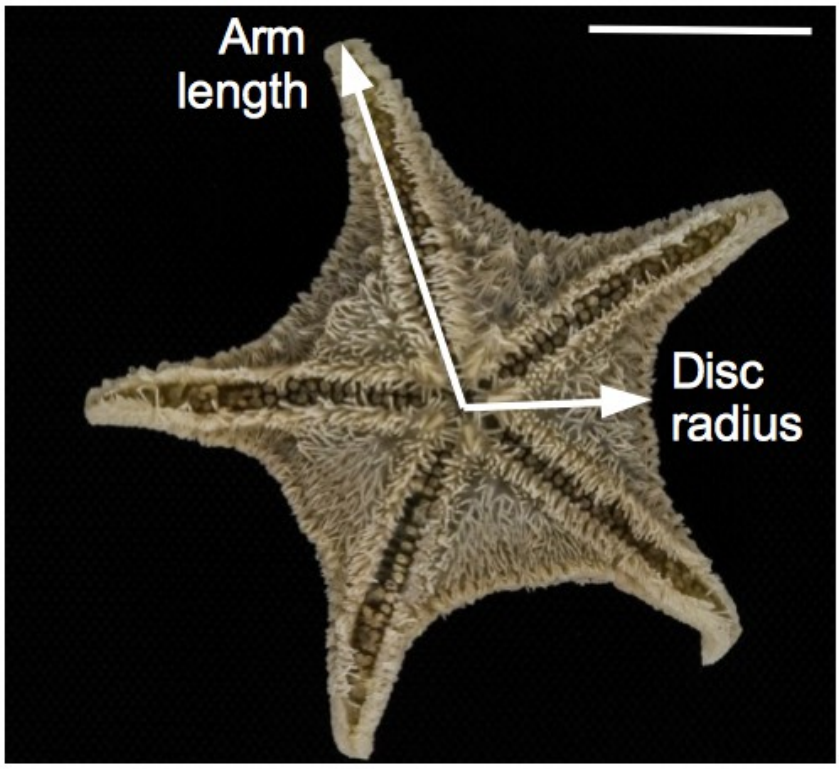

Fig. 2.2. Example of arm length and disc radius measurement in *Odontaster validus*. Bar = 1 cm (credit: Université libre de Bruxelles; picture by Pernet P).

Carbonates in the endoskeleton of animals are more enriched in ^{13}C than other tissue components, and their composition is not necessarily directly related to diet (DeNiro and Epstein, 1978). Sea stars endoskeleton is constituted of carbonates. Consequently, carbonates were removed from the ground samples by exposing subsamples to 37 % hydrochloric acid vapour during 48 hours (Hedges and Stern, 1984). Acidified subsamples were then kept at 60°C until further sample preparation. Contrary to carbonates, lipids are more depleted in ^{13}C than other tissues because of the preferential incorporation of ^{12}C during lipid synthesis (DeNiro and Epstein, 1977; Post et al., 2007). Nevertheless, they are linked to sea star diet. Therefore, lipids were not extracted except for several individuals in data found in the literature or provided by other institutions by using the chloroform/methanol methodology (Table 2.1; Bligh and Dyer, 1959). Considering the low lipid content of sea star tegument, this is not constituting a major cause of variation in our data.

The subsamples were then precisely weighed (*ca* 2.5-3 mg) in 5×8 tin cups with *ca* 3 mg of tungsten trioxide, and analysed with an elemental analyser (vario MICRO Cube, Elementar, Hanau, Germany) coupled to a continuous-flow isotope-ratio mass spectrometer (IsoPrime100, Elementar UK, Cheadle, United Kingdom). Stable isotope ratios of carbon, nitrogen and sulfur were expressed in δ notation ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ respectively; Coplen, 2011) in ‰ relative to international references (Vienna Pee Dee Belemnite for $\delta^{13}C$, N_2 in atmospheric air for $\delta^{15}N$ and Canyon Diablo troilites for $\delta^{34}S$) according to the formula:

$$\delta X_{sample} = \frac{(X/x)_{sample}}{(X/x)_{standard}} - 1 \quad (1)$$

where X is the heavy isotope (^{13}C, ^{15}N, or ^{34}S) and x is the lighter isotope (^{12}C, ^{14}N, or ^{32}S) and $(X/x)_{sample}$ and $(X/x)_{standard}$ are the ratios of both stable isotopes in the sample and the standard, respectively.

Shift or drift of stable isotope values may occur during SIA. Consequently, analytical standards with known stable isotope values were used to manage these potential drifts and thus improve the accuracy of the stable isotope measurements. Certified reference materials from the International Atomic Energy Agency (IAEA, Vienna, Austria) IAEA-N_1 (ammonium sulphate; $\delta^{15}N = 0.4 \pm 0.2$ ‰), IAEA C-6 (sucrose; $\delta^{13}C = -10.8 \pm 0.5$ ‰) and IAEA S-1 (silver sulphide; $\delta^{34}S = -0.3$ ‰) were used as primary standards for N, C and S analysis, respectively. Sulfanilic acid (Sigma-Aldrich; $\delta^{13}C = -25.6 \pm 0.4$‰; $\delta^{15}N = -0.13 \pm 0.4$‰, $\delta^{34}S = 5.9 \pm 0.5$‰; means ± SD) was used as secondary analytical standard. Finally, two randomly selected sea star samples were also used as replicates ($\delta^{13}C = -21.2 \pm 0.2$ ‰, $\delta^{15}N = 15.1 \pm 0.3$ ‰, $\delta^{34}S = 18.2 \pm 0.5$ ‰ for the first sample; $\delta^{13}C = -15.1 \pm$

0.3 ‰, $\delta^{15}N$ = 12.2 ± 0.2 ‰, $\delta^{34}S$ = 15.5 ± 0.4 ‰ for the second sample). Elemental data are expressed as a ratio between the relative concentrations of C and N (C/N mass ratio), measured relative to dry mass (%DM) and may be used as a proxy of the lipid content. The mean C/N ratio of samples (3.38 ± 0.42) and the lack of correlation between C/N ratios and $\delta^{13}C$ values ($r = –0.069$, $P < 0.001$) does indicate that lipids had no influence on $\delta^{13}C$ values. According to Le Bourg et al. (2020), correction factors were added to the $\delta^{13}C$ and $\delta^{34}S$ values of sea stars that were not stored frozen or dried to deal with the effects of preservation. Results of this experimental study assessing the effects of preservation methodology on stable isotope ratios in sea stars are detailed in chapter 3. For samples stored in ethanol, a correction factor of –0.6 ‰ was subtracted to $\delta^{13}C$ values. For samples fixed with formaldehyde and then stored in ethanol, a correction factor of 0.2 ‰ was added to $\delta^{13}C$ values to take into account the effects of both ethanol (–0.6 ‰) and formaldehyde (+0.8 ‰) on $\delta^{13}C$ values. A correction factor of 1.5 ‰ was also added to $\delta^{34}S$ values for samples fixed with formaldehyde.

The subsequent data analyses were performed using R 3.6.0 (current version; R Core Team, 2017).

2.3 A note about isotopic data representation and isotopic metrics

Stable isotope values are typically depicted on biplots (so-called “isotopic spaces”) where each point is the stable isotope values of an organism (Fig. 2.3 and 2.4). Usually, the x-axis shows $\delta^{13}C$ values and the y-axis the $\delta^{15}N$ values. Alternatively, the x-axis shows $\delta^{13}C$ values and the y-axis the $\delta^{34}S$ values.

The data analyses presented in the subsequent chapters heavily rely on the computation and interpretation of isotopic models and metrics. Indeed, the increasing use of SIA led to the development of various ecological metrics and models to ease the interpretation of data. For example, models have been developed to reconstruct the trophic pathways within communities or assemblages (Parnell et al., 2010; 2013). Other metrics have been developed to investigate the trophic level of organism groups (Quezada-Romegialli et al., 2018). Finally, various metrics are used to assess the trophic diversity between organisms within groups, populations or communities by using proxies of their trophic niches with stable isotope data (e.g. convex hulls, standard ellipses) and assessing the characteristics of these proxies (e.g. area, dispersion of individual stable isotope values; Layman et al., 2007; Jackson et al., 2011; Cucherousset and Villéger, 2015).

Mixing models (Parnell et al., 2010; 2013), Layman metrics (2007) and standard ellipses

(Jackson et al., 2011) are the most commonly used metrics in stable isotope studies. In particular, Bayesian methods have also been developed for these metrics to take into account the uncertainties in the stable isotope data and thus lower the potential effects of sampling bias: successive estimations of the metrics or model results produce a range of their probable values which is thus an estimate of the likely order of magnitude of their values or results, i.e. a credibility interval (Jackson et al., 2011). Pairwise comparison of the credibility intervals between two organism assemblages or groups can be done by calculating the percentage of the estimated metric values that differed between these credibility intervals. This percentage indicates the probability that a given organism assemblage or group has a higher or lower metric value than the other one. If the percentage of higher or lower metric values exceeds 95 %, the difference may be considered meaningful and both organism groups or communities have likely different metric values. As a result, Bayesian estimates of metric values can be quantitatively compared between organism assemblages or groups.

2.3.1 Mixing models

Mixing models (Parnell et al., 2010; 2013) have been developed to assess the relative contribution of several food sources to the diet of organism groups. This is done by using the stable isotope values of consumers and the stable isotope values of their potential food sources (e.g. primary producers, animal prey, and so on) adjusted by the Trophic Enrichment Factor (TEF), i.e. the theoretical enrichment in heavy isotopes in consumers relative to the food sources. Indeed, as highlighted by the famous quote “you are what you eat, plus a few per mil” (DeNiro and Epstein, 1976), stable isotope ratios in an organism are the result of the proportional mixing of the adjusted stable isotope ratios of its different food items. As a result, by knowing stable isotope values of an organism and its potential food sources and the TEF, it is possible to compute the contribution of the stable isotope ratios of each food source to the stable isotope ratios of the organism. Bayesian methods allow to take into account the natural variability of stable isotope values and TEFs, as well as the analytical error associated with their measurements. The results of Bayesian mixing models are thus the estimated proportions of each tested food source in the diet of the investigated consumers.

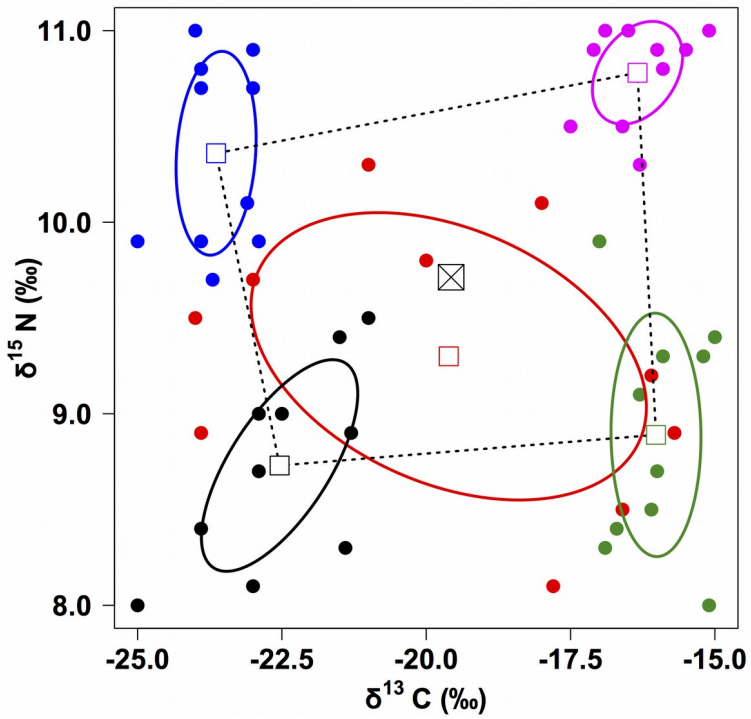

Fig. 2.3. Theoretical example of isotopic space showing individual (filled circles) and mean (open squares) stable isotope ratios of carbon ($\delta^{13}C$ values) and nitrogen ($\delta^{15}N$ values) for five groups of organisms (i.e. species for example; each colour standing for one group) and the resulting standard ellipses (coloured solid lines) based on individual values, convex hull (dashed line) based on group means and its centroid (crossed square).

2.3.2 Isotopic niches

2.3.2.1 Layman metrics

Layman (2007) metrics (Table 2.2) are an ensemble of six metrics that assess the isotopic diversity between organisms. These metrics have initially been presented as a way to assess the trophic diversity between organisms within communities or assemblages but may also be used to investigate the trophic diversity within an organism group. This is done by assessing the characteristics of the convex hull which encompasses the mean stable isotope values of all organism groups in the isotopic space (Fig. 2.3; Layman et al., 2007) or of the convex hull which encompass the individual stable isotope values of a given organism group. The first four metrics are community or assemblage-wide measures of the trophic diversity as they measure the total extent of spacing of mean stable isotope values within the isotopic space. The first two are the ranges of both mean stable isotope values (δx-range and δy-range). These metrics will increase if organisms with extreme isotopic values are present in the community. If stable isotopes of carbon and nitrogen are used to investigate a food web, the range of carbon may be used to estimate the source diversity for

a group of organisms while the range of nitrogen may help to estimate the trophic level diversity. The following metric is the total area (TA) of the convex hull. TA represents a measure of the total amount of the niche space that is occupied by the convex hull, and thus is a proxy for the total extent of trophic diversity within a community. Like the two previous metrics, its value increases when species with extreme isotopic values are present in the community. The following metric is the mean distance to centroid (CD), which is the average distance of each point included in the convex hull to the centre of gravity of the convex hull. Regardless of hull area, CD values increase when more species with extreme isotopic values are present in the community, but decrease when more species with similar values, and thus similar trophic ecology, are present. The two last metrics investigate the relative position of points to each other within the convex hull and can be used to estimate the trophic redundancy. These metrics are the mean (MNND) and the standard deviation (SDNND) of the nearest neighbour distance. MNND is a measure of the overall density of species packing, with smaller values indicating that a large proportion of the organism groups have similar stable isotope compositions and similar trophic ecologies (higher trophic redundancy). SDNND is a measure of the evenness of the species packing, with low values indicating a more even distribution of points in the isotopic space, and higher values indicating the presence of one or several high density regions in the isotopic space. Bayesian methods were developed for the estimation of Layman metrics. The main downside Layman metrics is that they are highly sensitive to the number of species used to build convex hulls, with larger convex hulls (and thus higher TA) and isotopic ranges and lower MNND for larger number of species (Jackson et al., 2011). Consequently, comparisons between communities containing different number of species have to be handled with caution.

Table 2.2 Summary of the six Layman (2007) metrics.

Metric	Abbreviation	Definition
δX range	δx-range	Range of stable isotope values on the x-axis (usually for $\delta^{13}C$ values)
δY range	δy-range	Range of stable isotope values on the y-axis (usually for $\delta^{15}N$ values)
Total area	TA	Area of the convex hull
Mean distance to centroid	CD	Mean of the distances between each point and the centroid of the convex hull
Mean of the nearest neighbour distance	MNND	Mean of the distances between each point and its closest neighbour in the convex hull
Standard deviation of the nearest neighbour distance	SDNND	Standard deviation of the distances between each point and its closest neighbour in the convex hull

2.3.2.2 Standard ellipses

Standard ellipses (Jackson et al., 2011) were developed to assess the isotopic and thus trophic diversity both within communities and between individuals inside groups of organisms. Standard ellipses are a bivariate representation of the standard deviation of both stable isotope ratios (Fig. 2.3 and 2.4) and are less sensitive to sample sizes than Layman metrics (Jackson et al., 2011). The characteristics of the standard ellipses include the lengths of the semi-major (a) and semi-minor (b) axes which are respectively the longest and shortest distances between the standard ellipse centroid and its perimeter (Fig. 2.4). These parameters can be sample-size corrected (a_C and b_C; Jackson et al., 2011) and are used for the computation of the standard ellipse area (SEA). SEA indicates the isotopic niche size of an organism group, population or a community, with a large ellipse showing important differences of stable isotope values, and thus of trophic ecology, between individuals within the organism group or population or between species within a community (i.e. generalist group, population or community) while a smaller ellipse highlight similar stable isotope values, and thus similar trophic ecology, within the organism group or population or between species within a community (i.e. specialist group, population or community). SEA can be sample-size corrected (SEA_C) to reduce the influence of small sample sizes on its computation (Jackson et al., 2011). Bayesian methods have also been developed for SEA estimations (SEA_B; Jackson et al., 2011). SEA_C and/or SEA_B are the most used standard ellipse metrics in stable isotope studies. However, other standard ellipse metrics may be used to investigate the trophic ecology of organisms. These other metrics can be estimated with Bayesian methods too.

The angle (θ) of the semi-major axis with the x-axis represents the inclination of the ellipses in the isotopic space (Fig. 2.4). This parameter may be used to investigate the trophic diversity within an organism group. For example, if the standard ellipse of an organism group is computed using the $\delta^{13}C$ and $\delta^{15}N$ values, θ values close to 0° represent higher dispersion along the $\delta^{13}C$ axis, and thus a potentially greater diversity of basal carbon sources used by this organism group. By contrast, θ values close to 90° highlight relative dispersion along the $\delta^{15}N$ axis, and thus potentially more variable trophic levels and/or nitrogen sources (Reid et al., 2016).

θ may be further used to project the ellipse's major (2a) on the x- and y-axes (i.e. pseudo-standard deviation PSD). This new metric may provide an estimation of the range of the most common stable isotope values measured in a community or an organism groups (Fig. 2.4). As a result, this metric would be less sensitive to sample size or extreme stable isotope values than the ranges of stable isotope values in Layman metrics. PSDs are calculated by using the length of the

semi-major a and the angle θ according to the following formula for the projection of a on the x-axis:

$$PSD_X = 2a\cos(|\theta|) \quad (2)$$

and according to the following formula for the projection of a on the y-axis:

$$PSD_Y = 2a\sin(|\theta|) \quad (3)$$

These metrics may be sample-size corrected (PSD_{XC} and PSD_{YC}) by computing with the sample-size corrected major ($2a_C$) or estimated with Bayesian methods (PSD_{XB} and PSD_{YB}).

The eccentricity (ε) of the ellipse is a numeric included between 0 and 1 that indicates the elongation of the ellipse. Consequently, ε provides information on the variance on the axes and thus on the variability of both stable isotope values. A ε value close to 0 indicates a similar variance on both axes (i.e. the "ellipse" is a circle, i.e. a = b), while a high ε indicates that the ellipse is more variable on one axis than on the other one (Reid et al., 2016).

Like for Layman (2007) metrics, the combination of the standard ellipse characteristics described here is useful to investigate the trophic ecology of organisms when combined with SEA_C and/or SEA_B. For example, two organism groups with both an eccentricity close to 1 (the ellipse is more variable on one axis than on the other one), an angle θ close to 90° (higher relative dispersion along the $\delta^{15}N$ axis) but different SEA could be differentiated, one of the groups feeding on a higher range of trophic levels than the other one. Similarly, two organism groups with both an eccentricity close to 1 (the ellipse is more variable on one axis than on the other one), an angle θ close to 0° (higher relative dispersion along the $\delta^{13}C$ axis) but different SEA could also be differentiated, one of the groups exploiting a wider range of basal food sources than the other.

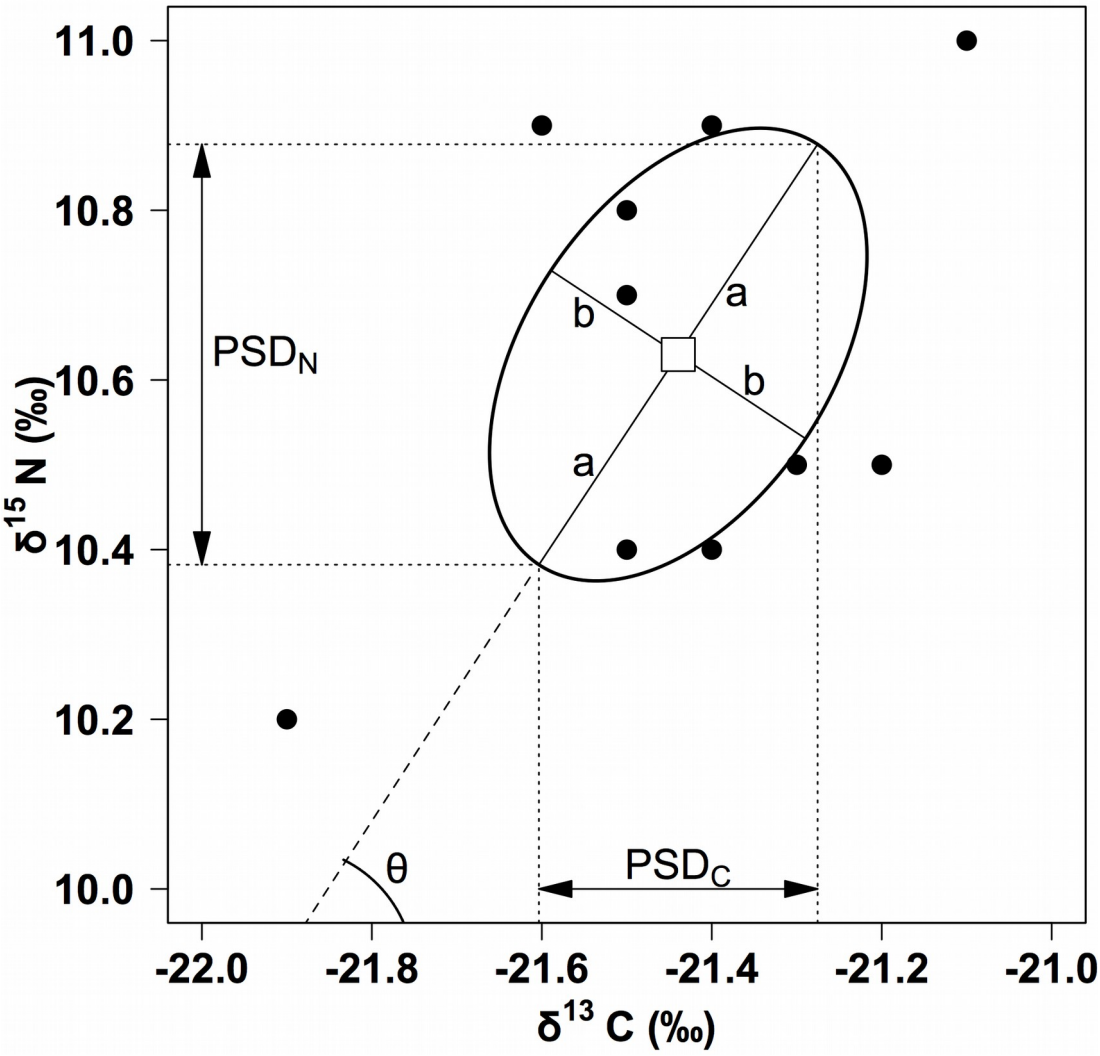

Fig. 2.4. Theoretical example of isotopic niche showing individual stable isotope values (black dots) and the derived standard ellipse (solid line) with its centroid (white square), its two semi-majors (a) and semi-minors (b) axes, as well as the angle (θ) with the x axis and the projection of its major (2a) on the x ($\delta^{13}C$ values) and y ($\delta^{15}N$ values) axes to measure the pseudo-standard deviations of $\delta^{13}C$ (PSD_C) and $\delta^{15}N$ values (PSD_N), respectively.

2.4 Data mean-correction methodology

Stable isotope values in organisms, and biological data in general, are influenced by various factors. For example, stable isotope values in organisms may differ between sampling locations or sampling periods as a result of spatial variation of stable isotope values of primary food sources at baseline of food webs (i.e. primary producers and/or organic matter pools at the basis of the food web) between sampling locations or periods (Harmelin-Vivien et al., 2008; McMahon et al., 2013; Veit-Köhler et al., 2013; Espinasse et al., 2019). These variations in isotopic baselines may be the result of changes in the nature of primary producers consumed at the baseline of the food web, between sampling locations or periods, but may also occur in a same type of primary producer because of primary production processes. In marine environments, this can be explained by different factors such as change in nutrient availability and phytoplankton growth rates (McMahon et al., 2013), different importance of terrestrial and river inputs (Harmelin-Vivien et al., 2008; McMahon et al., 2013) or differences in inputs of allochthonous and autochthonous matter in the food web (Wyatt et al., 2013).

While the differences of mean stable isotope values between factor levels may provide useful information on the trophic ecology of organisms, they may hinder more global studies using stable isotope values. Indeed, in case of significant differences of stable isotope values between the levels of a confounding factor, the pooling of the confounding factor levels to study another factor of interest may be prevented. While the effect of the confounding factor may be dealt with in several statistical analyses, they may be more problematic for other types of data analyses such as the computation of isotopic metrics. Indeed, differences of mean stable isotope values between the confounding factor levels may result in an increase of the variability and thus in an overestimation of isotopic metrics if the confounding factor levels are pooled. As a result, the differences of stable isotope values between the confounding factor levels may mask differences between levels of the factor of interest.

For example, fictional stable isotope data of a species sampled in 3 stations are presented on the figure 2.5. Mean stable isotope values differ between stations and it is not possible to determine if this is the result of different food sources or of changes of stable isotope values in a same type of food source in each station. Consequently, pooling the samples from the 3 stations would result in a overestimation of the general convex hull metrics, and thus of the trophic diversity (Fig. 2.5.a), especially if the different means of $\delta^{13}C$ and $\delta^{15}N$ values between stations result from the consumption of a same type of food source with different stable isotope values. Therefore, to assess

the trophic diversity of this species at the scale of whole study zone (i.e. by pooling the stations), it is crucial to account for inter-station differences (i.e. differences in mean stable isotope values of each station). In addition, the variability of stable isotope values within each station should be preserved, as computed metrics will use this parameter to determine the diversity of food web baselines and/or of trophic levels used by the species. This can be done by a correction of mean values without changing the variability of data within each station. This method may be used not only for stable isotope data, but also for any other kind of data. The principle is, knowing the general mean of all values and the means of each station, to remove the relevant "station" effect to each individual isotope value. The researched result is that all the stations have the same mean without removing the differences of values between individuals within each station. The figure 2.5.b shows that the means of the 3 stations are all at the same point after mean-correction. The extent and the shape of the convex hulls of each station has not been modified in the process and thus the variability of stable isotope values within each station is preserved, and so is the ecological info that it provides.

If we have a variable X (e.g. $\delta^{13}C$ or $\delta^{15}N$ values in figure 2.5) for an individual i belonging to the factor K (e.g. station in figure 2.5), the value of X for this individual i belonging to the factor level k (X_{ik}) is the sum of the mean of X ($\overline{X}$), the coefficient of the factor K (coefK) and the residual (e_{ik}):

$$X_{ik} = \overline{X} + coefK + e_{ik} \quad (4)$$

Where X_{ik} is the value of the variable X for the individual i belonging to the factor level k. $\overline{X}$ is the general mean of the variable X for all the individuals i, all factor levels considered. coefK is the difference between the mean of X in the factor level k ($\overline{X}_k$) and $\overline{X}$:

$$coefK = (\overline{X}_k - \overline{X}) \quad (5)$$

e_{ik} is the difference between X_{ik} and $\overline{X}_k$:

$$e_{ik} = X_{ik} - \overline{X}_k \quad (6)$$

Consequently, the equation (4) can then be written like this:

$$X_{ik} = \overline{X} + (\overline{X}_k - \overline{X}) + (X_{ik} - \overline{X}_k) \quad (7)$$

The potential effect of K on X is corrected by removing coefK from the equation (7). Consequently, the equation for the factor-corrected X value in the individual i from the factor level k ($corX_{ik}$) is:

$$corX_{ik} = \overline{X} + (X_{ik} - \overline{X}_k) \quad (8)$$

or more simply:

$$corX_{ik} = X_{ik} - (\overline{X}_k - \overline{X}) \quad (9)$$

With this method, data from the different factor levels of K have the same mean for the variable X while the variability of X each factor level is preserved. Thus, the variability of X for pooled factor levels is thus no more the result of differences of X between these factor levels (Fig. 2.5.b).

For example, let us consider the $\delta^{13}C$ and $\delta^{15}N$ values of the individual 1 belonging to the station 1 in the figure 2.5 and in the table 2.3. The mean of all $\delta^{13}C$ values is –12.4, the mean of $\delta^{13}C$ values in the station 1 is –15.0 and the $\delta^{13}C$ value of the individual 1 is –15.0. Then, the corrected value is –15.0 – (–15.0 + 12.4) = –12.4. Similarly, the mean of all $\delta^{15}N$ values is 12.1, the mean of $\delta^{15}N$ values in the station 1 is 10.3 and the $\delta^{15}N$ value of the individual 1 is 8.0. Then, the corrected value is 8.0 – (10.3 – 12.1) = 9.8.

In this thesis, the mean-correction method has mostly been used to correct spatial and/or temporal differences of stable isotope values between sampling stations to allow the inclusion of these stations together in larger groups for a given data analysis without their differences risking to bias the results. It has notably been used to assess the relationship between sea star size and stable isotope values in all stations of Ezcurra Inlet in chapter 5, as well as to group very distant stations into larger groups in chapter 6.

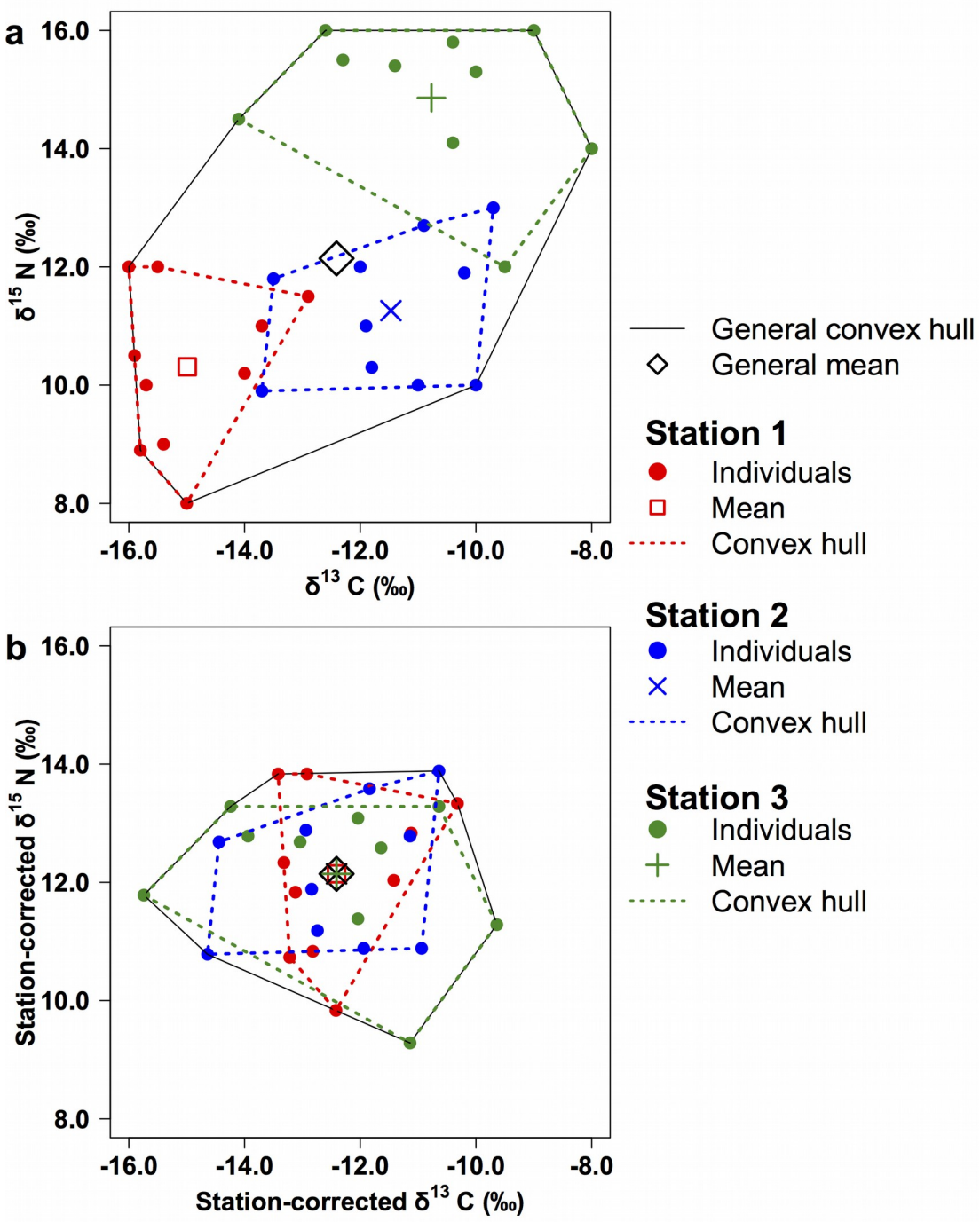

Fig. 2.5. Theoretical example of mean-correction of $\delta^{13}C$ and $\delta^{15}N$ values for organisms of a same species sampled in 3 stations with individual and mean values and the resulting convex hull for each station. By looking at the raw data (a), it appears that samples from the 3 stations have different mean $\delta^{13}C$ and $\delta^{15}N$ values, resulting in an overestimation of the general convex hull when pooling the data. After mean-correction by the station (b), data from the 3 stations have the same mean $\delta^{13}C$ and $\delta^{15}N$ values while the convex hull shapes for each station are preserved and the size of the general convex hull is thus no more the result of differences of $\delta^{13}C$ and $\delta^{15}N$ values between the stations. Computation of station-corrected $\delta^{13}C$ and $\delta^{15}N$ values are provided in the table 2.3.

Table 2.3. Mean-correction of the stable isotope values in the figure 2.5 with individual stable isotope values, mean isotopic values in each station and mean isotopic values for all samples.

Individual i	Station k	$\delta^{13}C_{ik}$	–	(	Mean $\delta^{13}C_k$	–	Total mean $\delta^{13}C$	)	=	cor$\delta^{13}C_{ik}$	/	$\delta^{15}N_{ik}$	–	(	Mean $\delta^{15}N_k$	–	Total mean $\delta^{15}N$	)	=	cor$\delta^{15}N_{ik}$
Individual 1	Station 1	–15.0	–	(	–15.0	–	–12.4	)	=	–12.4	/	8.0	–	(	10.3	–	12.1	)	=	9.8
Individual 2	Station 1	–16.0	–	(	–15.0	–	–12.4	)	=	–13.4	/	12.0	–	(	10.3	–	12.1	)	=	13.8
Individual 3	Station 1	–15.5	–	(	–15.0	–	–12.4	)	=	–12.9	/	12.0	–	(	10.3	–	12.1	)	=	13.8
Individual 4	Station 1	–13.7	–	(	–15.0	–	–12.4	)	=	–11.1	/	11.0	–	(	10.3	–	12.1	)	=	12.8
Individual 5	Station 1	–15.4	–	(	–15.0	–	–12.4	)	=	–12.8	/	9.0	–	(	10.3	–	12.1	)	=	10.8
Individual 6	Station 1	–15.7	–	(	–15.0	–	–12.4	)	=	–13.1	/	10.0	–	(	10.3	–	12.1	)	=	11.8
Individual 7	Station 1	–15.9	–	(	–15.0	–	–12.4	)	=	–13.3	/	10.5	–	(	10.3	–	12.1	)	=	12.3
Individual 8	Station 1	–12.9	–	(	–15.0	–	–12.4	)	=	–10.3	/	11.5	–	(	10.3	–	12.1	)	=	13.3
Individual 9	Station 1	–15.8	–	(	–15.0	–	–12.4	)	=	–13.2	/	8.9	–	(	10.3	–	12.1	)	=	10.7
Individual 10	Station 1	–14.0	–	(	–15.0	–	–12.4	)	=	–11.4	/	10.2	–	(	10.3	–	12.1	)	=	12.0
Individual 11	Station 2	–12.0	–	(	–11.5	–	–12.4	)	=	–12.9	/	12.0	–	(	11.3	–	12.1	)	=	12.9
Individual 12	Station 2	–11.0	–	(	–11.5	–	–12.4	)	=	–11.9	/	10.0	–	(	11.3	–	12.1	)	=	10.9
Individual 13	Station 2	–10.0	–	(	–11.5	–	–12.4	)	=	–10.9	/	10.0	–	(	11.3	–	12.1	)	=	10.9
Individual 14	Station 2	–11.9	–	(	–11.5	–	–12.4	)	=	–12.8	/	11.0	–	(	11.3	–	12.1	)	=	11.9
Individual 15	Station 2	–13.7	–	(	–11.5	–	–12.4	)	=	–14.6	/	9.9	–	(	11.3	–	12.1	)	=	10.8
Individual 16	Station 2	–9.7	–	(	–11.5	–	–12.4	)	=	–10.6	/	13.0	–	(	11.3	–	12.1	)	=	13.9
Individual 17	Station 2	–10.9	–	(	–11.5	–	–12.4	)	=	–11.8	/	12.7	–	(	11.3	–	12.1	)	=	13.6
Individual 18	Station 2	–10.2	–	(	–11.5	–	–12.4	)	=	–11.1	/	11.9	–	(	11.3	–	12.1	)	=	12.8
Individual 19	Station 2	–11.8	–	(	–11.5	–	–12.4	)	=	–12.7	/	10.3	–	(	11.3	–	12.1	)	=	11.2
Individual 20	Station 2	–13.5	–	(	–11.5	–	–12.4	)	=	–14.4	/	11.8	–	(	11.3	–	12.1	)	=	12.7
Individual 21	Station 3	–9.0	–	(	–10.8	–	–12.4	)	=	–10.6	/	16.0	–	(	14.9	–	12.1	)	=	13.3
Individual 22	Station 3	–8.0	–	(	–10.8	–	–12.4	)	=	–9.6	/	14.0	–	(	14.9	–	12.1	)	=	11.3
Individual 23	Station 3	–9.5	–	(	–10.8	–	–12.4	)	=	–11.1	/	12.0	–	(	14.9	–	12.1	)	=	9.3
Individual 24	Station 3	–12.3	–	(	–10.8	–	–12.4	)	=	–13.9	/	15.5	–	(	14.9	–	12.1	)	=	12.8
Individual 25	Station 3	–14.1	–	(	–10.8	–	–12.4	)	=	–15.7	/	14.5	–	(	14.9	–	12.1	)	=	11.8
Individual 26	Station 3	–10.4	–	(	–10.8	–	–12.4	)	=	–12.0	/	15.8	–	(	14.9	–	12.1	)	=	13.1
Individual 27	Station 3	–12.6	–	(	–10.8	–	–12.4	)	=	–14.2	/	16.0	–	(	14.9	–	12.1	)	=	13.3
Individual 28	Station 3	–11.4	–	(	–10.8	–	–12.4	)	=	–13.0	/	15.4	–	(	14.9	–	12.1	)	=	12.7
Individual 29	Station 3	–10.4	–	(	–10.8	–	–12.4	)	=	–12.0	/	14.1	–	(	14.9	–	12.1	)	=	11.4
Individual 30	Station 3	–10.0	–	(	–10.8	–	–12.4	)	=	–11.6	/	15.3	–	(	14.9	–	12.1	)	=	12.6

Chapter 3: Investigation of the usability of chemically preserved sea stars for stable isotope analysis*

Archived sea star samples from the French National Museum of Natural History (picture by Le Bourg B).

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3.1 Introduction

Freezing and drying are usually the recommended method of sample preservation before stable isotope analysis (SIA). However, many of the sea star samples used in this study were provided by other institutions that did not initially sample sea stars for SIA, and many of these samples were fixed and stored with preservative fluids (formaldehyde and ethanol). Unfortunately, preservative fluids are known to alter stable isotopes ratios in samples (Kaehler and Pakhomov, 2001; Sarakinos et al., 2002; Fanelli et al., 2010). Furthermore, impacts of preservation methods are taxon-specific and studies of these impacts on particular taxa are necessary.

Teleosts is the taxon where effects of preservation methodology on stable isotope values have been most studied (e.g. Bosley and Wainright, 1999; Kaelher and Pakhomov, 2001; Edwards et al., 2002; Lau et al., 2012; González-Bergonzoni et al., 2015; Stallings et al., 2015). The influence of preservation methodology on stable isotope values has also been investigated in various other taxa such as elasmobranchs (Kim and Koch, 2012; Olin et al., 2014), chelonians (Barrow et al., 2008), birds (Bugoni et al., 2008), marine (Kiszka et al., 2014) and terrestrial mammals (Javornik et al., 2019) and even photosynthetic organisms (Kaelher and Pakhomov, 2001; Oczkowski et al., 2015). The influence of preservation methodology on stable isotope values has also been investigated in several invertebrate taxa such as cnidarians (Carabel et al., 2009; Fleming et al., 2011), molluscs (e.g. Kaelher and Pakhomov, 2001; Carabel et al., 2009; Fanelli et al., 2010; Syväranta et al., 2011; Umbricht et al., 2018), polychaetes (Fanelli et al., 2010; Umbricht et al., 2018), sipunculid (Fanelli et al., 2010) and aquatic (e.g. Bosley and Wainright, 1999; Lau et al., 2012; Rennie et al., 2012) and terrestrial arthropods (e.g. Krab et al., 2012; Jesus et al., 2015). With some exceptions (Feuchtmayr and Grey, 2003; Fleming et al., 2011; Syväranta et al., 2011; Oczkowski et al., 2015), most of these studies agree that freezing and drying do not alter stable isotope ratios and that preservation and/or fixation of organisms with formaldehyde induce a negative shift of $\delta^{13}C$ values. However, more conflicting results have been reported on the impact of ethanol on $\delta^{13}C$ values, with either no significant changes or increasing $\delta^{13}C$ values being observed. The study of the impact of formaldehyde and ethanol on $\delta^{15}N$ values also led to conflicting results. A summary of the previous studies investigating the influence of preservation on $\delta^{13}C$ and $\delta^{15}N$ values is provided by the table 3.1.

Table 3.1. Examples of reported shifts (mean ± SD) of preservation methods on stable isotope values in aquatic animals.

Method	Phylum	Species	Experiment duration	$\Delta\delta^{13}C$ (‰)	$\Delta\delta^{15}N$ (‰)	Reference
Freezing	Cnidarians	*Aurelia aurita*	6 months	Not significant	↓ –2.1	Fleming et al., 2011
	Mollusks	*Corbicula fluminea*	12 months	↑ +2.1 ± 0.3	↑ +1.0 ± 0.3	Syväranta et al., 2011
		Octopus vulgaris	12 weeks	Not significant	Not significant	Kaehler and Pakhomov, 2001
	Crustaceans	Bulk zooplankton	4 days	↓ –0.9	↑ +0.6	Feuchtmayr and Grey, 2003
	Echinoderms	*Marthasterias glacialis*	24 months	Not significant	Not significant	This study
	Teleosts	*Argiosomus hololepidotus*	12 weeks	Not significant	Not significant	Kaehler and Pakhomov, 2001
		Various species	1 month	Not significant	Not significant	Stallings et al., 2015
Drying	Mollusks	*Octopus vulgaris*	12 weeks	Not significant	Not significant	Kaehler and Pakhomov, 2001
	Echinoderms	*Marthasterias glacialis*	24 months	Not significant	Not significant	This study
	Teleosts	*Argiosomus hololepidotus*	12 weeks	Not significant	Not significant	Kaehler and Pakhomov, 2001
		Various species	625 days	Not significant	Not significant	Xu et al., 2011
Formaldehyde	Polychaetes	*Chirimia biceps*	12 months	↓ –4.1	Not significant	Fanelli et al., 2010
		Magelona spp.	18 weeks	↓ –2.1	↓ –1.0	Umbricht et al., 2018
		Nephtys hystricis	12 months	↓ –3.1	Not significant	Fanelli et al., 2010
	Sipunculid	*Sipunculus norvegicus*	12 months	↓ –3.5	Not significant	Fanelli et al., 2010
	Mollusks	*Corbicula fluminea*	12 months	↑ +2.2 ± 0.3	↑ +1.0 ± 0.2	Syväranta et al., 2011
		Abra longicalus	12 months	↓ –2.1	Not significant	Fanelli et al., 2010
		Octopus vulgaris	12 weeks	↓ –0.3 ± 0.1	Not significant	Kaehler and Pakhomov, 2001
		Mya arenaria	18 weeks	↓ –1.5 ± 0.8	Not significant	Umbricht et al., 2018
		Tellina fabula	18 weeks	↓ –2.7 ± 0.3	Not significant	Umbricht et al., 2018
	Crustaceans	Bulk zooplankton	4 days	↑ +1.1	↑ +0.8	Feuchtmayr and Grey, 2003
	Echinoderms	*Molpadia musculus*	12 months	↑ +3.9 (6 months) ↓ –2.6 (12 months)	Not significant	Fanelli et al., 2010
		Marthasterias glacialis	24 months	↓ –0.8 ± 0.5	Not significant	This study
	Teleosts	*Argiosomus hololepidotus*	12 weeks	↓ –0.5 ± 0.1	Not significant	Kaehler and Pakhomov, 2001
		Various species	625 days	↓ –1.0	Not significant	Xu et al., 2011
Ethanol	Cnidarians	*Aurelia aurita*	6 months	Not significant	↓ –2.4	Fleming et al., 2011
	Polychaetes	*Chirimia biceps*	12 months	Not significant	Not significant	Fanelli et al., 2010
		Magelona spp.	18 weeks	↑ +1.4 ± 0.2	↑ +0.9 ± 0.0	Umbricht et al., 2018
		Nephtys hystricis	12 months	Not significant	Not significant	Fanelli et al., 2010
	Sipunculid	*Sipunculus norvegicus*	12 months	Not significant	↓ –1.7	Fanelli et al., 2010
	Mollusks	*Abra longicalus*	12 months	Not significant	Not significant	Fanelli et al., 2010
		Corbicula fluminea	12 months	↑ +1.3 ± 0.3	↑ +0.9 ± 0.2	Syväranta et al., 2011
		Octopus vulgaris	12 weeks	↑ +1.6 ± 0.3	Not significant	Kaehler and Pakhomov, 2001
		Mya arenaria	18 weeks	↓ –1.4 ± 6.5	Not significant	Umbricht et al., 2018
		Tellina fabula	18 weeks	↑ +0.8	↑ +0.6	Umbricht et al., 2018
	Crustaceans	Bulk zooplankton	4 days	Not significant	↑ +0.8	Feuchtmayr and Grey, 2003
	Echinoderms	*Molpadia musculus*	12 months	↑ +3.6	Not significant	Fanelli et al., 2010
		Marthasterias glacialis	24 months	↑ +0.6 ± 0.5	Not significant	This study
	Teleosts	*Argiosomus hololepidotus*	12 weeks	↑ +0.7 ± 0.2	Not significant	Kaehler and Pakhomov, 2001
		Various species	625 days	↑ +0.7	↑ +0.4	Xu et al., 2011
		Various species	1 month	↑ +0.4 ± 0.4	↑ +0.6 ± 0.4	Stallings et al., 2015

Contrary to $\delta^{13}C$ and $\delta^{15}N$ values, the impact of preservation on $\delta^{34}S$ values has been poorly investigated so far. The few studies that investigated the effects of preservation on $\delta^{34}S$ values values reported different results, with an increase of mean $\delta^{34}S$ values being observed in teleosts fixed with formaldehyde and then stored in ethanol (Edwards et al., 2002) and no effects of ethanol preservation being observed on $\delta^{34}S$ values in bear tissues (Javornik et al., 2019). Furthermore, only one study investigated the impact of preservation on mixing model performance (Xu et al., 2011), but its influence on isotopic niche modelling has never been tested. Finally, the influence of preservation methodology on stable isotope values remains poorly investigated in several taxa. In particular, the impact of preservation on stable isotope ratios in sea stars was never investigated so far.

Consequently, in order to use stable isotope data from stored sea star samples in this study, it is necessary to determine what are the effects of preservation methods on stable isotope values for this group and how to deal with preservation-induced alteration of stable isotope values. As a result, an experimental study was conducted to assess the modification of stable isotope values in sea star tissues preserved up to two years with different preservation methods (freezing, drying, formaldehyde, ethanol). Furthermore, the influence of these modifications on the resulting isotopic niches and associated parameters (Jackson et al., 2011) was investigated.

3.2 Material and methods

3.2.1 Sampling and stable isotope analysis

Sea stars of the species *Marthasterias glacialis* (n = 20) were collected in the Atlantic Ocean, near the Roscoff biological station (Brittany, France), in April 2016. Sea stars were maintained alive until their transfer to the laboratory. For each sea star, arms were separated from the central disc. Internal organs were removed in each arm. The first arm of each sea star was immediately dried and homogenised into powder (T_0). The other arms were randomly assigned to each preservation method (freezing, drying, formaldehyde, ethanol) and cut in six sections, each section being randomly assigned to a time of analysis (1, 3, 6, 9, 12 and 24 months; n = 20 samples per method and per time of analysis). Each arm section was individually either frozen at –28°C, oven dried, preserved in 3.7 % formaldehyde or in 99.8 % ethanol. At the assigned date of analysis, with the exception of the already dried samples, arm sections were rinsed with distilled water and dried. The details of the sample preparation (grinding, removal of carbonates) and stable isotope analysis are provided in the section 2.2 of the chapter 2.

Certified reference materials from the International Atomic Energy Agency (IAEA, Vienna, Austria), IAEA N-1 (ammonium sulphate; $\delta^{15}N = 0.4 \pm 0.2$ ‰), IAEA C-6 (sucrose; $\delta^{13}C = -10.8 \pm 0.5$ ‰) and IAEA S-1 (silver sulphide; $\delta^{34}S = -0.3$ ‰) were used as primary standards. Sulfanilic acid (Sigma-Aldrich, Overijse, Belgium; $\delta^{13}C = -25.6 \pm 0.4$ ‰; $\delta^{15}N = -0.1 \pm 0.4$ ‰; $\delta^{34}S = 5.9 \pm 0.5$ ‰; means ± SD) and one of the samples (randomly selected; $\delta^{13}C = -15.1 \pm 0.3$ ‰, $\delta^{15}N = 12.3 \pm 0.2$ ‰; $\delta^{34}S = 16.9 \pm 0.8$ ‰) were used as secondary analytical standard and replicate, respectively and were analysed before and after a sequence of 12 samples. T_0 samples were analysed four times, i.e. once per method, in order to have a balanced data design. Elemental data are expressed as a ratio between the relative concentrations of C and N (C/N mass ratio), measured relative to dry mass (%DM).

3.2.2 Data analysis

All the data analyses were performed using R 3.6.0 (R Core Team, 2017).

Two-way repeated measures analyses of variance (ANOVA) were performed on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values and on C/N ratios to assess the effects of preservation methods and time of preservation on those parameters. In case of significant differences, subsequent one-way repeated measures ANOVA were performed in each preservation method to assess the effect of time of preservation on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values and on C/N ratios. In case of significant differences, pairwise comparisons with Bonferroni correction (Rice, 1989) were computed to compare $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values between T_0 and preserved samples at each time to determine when preservation is altering stable isotopes values. Normality of residuals was checked for all models using Q-Q plots and Shapiro tests. In case of a consistent effect of preservation time, i.e. a significant change of $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values at a given time of preservation that still occurs after this time, correction factors were computed. To do so, mean differences of mean $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values between T_0 samples and significantly different preserved samples ($\Delta\delta^{13}C$, $\Delta\delta^{15}N$ and $\Delta\delta^{34}S$, respectively) were calculated: the correction factors are the opposite values of these calculated differences. One-way repeated measures ANOVAs and subsequent post-hoc analyses were then performed to compare the differences between corrected $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values and non-corrected $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values from previous times of analysis and T_0 samples.

For each preservation method and for each time of analysis, standard ellipses representing isotopic niches were computed using the $\delta^{13}C$ and $\delta^{15}N$ values, or the $\delta^{13}C$ and $\delta^{34}S$ values and the temporal evolution of following parameters was investigated: lengths of the semi-major (a_C) and

semi-minor (b_C) axes (sample size corrected), angle (θ) of the semi-major axis with the x axis, eccentricity (ε) of the ellipse ($\varepsilon = 0$ means that the "ellipse" is a circle i.e. $a_C = b_C$). Finally, sample size corrected (SEA_C) and Bayesian (based on 5.10^5 successive iterations; SEA_B) estimates of standard ellipse area (SEA) were computed with the SIBER package (Jackson et al., 2011). For each method of preservation, the SEA_B was directly compared with the SEA_B of T_0 samples by assessing the proportion of estimated SEA computed by the SIBER package for which SEA values of preserved samples were higher or lower than those of the T_0 samples (p). If this proportion of higher or lower SEA values exceeded 95 %, SEA_B of fresh and preserved samples were considered as being different.

3.3 Results

Significant influences of the preservation method ($F_{3,57} = 113.338$, $P < 0.001$) and of its interaction with the time of analysis ($F_{18,342} = 6.718$, $P < 0.001$) were observed on $\delta^{13}C$ values. Subsequent ANOVAs performed in each preservation method revealed different effects of preservation on $\delta^{13}C$ values. $\delta^{13}C$ values are strongly altered by formaldehyde preservation ($F_{6,114} = 14.360$, $P < 0.001$): $\delta^{13}C$ values immediately decreased at the first month of preservation and then remained stable throughout the experiment (Fig. 3.1.a). The difference in $\delta^{13}C$ values between T_0 samples and preserved samples was -0.8 ± 0.5 ‰. Consequently, adding 0.8 ‰ to the $\delta^{13}C$ values of samples preserved in formaldehyde suppressed significant differences of $\delta^{13}C$ values between T_0 samples and preserved samples whatever the treatment time ($F_{6,114} = 0.374$, $P = 0.894$). Ethanol had a significant effect on $\delta^{13}C$ values ($F_{6,114} = 5.701$, $P < 0.001$) with $\delta^{13}C$ values increasing through time until reaching an asymptote (Fig. 3.1.a). Subsequent pairwise comparisons with Bonferroni correction showed that a significant change of $\delta^{13}C$ values occurred at 9 months of preservation and was still present after 12 and 24 months of preservation (Table 3.2). The difference of $\delta^{13}C$ values between T_0 samples and preserved samples after 9 months was 0.6 ± 0.5 ‰. Adding –0.6 ‰ from $\delta^{13}C$ values of samples preserved in ethanol after 9 months suppressed significant differences of $\delta^{13}C$ values between T_0 samples and preserved samples but some differences appeared between time of analysis ($F_{6,114} = 4.532$, $P < 0.001$; Table 3.2).

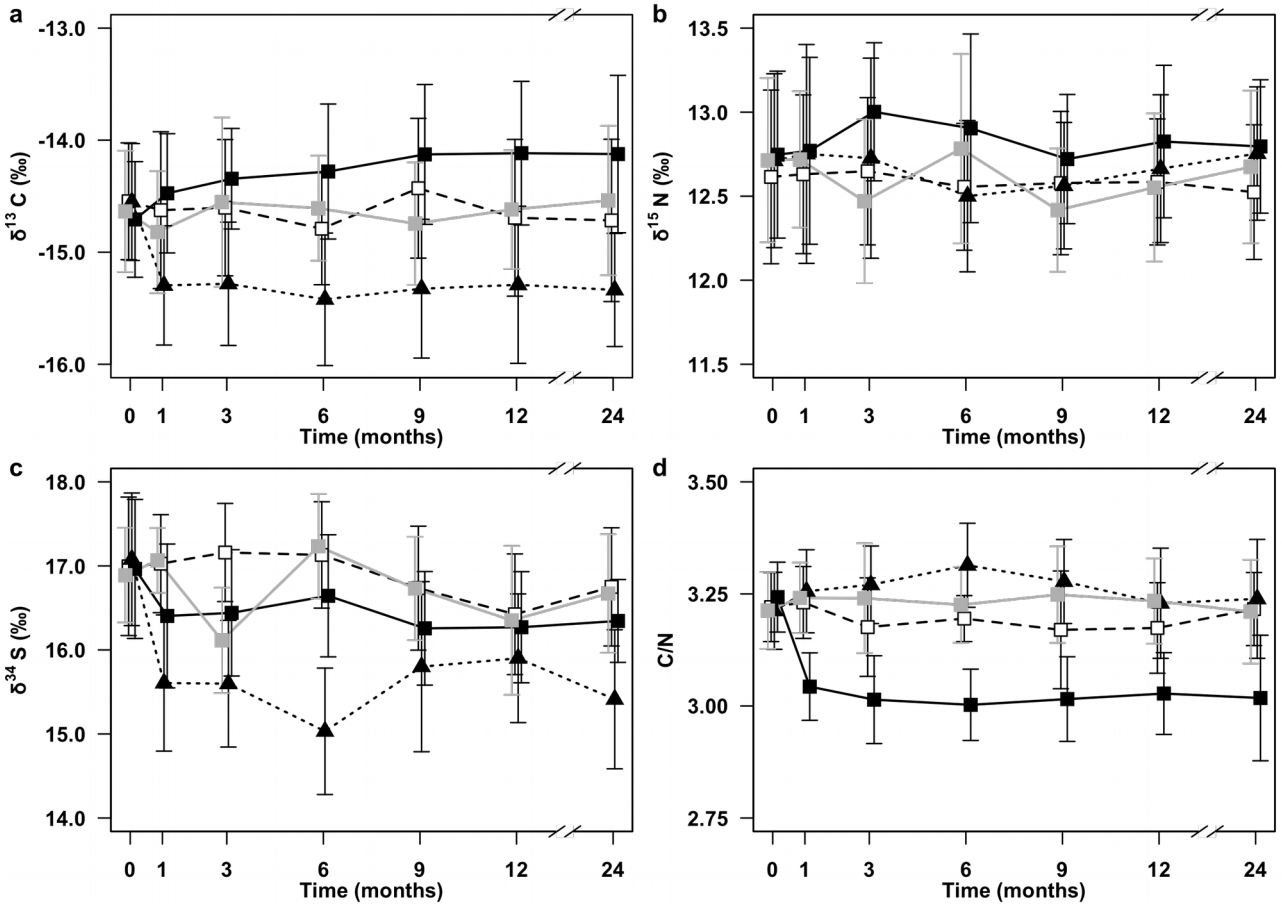


Fig. 3.1. Evolution of mean ± SD of a) $\delta^{13}C$ values, b) $\delta^{15}N$ values, c) $\delta^{34}S$ values, and d) C/N ratios in *Marthasterias glacialis* tissues stored frozen (white squares and dashed lines), dried (grey squares and lines), in formaldehyde (black triangles and dotted lines) or in ethanol (black squares and solid lines) for 24 months.

Table 3.2. Results (P-values) of the post-hoc analyses with Bonferroni correction computed after the ANOVAs assessing the effect of time of preservation on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values and on C/N ratios in *Marthasterias glacialis* samples stored frozen, dried, in formaldehyde or in ethanol during two years. Bold results are significant. Post-hoc analyses are not available (NA) when the ANOVA is not significant. Asterisks indicate times of analysis for which correction factors were used.

Freezing

$\delta^{13}C$

	0	1	3	6	9	12	24
0							
1							
3							
6				NA			
9							
12							
24							

$\delta^{15}N$

	0	1	3	6	9	12	24
0							
1							
3							
6				NA			
9							
12							
24							

$\delta^{34}S$

	0	1	3	6	9	12	24
0	-						
1	1,000	-					
3	1,000	1,000	-				
6	1,000	1,000	1,000	-			
9	1,000	1,000	1,000	1,000	-		
12	0,939	0,120	**0,002**	0,338	1,000	-	
24	1,000	1,000	1,000	0,878	1,000	1,000	-

C/N

	0	1	3	6	9	12	24
0	–						
1	1,000	–					
3	1,000	0,430	–				
6	1,000	1,000	1,000	–			
9	1,000	1,000	1,000	1,000	–		
12	0,440	0,510	1,000	1,000	1,000	–	
24	1,000	1,000	1,000	1,000	1,000	1,000	–

Drying

$\delta^{13}C$

	0	1	3	6	9	12	24
0							
1							
3							
6				NA			
9							
12							
24							

$\delta^{15}N$

	0	1	3	6	9	12	24
0	–						
1	1,000	–					
3	0,562	0,283	–				
6	1,000	1,000	0,245	–			
9	0.138	**0.024**	1,000	0.061	–		
12	1,000	0,398	1,000	**0,016**	1,000	–	
24	1,000	1,000	0,330	1,000	**0.026**	**0,011**	–

$\delta^{34}S$

	0	1	3	6	9	12	24
0	–						
1	1,000	–					
3	**0,017**	**< 0.001**	–				
6	1,000	1,000	**< 0.001**	–			
9	1,000	1,000	0,178	0,100	–		
12	1,000	0,104	1,000	**0,033**	1,000	–	
24	1,000	0,342	0,606	0,276	1,000	1,000	–

C/N

	0	1	3	6	9	12	24
0							
1							
3							
6				NA			
9							
12							
24							

Table 3.2. continued.

Formaldehyde

$\delta^{13}C$

	0	1	3	6	9	12	24
0	–						
1	**< 0.001**	–					
3	**< 0.001**	1,000	–				
6	**< 0.001**	1,000	1,000	–			
9	**< 0.001**	1,000	1,000	1,000	–		
12	**< 0.001**	1,000	1,000	1,000	1,000	–	
24	**< 0.001**	1,000	1,000	1,000	1,000	1,000	–

$\delta^{13}C$ correction

	0	1*	3*	6*	9*	12*	24*
0							
1*							
3*							
6*				NA			
9*							
12*							
24*							

$\delta^{15}N$

	0	1	3	6	9	12	24
0	–						
1	1,000	–					
3	1,000	1,000	–				
6	1,000	1,000	0,766	–			
9	1,000	1,000	0,684	1,000	–		
12	1,000	1,000	1,000	1,000	1,000	–	
24	1,000	1,000	1,000	**0,027**	**0,008**	1,000	–

$\delta^{34}S$

	0	1	3	6	9	12	24
0	–						
1	**< 0.001**	–					
3	**0.002**	1,000	–				
6	**< 0.001**	0,256	0,797	–			
9	**0,006**	1,000	1,000	0,214	–		
12	**0,015**	1,000	0,877	0,059	1,000	–	
24	**< 0.001**	1,000	1,000	1,000	1,000	1,000	–

$\delta^{34}S$ correction

	0	1*	3*	6*	9*	12*	24*
0	–						
1*	1,000	–					
3*	1,000	1,000	–				
6*	0.680	0,256	0,797	–			
9*	1,000	1,000	1,000	0,214	–		
12*	1,000	1,000	0,877	0,059	1,000	–	
24*	1,000	1,000	1,000	1,000	1,000	1,000	–

C/N

	0	1	3	6	9	12	24
0	–						
1	1,000	–					
3	0.739	1,000	–				
6	**0.005**	0.276	0,797	–			
9	0,310	1,000	1,000	1,000	–		
12	1,000	1,000	1,000	0,086	0,211	–	
24	1,000	1,000	1,000	0,120	1,000	1,000	–

Ethanol

$\delta^{13}C$

	0	1	3	6	9	12	24
0	–						
1	1,000	–					
3	0,084	1,000	–				
6	0,075	1,000	1,000	–			
9	**0.008**	0.253	0.527	1,000	–		
12	**< 0.001**	0,068	1,000	1,000	1,000	–	
24	**0,003**	0,551	1,000	1,000	1,000	1,000	–

$\delta^{13}C$ correction

	0	1	3	6	9*	12*	24*
0	–						
1	1,000	–					
3	0.084	1,000	–				
6	0.075	1,000	1,000	–			
9*	1,000	1,000	**0.008**	0.380	–		
12*	1,000	0.732	0.261	**0.008**	1,000	–	
24*	1,000	1,000	0.409	0.169	1,000	1,000	–

$\delta^{15}N$

	0	1	3	6	9	12	24
0							
1							
3							
6				NA			
9							
12							
24							

$\delta^{34}S$

	0	1	3	6	9	12	24
0	–						
1	0,415	–					
3	1,000	1,000	–				
6	1,000	1,000	1,000	–			
9	0,245	1,000	1,000	0,754	–		
12	0,146	1,000	1,000	0,997	1,000	–	
24	**0,025**	1,000	1,000	1,000	1,000	1,000	–

$\delta^{34}S$ correction

	0	1	3	6	9	12	24*
0	–						
1	0,415	–					
3	1,000	1,000	–				
6	1,000	1,000	1,000	–			
9	0,245	1,000	1,000	0,754	–		
12	0,146	1,000	1,000	0,997	1,000	–	
24*	1,000	0.347	0.061	1,000	**0.018**	**0.012**	–

C/N

	0	1	3	6	9	12	24
0	–						
1	**< 0.001**	–					
3	**< 0.001**	1,000	–				
6	**< 0.001**	1,000	1,000	–			
9	**< 0.001**	1,000	1,000	1,000	–		
12	**< 0.001**	1,000	1,000	1,000	1,000	–	
24	**< 0.001**	1,000	1,000	1,000	1,000	1,000	–

Significant influences of the preservation method ($F_{3,57} = 22.848$, $P < 0.001$) and of its interaction with the time of analysis ($F_{18,342} = 2.986$, $P < 0.001$) were observed on $\delta^{15}N$ values. Subsequent ANOVAs performed in each preservation method revealed inconsistent effects of drying on $\delta^{15}N$ values ($F_{6,114} = 4.436$, $P < 0.001$, Fig. 3.1.b) as there was no significant differences of $\delta^{15}N$ values between T_0 and other times of analysis, but some differences between times of analysis (Table 3.2). Furthermore, storage in formaldehyde ($F_{6,114} = 2.136$, $P = 0.055$) and ethanol ($F_{6,114} = 2.178$, $P = 0.050$) appeared to have a marginally significant effect on $\delta^{15}N$ values (Fig. 3.1.b).

Results of the two-way repeated measures ANOVA showed an influence of preservation method ($F_{3,57} = 87.415$, $P < 0.001$), time of analysis ($F_{6,114} = 7.371$, $P < 0.001$) and of their interaction ($F_{18,342} = 6.617$, $P < 0.001$) on $\delta^{34}S$ values. $\delta^{34}S$ values inconsistently changed in frozen samples ($F_{6,114} = 3.168$, $P = 0.007$), with samples stored during 3 and 12 months having significantly different $\delta^{34}S$ values (Fig. 3.1.c, Table 3.2). Inconsistent changes of $\delta^{34}S$ values also occurred in dried samples ($F_{6,114} = 7.255$, $P < 0.001$), with significant deviance from $\delta^{34}S$ values of T_0 samples occurring only at 3 months of preservation but not earlier or later (Fig. 3.1.c). $\delta^{34}S$ values significantly changed in samples stored in formaldehyde ($F_{6,114} = 11.950$, $P < 0.001$). $\delta^{34}S$ values of preserved samples were significantly lower than those of T_0 samples for all time periods, with the mean shift of $\delta^{34}S$ values between T_0 and those times of analysis being -1.5 ± 1.2 ‰ (Fig. 3.1.c). Adding 1.5 to $\delta^{34}S$ values of samples preserved in formaldehyde suppressed any significant differences in $\delta^{34}S$ values between times of analysis appeared despite the ANOVA remaining significant, but with a very low F value ($F_{6,114} = 2.327$, $P = 0.037$; Table 3.2). A significant influence of ethanol preservation on $\delta^{34}S$ values was observed ($F_{6,114} = 2.659$, $P = 0.018$) but different $\delta^{34}S$ values could be seen only between T_0 samples and samples stored during 24 months in the post-hoc analysis (Fig. 3.1.c, Table 3.2). The mean shift of $\delta^{34}S$ values between T_0 samples and samples stored in ethanol during 24 months was -0.7 ± 1.0 ‰. Adding 0.7 to $\delta^{34}S$ values of samples preserved during 24 months in ethanol suppressed the slightly significant difference of $\delta^{34}S$ values between them and T_0 samples. However, this correction created differences between $\delta^{34}S$ values of samples stored during 24 months and other times of analysis appeared (Table 3.2), and caused an increase of the ANOVA's F value ($F_{6,114} = 4.323$, $P < 0.001$).

Significant influences of preservation method ($F_{3,57} = 162.972$, $P < 0.001$), time of analysis ($F_{6,114} = 2.641$, $P = 0.020$) and of their interaction ($F_{18,342} = 10.209$, $P < 0.001$) were observed on C/N ratios. Subsequent ANOVAs and post-hoc analyses in each preservation method showed marginal effects of freezing on C/N ratios ($F_{6,114} = 2.252$, $P = 0.043$) and pairwise comparisons with

Bonferroni correction did not detect any significant change in C/N ratios (Table 3.2). Storage in formaldehyde ($F_{6,114} = 3.948$, $P = 0.001$) and ethanol ($F_{6,114} = 20.740$, $P < 0.001$, Fig. 3.1.d) induced changes of C/N ratios. For samples stored in formaldehyde, higher C/N ratios were observed at 6 months of preservation than in T_0 samples (Table 3.2). For ethanol, the C/N ratios immediately decreased at the first month of preservation and then remained stable throughout the experiment (Table 3.2). In this case, the difference of C/N ratios between T_0 samples and preserved samples was 0.22 ± 0.10.

When computed with $\delta^{13}C$ and $\delta^{15}N$ values, the ellipse parameters changed little and inconsistently and, as a result, they were similar at the beginning and at the end of the experiment (Fig. 3.2). Changes in SEA_B occurred between T_0 samples and each time of preservation for samples stored dried or ethanol (Fig. 3.3). For samples stored dried, SEA_B for samples stored during 3 months were higher than for T_0 ones ($p = 95.3$ %; Fig. 3.3.b). For samples stored in ethanol, SEA_B for samples stored during 1 month ($p = 98.4$ %) and 24 months ($p = 95.5$ %) were higher than for the T_0 ones (Fig. 3.3.d). Yet, these changes did not occur consistently for other times of preservation. The overlap between T_0 ellipses and ellipses for other times of analysis appeared to be weak in samples stored in formaldehyde and in ethanol (Fig. 3.4) because of the shift of mean $\delta^{13}C$ values previously observed for these two preservative fluids (Fig. 3.1.a).

When the standard ellipses were computed with $\delta^{13}C$ and $\delta^{34}S$ values, more important and more inconsistent changes in the parameters occurred (Fig. 3.5). Indeed, changes of the length of ellipses' axes frequently exceeded 0.1 ‰ (Fig. 3.5.a and 3.5.b). In all methods, the angles of the ellipses were the opposite of the angle of ellipses from T_0 samples at least at one time of analysis and even the angles of ellipses from T_0 samples were different between preservation methods (Fig. 3.5.c), resulting in inverted orientation of the ellipses. Changes in the SEA_B did not occur during the experiment (Fig. 3.6). The absence of overlap between T_0 ellipses and ellipses for other times of analysis that appeared in samples stored in formaldehyde, as well as the weak overlap that appeared in ethanol (Fig. 3.7) is mostly the result of the shift of both mean $\delta^{13}C$ and $\delta^{34}S$ values previously observed for these two preservative fluids (Fig. 3.1.a and 3.1.c).

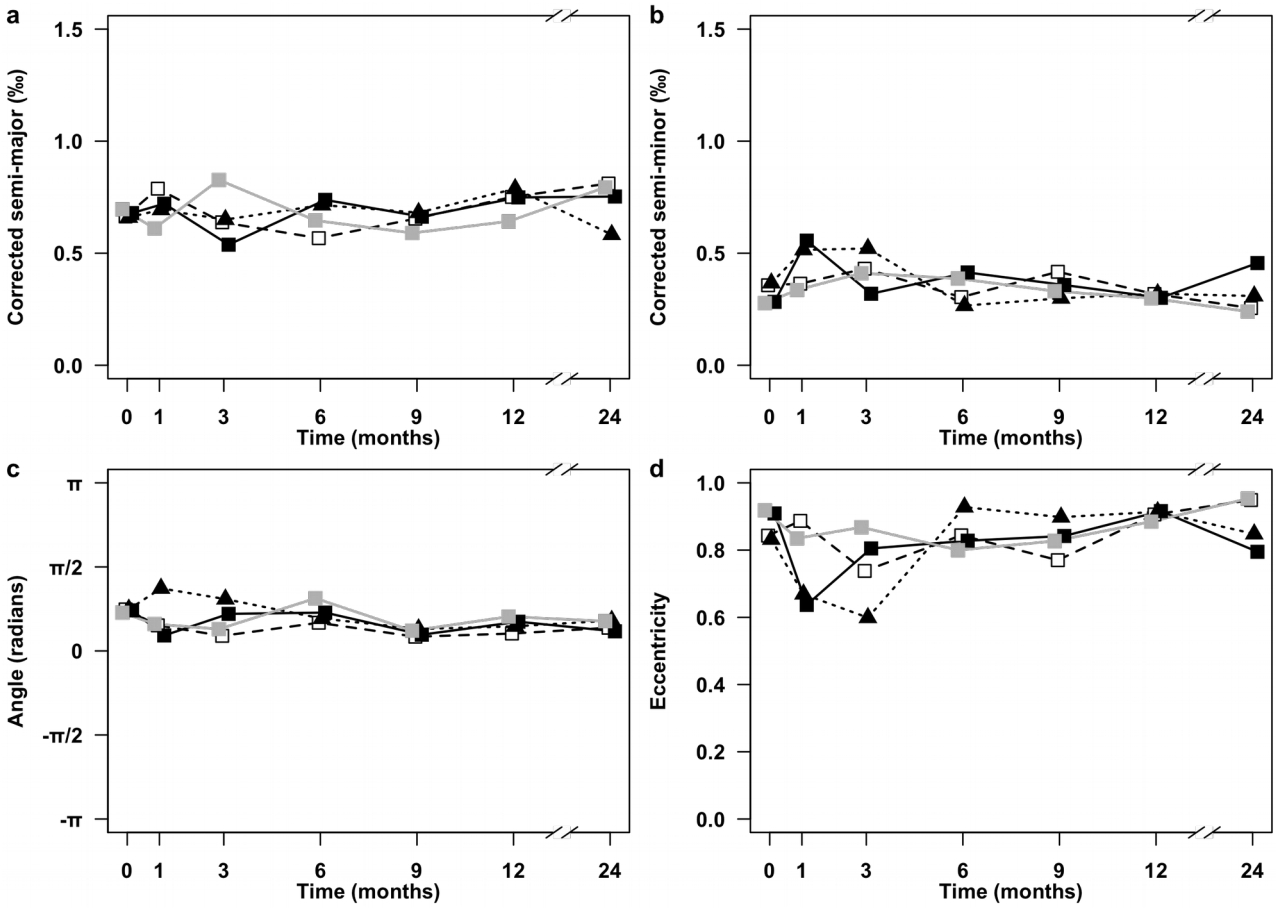


Fig. 3.2. Evolution of standard ellipse parameters computed with $\delta^{13}C$ and $\delta^{15}N$ values in *Marthasterias glacialis* tissues stored frozen (white squares and dashed lines), dried (grey squares and lines), in formaldehyde (black triangles and dotted lines), or in ethanol (black squares and full lines) during 24 months: a) length of the ellipse's semi-major axis corrected for sample size, b) length of the ellipse's semi-minor axis corrected for sample size, c) angle of the semi-major axis with the x axis and d) ellipse's eccentricity.

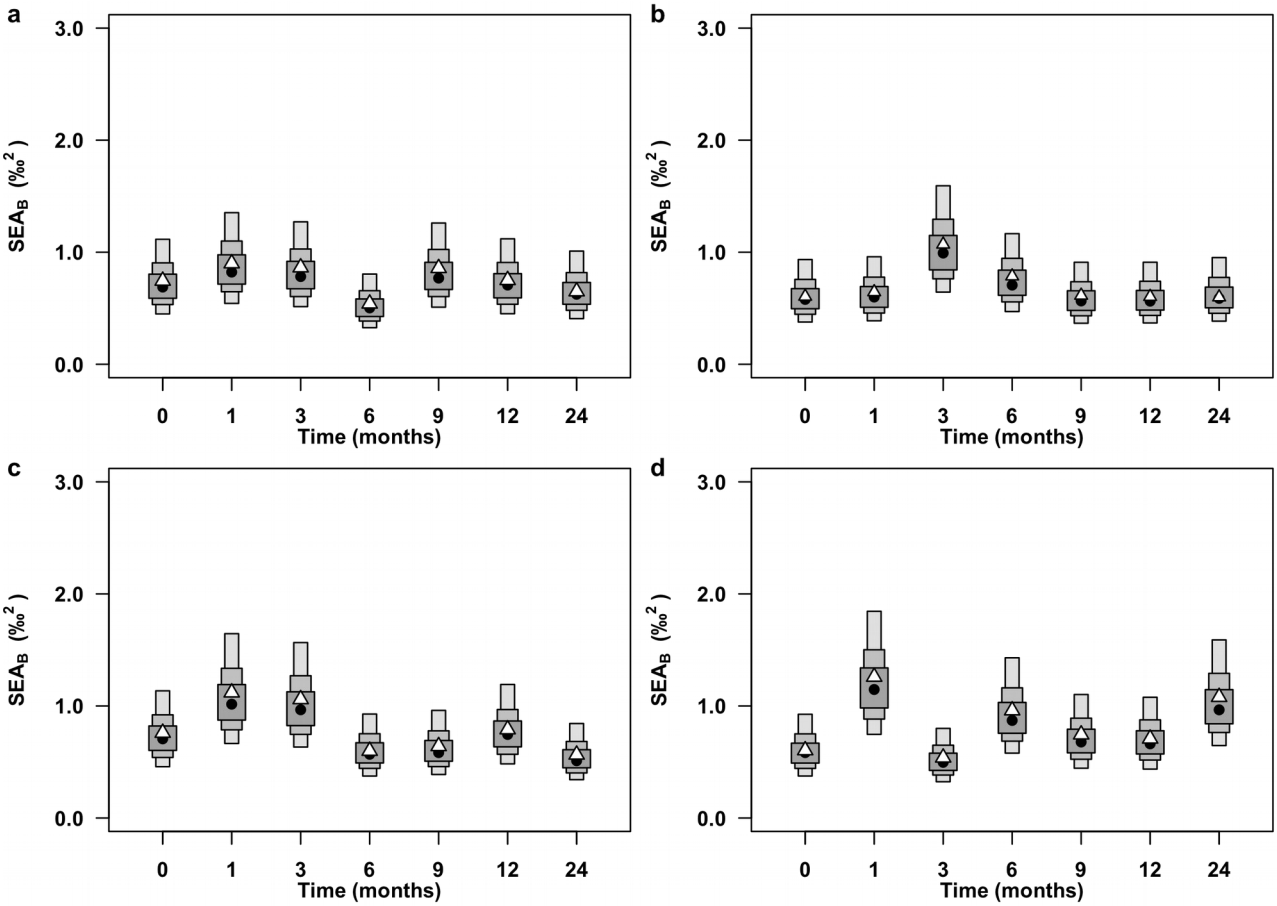


Fig. 3.3. SIBER density plots depicting evolution of standard ellipse areas computed with $\delta^{13}C$ and $\delta^{15}N$ values and estimated with Bayesian analysis, as well as standard ellipse areas corrected for sample size, in *Marthasterias glacialis* tissues stored a) frozen, b) dried, c) in formaldehyde, or d) in ethanol during 24 months. Black dots are the modes. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals, from dark to light grey. White triangles are standard ellipse areas corrected for sample size.

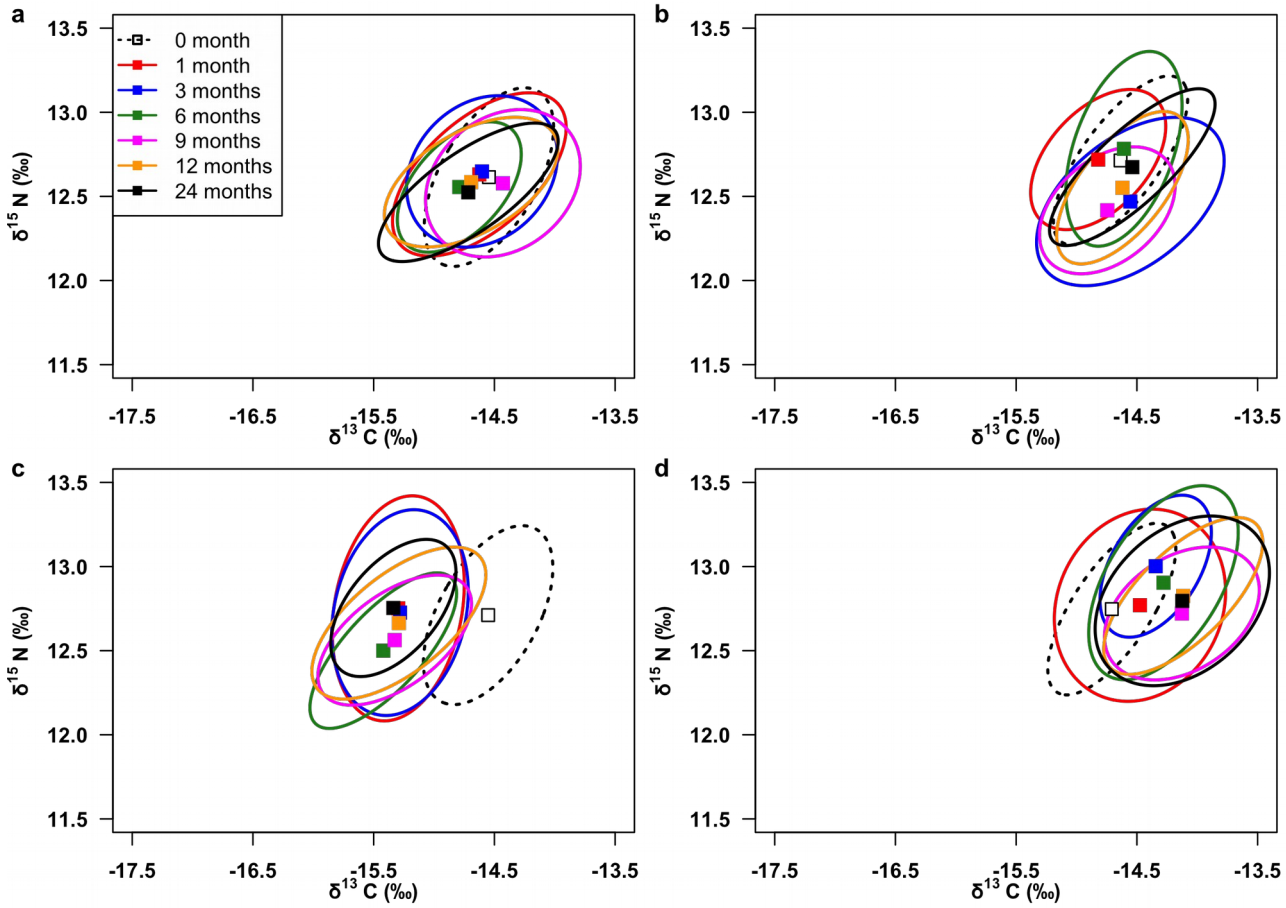


Fig. 3.4. Evolution of mean stable isotope ratios and isotopic niche computed with $\delta^{13}C$ and $\delta^{15}N$ values in *Marthasterias glacialis* tissues stored a) frozen, b) dried, c) in formaldehyde, or d) in ethanol during 24 months.

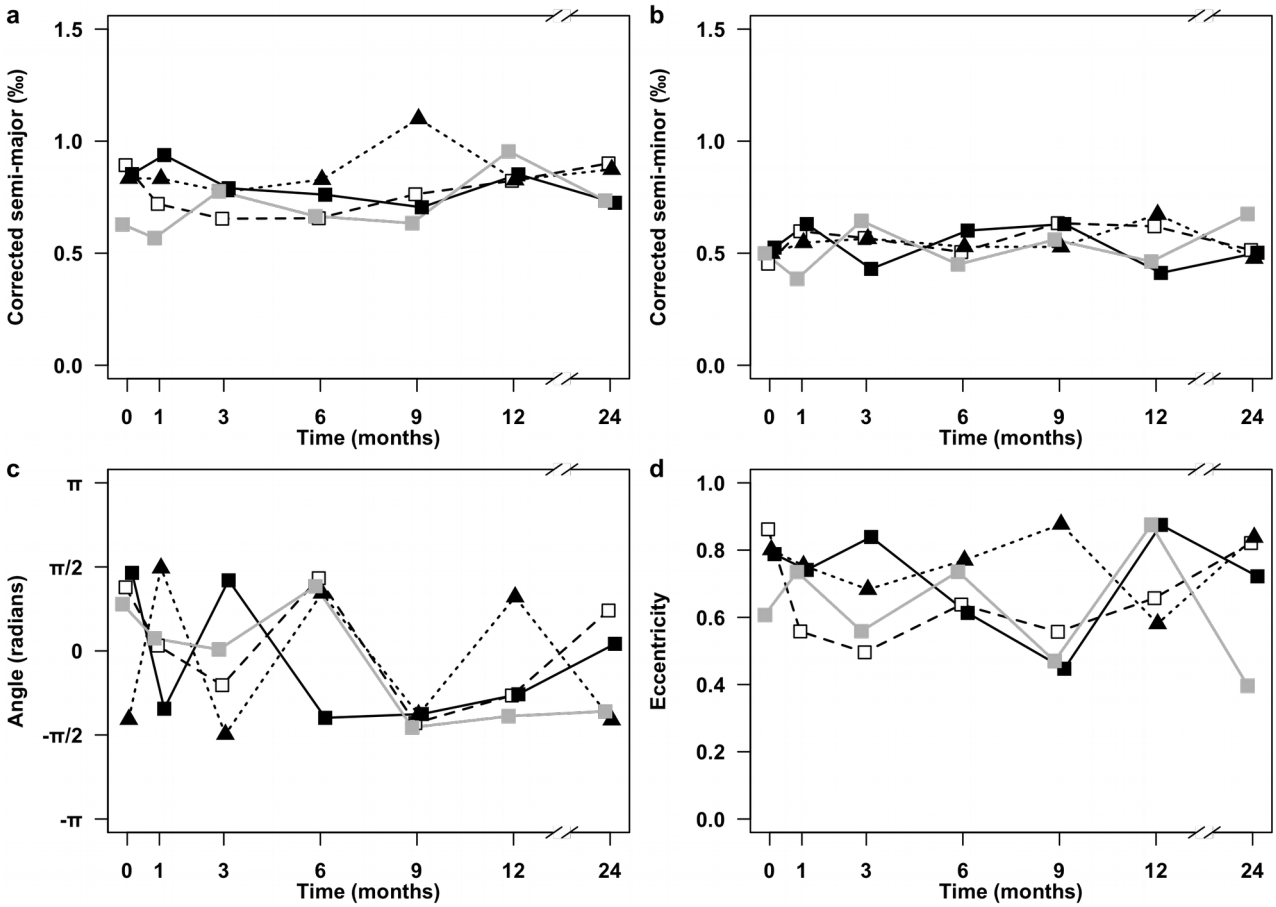


Fig. 3.5. Evolution of standard ellipse parameters computed with $\delta^{13}C$ and $\delta^{34}S$ values in *Marthasterias glacialis* tissues stored frozen (white squares and dashed lines), dried (grey squares and lines), in formaldehyde (black triangles and dotted lines), or in ethanol (black squares and full lines) during 24 months: a) length of the ellipse's semi-major axis corrected for sample size, b) length of the ellipse's semi-minor axis corrected for sample size, c) angle of the semi-major axis with the x axis and d) ellipse's eccentricity.

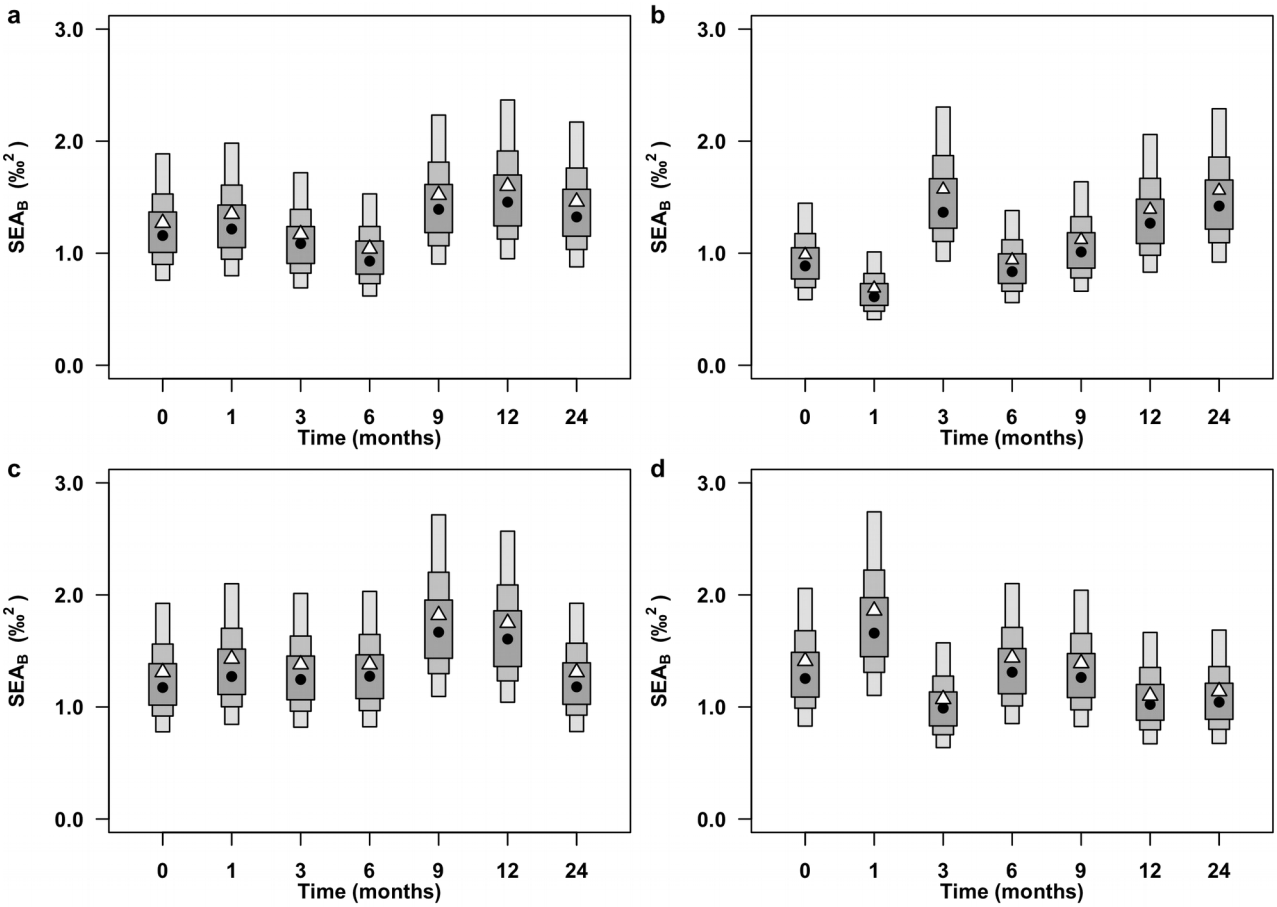


Fig. 3.6. SIBER density plots depicting evolution of standard ellipse area computed with $\delta^{13}C$ and $\delta^{34}S$ values and estimated with Bayesian analysis, as well as standard ellipse areas corrected for sample size, in *Marthasterias glacialis* tissues stored a) frozen, b) dried, c) in formaldehyde, or d) in ethanol during 24 months. Black dots are the modes. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals, from dark to light grey. White triangles are sample size corrected standard ellipse areas corrected for sample size.

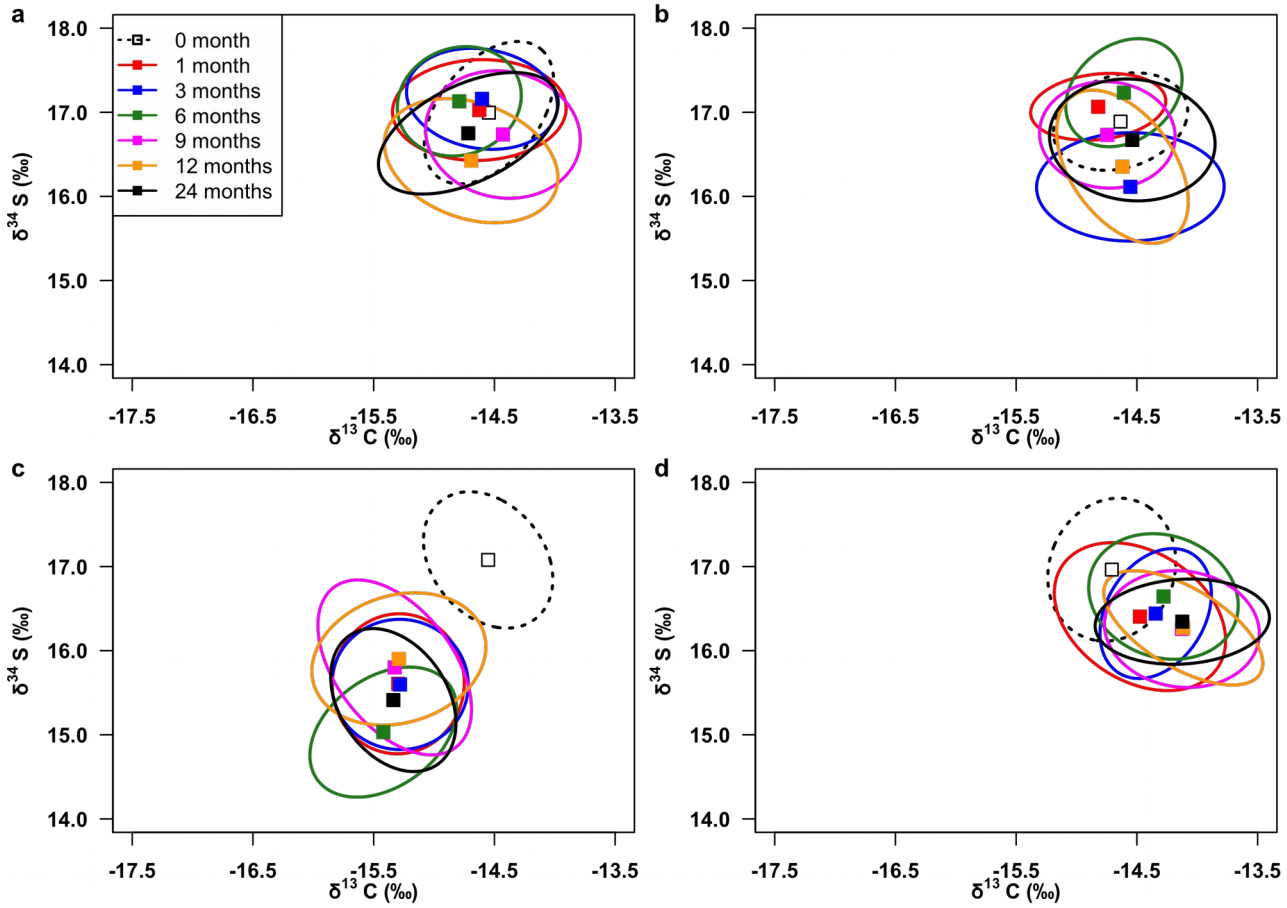


Fig. 3.7. Evolution of mean stable isotope ratios and isotopic niche computed with $\delta^{13}C$ and $\delta^{34}S$ values in *Marthasterias glacialis* tissues stored a) frozen, b) dried, c) in formaldehyde, or d) in ethanol during 24 months.

3.4 Discussion

Contrasting effects of preservation on $\delta^{13}C$ values in sea stars were observed. Freezing and drying had no or marginal effect on $\delta^{13}C$ values throughout time. Formaldehyde induced a rapid decrease of –0.8 ± 0.5 ‰ for $\delta^{13}C$ values during the first month of preservation. Those values were subsequently stable throughout the experiment. Decrease followed by stability in $\delta^{13}C$ values were frequently observed for organisms stored in formaldehyde (Kaehler and Pakhomov, 2001; Sarakinos et al., 2002; Xu et al., 2011). However, the time at which the change in $\delta^{13}C$ values occurs may differ, going from several weeks (Kaehler and Pakhomov, 2001; Sarakinos et al., 2002; Xu et al., 2011) to one year (Fanelli et al., 2010). Furthermore, the decrease of $\delta^{13}C$ values we observed is usually lower than the previously reported shift induced by formaldehyde. After the initial change, $\delta^{13}C$ values seems to remain stable during longer term preservation (Rennie et al., 2012). Proteins lysis (Sarakinos et al., 2002) and/or integration of C from the preservative liquid into the samples (Kaehler and Pakhomov, 2001; Edwards et al., 2002; Sarakinos et al., 2002) are proposed mechanisms to explain this phenomenon. Increasing C/N ratios in samples stored in formaldehyde (Fanelli et al., 2010; Lau et al., 2012) support this hypothesis, and higher C/N ratios were observed at 6 months of preservation in our experiment. Considering that $\delta^{13}C$ values are not further altered by formaldehyde following the initial change, we recommend to use a correction factor for $\delta^{13}C$ values of sea star samples in formaldehyde for more than 1 month no matter how long they have been preserved. Indeed, adding 0.8 ‰ to $\delta^{13}C$ values of samples stored in formaldehyde resulted in similar carbon isotopic ratios between fresh and preserved samples in our experiment. Testing the influence of ethanol on isotopic values led to conflicting results: either stable (Sarakinos et al., 2002; Fanelli et al., 2010) or increasing (Kaehler and Pakhomov, 2001; Sarakinos et al., 2002; Fanelli et al., 2010; Xu et al., 2011) $\delta^{13}C$ values in samples were previously observed. In *Marthasterias glacialis*, a gradual increase in $\delta^{13}C$ values was observed. This increase became significant after 9 months of preservation where it went up to 0.6 ± 0.5 ‰. This phenomenon may be explained by the extraction of lipids by ethanol (Von Endt, 1994), as highlighted by the decrease in C/N ratios we observed for samples stored in ethanol. Long-term preservation in ethanol could also induce leaching of other compounds such as amino acids (Von Endt, 1994). These results suggest that using a correction factor for $\delta^{13}C$ values of ethanol-preserved sea stars stored during more than 9 months is advised. Indeed, adding –0.6 ‰ to $\delta^{13}C$ values of samples stored more than 9 months in ethanol suppressed significant differences between fresh and preserved samples in our experiment.

No major $\delta^{15}N$ changes were recorded for any of the preservation methods. Freezing, formaldehyde and ethanol did not lead to any significant differences. Some differences were present in the drying experiment, but these changes were not consistent over time and occurred between times of analysis and not between $\delta^{15}N$ values of dried samples and those of T_0 samples. Seasonal variations in temperature and humidity in the storage room could contribute to this inconsistent variability in $\delta^{15}N$ values throughout the experiment. Conflicting results were usually reported on the impact of formaldehyde and ethanol on $\delta^{15}N$ values (e.g. Sarakinos et al., 2002; Fanelli et al., 2010; Lau et al., 2012; Rennie et al., 2012), suggesting that $\delta^{15}N$ values are generally not affected by preservation.

In this study, $\delta^{34}S$ of sea stars was much more variable than the two other isotopic ratios. Standard deviation on a sea star sample randomly chosen as secondary analytical standard was 0.3 ‰ for $\delta^{13}C$ values, 0.2 ‰ for $\delta^{15}N$ values, but 0.8 ‰ for $\delta^{34}S$ values. This could be caused by a higher natural variability of this parameter in sea stars, but also because of a higher analytical error, as sea star tissues contain low amounts of total sulfur. Our results therefore have to be interpreted with caution. Nevertheless, they suggest that formaldehyde, and possibly ethanol reduce $\delta^{34}S$ values. In formaldehyde, $\delta^{34}S$ values of preserved samples were significantly lower than $\delta^{34}S$ values of fresh samples after the first month of preservation. However, adding a correction factor of 1.5 to $\delta^{34}S$ values of preserved samples in our experiment allowed correcting the effects of preservation, despite the within-treatment error being close to the average $\delta^{34}S$ value shift (–1.5 ± 1.2 ‰). A weaker and slower decrease in $\delta^{34}S$ values occurred in samples stored in ethanol, with the decrease being slightly significant only at 24 months of preservation. By comparison, previous studies observed different effects of preservative fluids on $\delta^{34}S$ values. Indeed, an increase in mean $\delta^{34}S$ values was observed in teleosts fixed with formaldehyde and then stored in ethanol (0.8 ± 0.5 ‰; Edwards et al., 2002) while no effects of ethanol preservation were observed on $\delta^{34}S$ values in bear tissues (Javornik et al., 2019). Our results suggest that a using a correction factor to mitigate the effects of ethanol on $\delta^{34}S$ values is not adequate. The within-treatment error was indeed higher than the average $\delta^{34}S$ value shift (–0.7 ± 1.0 ‰). Moreover, although using this correction factor prevented significant differences between $\delta^{34}S$ values of T_0 samples and $\delta^{34}S$ values of samples stored during 24 months, it created previously non-existing significant differences between samples stored during 24 months and several other times of analysis. Furthermore, use of this correction factor seemed to increase the overall inter-treatment variability, as shown by the higher ANOVA F value. Considering these results, we do not advise using correction factors for $\delta^{34}S$ values of star

tissues preserved in ethanol. For samples stored frozen or dried, no significant or consistent differences in $\delta^{34}S$ values between fresh and preserved samples were observed.

Ellipse parameters computed with $\delta^{13}C$ and $\delta^{15}N$ values were slightly affected by preservation, resulting in estimation of SEA_B being inconsistently affected in samples stored dried or in ethanol while not affected by freezing and formaldehyde. Consequently, preservation does not seem to be an obstacle to the study of isotopic niches computed with $\delta^{13}C$ and $\delta^{15}N$ values, and thus trophic niches, of sea stars using ellipses-based methods and the lack of overlap between fresh and preserved samples is more likely the result of the changes in mean $\delta^{13}C$ values. By contrast, inconsistent variations in ellipse parameters occurred when computed with $\delta^{13}C$ and $\delta^{34}S$ values, because of both the preservation-induced changes in $\delta^{34}S$ values and the higher variability of this parameter. While these results need to be further tested both in sea stars and other taxa, caution is advised when dealing with sulfur isotopic ratios of fluid-preserved samples.

To summary, our results show that the preservation method has to be taken into account when analysing stable isotope ratios of carbon in sea stars. Both freezing and drying appear as the best preservation methods (Table 3.3). Freezing did not induce changes in $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ values or ellipse parameters when computed with $\delta^{13}C$ and $\delta^{15}N$ values. This result is in accordance with previous studies where freezing is generally considered as one of the best preservation methods with no effect on stable isotope ratios being observed (Bosley and Wainright, 1999; Kaehler and Pakhomov, 2001; Sweeting et al., 2004 Oczkowski et al., 2015), although some exceptions occurred (Feuchtmayr and Grey, 2003; Syväranta et al., 2011; Jesus et al., 2015). Drying appeared to have no effect on $\delta^{13}C$ values and minimal effect on $\delta^{34}S$ values but long-term drying could induce inconsistent variability of $\delta^{15}N$ values. While formaldehyde induced a sharp decrease of -0.8 ± 0.5 ‰ in $\delta^{13}C$ values during the first month of preservation, $\delta^{13}C$ values remained stable once altered and it is thus possible to correct the effects of preservation with a same correction factor, no matter how long sea stars were stored in formaldehyde. A decrease and then stability of $\delta^{13}C$ values in samples stored in formaldehyde was previously observed (Kaehler and Pakhomov, 2001; Sarakinos et al., 2002; Xu et al., 2011), including at the decadal scale (Rennie et al., 2012). Furthermore, $\delta^{15}N$ values and ellipse parameters computed with $\delta^{13}C$ and $\delta^{15}N$ values did not appear to be strongly affected by preservation in formaldehyde, and the change of the position of the ellipse is the result of the changes of mean $\delta^{13}C$ values. $\delta^{34}S$ values decreased in samples stored in formaldehyde but this change can be corrected for. The results showed that $\delta^{13}C$ values are affected by storage in ethanol, likely because of lipid extraction. Considering the significant increase in $\delta^{13}C$ values

observed in other taxa (Kaehler and Pakhomov, 2001; Sarakinos et al., 2002; Fanelli et al., 2010), some knowledge on the lipid (or other ethanol-soluble compounds) content of samples may be beneficial before analysing sea star samples stored in ethanol. By contrast, $\delta^{15}N$ values were not affected by ethanol preservation. Furthermore, long-term preservation in ethanol appeared to induce a decrease in $\delta^{34}S$ values. However, using a correction factor for $\delta^{34}S$ values in sea star samples stored in ethanol is not advised. Overall, the four preservation methods tested in this experiment either minimally impacted stable isotope ratios or induced impacts that could be dealt with by using correction factors. Such results tend to indicate that sea stars samples stored in preservative fluids, and thus, those stored by museums, may be used for trophic ecology studies using stable isotope ratios.

Table 3.2. Summary of the influence of preservation methods on $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ values, C/N ratios, Bayesian estimation standard ellipse area (SEA_B) computed with $\delta^{13}C$ and $\delta^{15}N$ and with $\delta^{13}C$ and $\delta^{34}S$ in *Marthasterias glacialis* tissues preserved during 24 months.

	$\Delta\delta^{13}C$ (‰)	$\Delta\delta^{15}N$ (‰)	$\Delta\delta^{34}S$ (‰)	C/N	SEA_B with $\delta^{13}C$ and $\delta^{15}N$	SEA_B with $\delta^{13}C$ and $\delta^{34}S$
Freezing	Not significant	Not significant	Inconsistent	Not significant	Not significant	Not significant
Drying	Not significant	Inconsistent	Inconsistent	Not significant	Inconsistent	Not significant
Formaldehyde	↓ –0.8 ± 0.5 ‰	Not significant	↓ –1.5 ± 1.2 ‰	Inconsistent	Not significant	Not significant
Ethanol	↑ +0.6 ± 0.5 ‰	Not significant	↓ –0.7 ± 1.0 ‰*	↑ +0.22 ± 0.10	Inconsistent	Not significant

* Significant difference only between samples at T_0 and preserved samples at 24 months.

Chapter 4: Food web structure of a Subantarctic nearshore community: main food chains and trophic role of sea stars

View of Port-aux-Français scientific station in Kerguelen Islands (picture by Patoir A).

4.1 Introduction

Knowledge on the food web structure and functioning is mandatory for proper environmental management, and to understand how future environmental changes could impact ecosystems. Indeed, identifying the various trophic groups of a food web is necessary as each trophic group directly or indirectly influences each other. Organisms directly influencing each others' abundance thanks to trophic relationships is a well-known phenomenon (e.g. Krebs et al., 2001; Sala et al., 2011) which was modelled early (Lotka, 1925; Volterra, 1926). However, indirect interactions may also occur. For example, basal food sources and higher predators indirectly influence each other by bottom-up (e.g. Ware and Thomson, 2005; Tulloch et al., 2019) or top-down control (e.g. Morris and Letnic, 2017; Burt et al., 2018). Another kind of indirect interaction may be competition between organisms of a same trophic group, and thus with similar trophic resources in an environment where their availability is limited. Indeed, competition may lead to trophic niche reduction (Tran et al., 2015; Jackson et al., 2016; Costa-Pereira et al., 2019) or expansion (Svanbäck and Bolnick, 2007; Costa-Pereira et al., 2019) or exclusion of one organism from the food web (Bøhn et al., 2008).

Food web structure in shallow (≤ 30 m) coastal Antarctic communities has been regularly studied. These communities are supported by a wide range of primary food sources, including pelagic production (Zenteno et al., 2019) and detritus (Dunton, 2001), but also micro- (Gillies et al., 2012) and macrophytobenthos (Dunton, 2001; Gillies et al., 2012; Zenteno et al., 2019). In comparison with their Antarctic counterpart, studies of benthic food webs in Subantarctic regions have been more limited, with studies mostly restricted to Patagonia (Dayton, 1985; Castilla, 1985; Adami and Gordillo, 1999; Andrade et al., 2016; Riccialdelli et al., 2017) while stations deeper than 30 m were considered as coastal in studies in Prince Edwards Islands (Kaehler et al., 2000; Puccinelli et al., 2018). In particular, several of these studies assessed the importance of kelp in the Subantarctic benthic food web functioning (Dayton, 1985; Castilla, 1985; Kaehler et al., 2000; 2006). Results from Patagonia indicate that Subantarctic food webs are mostly supported by benthic organic matter from both macrophytobenthos and sediment (Andrade et al., 2016; Riccialdelli et al., 2017). In Prince Edwards Islands, two kinds of nearshore food web were observed, with kelp-associated food webs being mostly supported by kelp but other nearshore food webs are supported by a mixture of pelagic organic matter and kelp (Kaehler et al., 2000).

Kelp forests refer to communities dominated by kelp, with the word "kelp" mostly referring to large Phaeophyceae from the order Laminariales. Among kelp species, *Macrocystis pyrifera* has a

wide distribution along the Pacific American coast, as well as in Subantarctic islands and on the Atlantic South American coast (Macaya and Zuccarello, 2010; Teagle et al., 2017; Fig. 4.1).

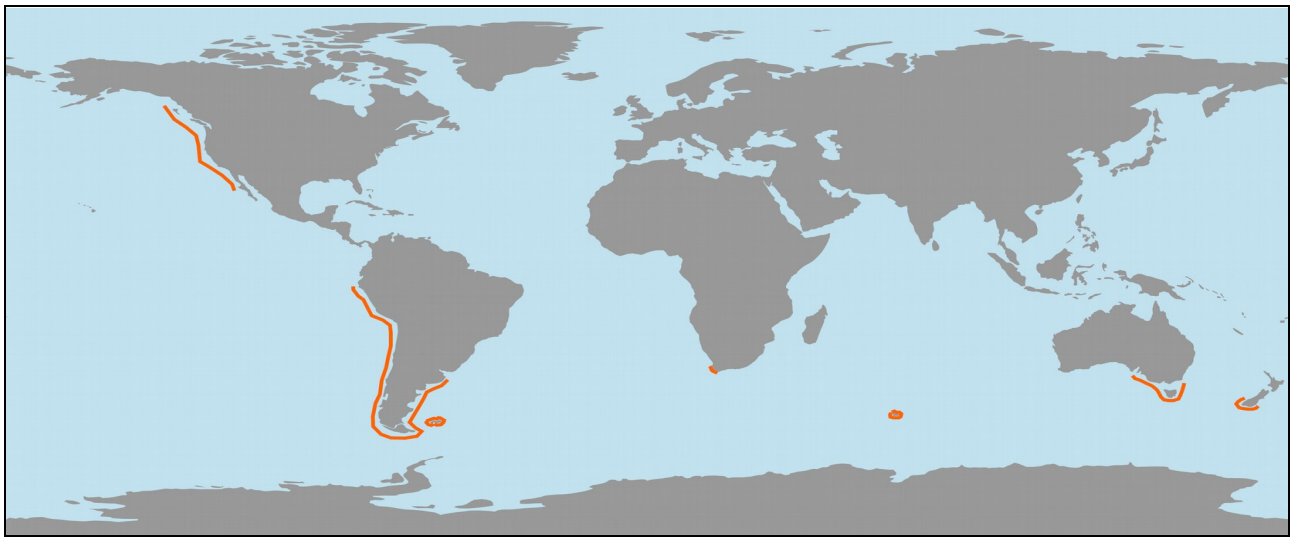


Fig. 4.1. Approximate worldwide distribution of *Macrocystis pyrifera* according to Teagle et al. (2017).

Kelp provides a physical habitat to productive communities (Miller et al., 2015; 2018; Teagle et al., 2017) and contribute to organism dispersal after being detached from the bottom by being transported over long distances along with their attached organisms (Helmuth et al., 1994; Hobday, 2000; Fraser et al., 2011; Nikula et al., 2013). However, in the Southern Ocean, the species *Durvillaea antarctica* is a better candidate than *Macrocystis pyrifera* for contributing to organism dispersal thanks to higher buoyancy (Smith, 2002; Fraser et al., 2011). In particular, the buoyancy of *Durvillaea antarctica* thalli allows to transport organisms by circumnavigating the Antarctic continent thanks to the Antarctic Circumpolar Current (ACC), as highlighted by specimens originating from Kerguelen and South Georgia Islands reaching King George Island by being transported eastward along the ACC (Fraser et al., 2018). Kelp is also a potential food source in benthic food webs (Page et al., 2008; Koenigs et al., 2015), but its importance for suspension feeders via detrital pathways seems variable (Page et al., 2008; Miller and Page, 2012; Renaud et al., 2015). However, most of the studies on food web functioning of kelp forests, dominated by *Macrocystis pyrifera* or not, focused on northern regions. Along the Pacific coast, *Macrocystis pyrifera* is an important food source for sea urchins, that can significantly reduce *Macrocystis pyrifera* abundance in case of overgrazing (Burt et al., 2018). Sea urchins themselves are the main prey of sea otters *Enhydra lutris* (Burt et al., 2018). The role of sea stars as a predator in the food

web functioning of kelp forest was initially considered as negligible (Harrold and Pearse, 1987). Nevertheless, studies have shown that sea stars contribute to prevent sea urchin pullulation by targeting small and medium individuals (Schroeter et al., 1983; Pearse and Hines, 1987; Schultz et al., 2016; Burt et al., 2018). In turn, the predation on sea urchins by sea otters and sea stars prevent kelp overgrazing by sea urchins (Schultz et al., 2016; Burt et al., 2018), and the absence of one of these predators is sufficient to release sea urchins from top-down control, resulting in an increased impact on kelp abundance despite the other predator being present (Burt et al., 2018). However, the distribution of sea otters is limited to the Northern Pacific and this species is thus absent from the Southern Pacific and the Southern Ocean (Tinker et al., 2018). As a result, food web dynamics are likely different between the northern and southern kelp forests and/or the importance of sea stars in regulating kelp consumers may be higher in southern kelp forests. On the one hand, in early studies on kelp forests from Patagonia, top-down control of kelp by sea urchins appeared to be more limited as the sea urchin *Loxechinus albus* mostly targets drifting kelp (Castilla, 1985) although overgrazing of live kelp may locally occur (Dayton, 1985). On the other hand, sea stars may still contribute to reduce the grazing pressure exerted by sea urchins in this region by excluding urchins from the areas where they are present (Dayton, 1985).

Kerguelen Islands are a Subantarctic archipelago in the Indian Ocean. Because of its proximity to the Polar Front, this archipelago has unique environmental characteristics. For example, higher levels of pelagic primary production than in the surrounding ocean may be observed on the Kerguelen plateau (Mongin et al., 2008), thanks to terrestrial inputs (Robinson et al., 2016) and to coastal upwelling (Schallenberg et al., 2018) leading, respectively, to downstream and upward transfer of dissolved iron to the continental shelf. Furthermore, Kerguelen waters are the habitat of an important benthic community (Améziane et al., 2011). The subtidal environment in coastal areas of Kerguelen Islands is characterised by kelp forests dominated by the Phaeophyceae *Macrocystis pyrifera* (Duchêne, 1984; Belsher and Mouchot, 1992) which are separated from the intertidal zone by successive belts of macrophytobenthos with each belt being dominated by a different group of species. The closest belt to the kelp forest is dominated by Rhodophycae but seasonal periods of abundance of the Phaeophyceae *Adenocystis* sp. may also occur. The second belt is dominated by the Ulvophyceae *Codium* sp. Finally, the Phaeophyceae *Durvillaea antarctica* dominates the belt closer to the shore (Duchêne, 1984).

Investigating the food web of kelp forests from Kerguelen Island may provide new insights on the food web functioning of coastal environments in Subantarctic islands and may also allow to

compare differences in the kelp forest ecosystem functioning between temperate, Patagonian and other Subantarctic environments. In this study, the food web structure of a nearshore kelp forest of the Subantarctic Kerguelen Islands was assessed by analysing stable isotope ratios of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulfur ($\delta^{34}S$) in various organism groups and by reconstructing trophic relationships between organisms with mixing models. By doing so, this study tries to assess the presence of consumers of *Macrocystis pyrifera* and of predators of these consumers in the Kerguelen nearshore subtidal ecosystem. In particular, this study would provide a first indication whether, like in northern kelp forests, sea stars may have a potential positive effect on kelp abundance by consuming their potential grazer.

4.2 Material and methods

4.2.1 Sampling, sample preparation and stable isotope analysis

Sampling occurred in Kerguelen archipelago, during the Proteker 5 campaign, from November 17th to December 4th 2016 and on the subtidal BIOMAR sampling site, near the Port-aux-Français scientific station (*ca* 49° 21' S and 70° 13' E, Fig. 4.2). Data from other sampling stations and intertidal areas were not included in this study. Benthic organisms and organic matter sources were collected by a scuba diver between 5 and 13 m deep. These samples include macrophytobenthos, macrophytobenthic detritus, surface sediment and benthic invertebrates (Table 4.1 and Fig. 4.3). Furthermore, subsurface seawater samples (volumes: from 1.8 to 2.1 dm^3) were collected and filtered on pre-combusted (400°C, 4 h) GF/F filters to recover suspended particulate organic matter (POM). Samples were either immediately dissected and dried at 60°C during 72 hours, or preliminary stored at –20°C before dissection. Samples were then homogenised into powder prior to stable isotope analysis (SIA) using a mortar and a pestle or a mixer mill (MM301, Retsch, Haan, Germany), depending on their toughness. "Champagne tests" (Jaschinski et al., 2008), i.e. dropping a small amount of the sample in 37 % hydrochloric acid, were conducted for each type of sample to assess the presence of carbonates. When effervescence was observed during the "champagne test", carbonates were removed from the samples. To do so, subsamples were exposed to 37 % hydrochloric acid vapours during 48 hours, and then kept at 60°C until further sample preparation (Hedges and Stern, 1984). The list of the tissues selected for each item, and whether they were acidified for subsequent stable isotope analyses is reported in Table 4.1. Subsamples were then precisely weighed (*ca* 10 mg for POM, 25 mg for sediment, 1.5-5 mg for macrophytobenthos and 2.5-3 mg for invertebrates) in 5×8 tin cups. *Ca* 3 mg of tungsten trioxide was added in the cups

containing macrophytobenthos or invertebrate subsamples, but not in the cups containing sediment. Stable isotope ratios of carbon, nitrogen and sulfur were then analysed with an elemental analyser (vario MICRO Cube, Elementar, Hanau, Germany) coupled to a continuous-flow isotope-ratio mass spectrometer (IsoPrime100, Elementar UK, Cheadle, United Kingdom) according to the procedure described in the section 2.2 of the chapter 2. The organic and inorganic matters in sediment were not separated. Consequently, because SIA cannot distinguish organic and inorganic matters and the different sulfur species in sediment have different levels of ^{34}S enrichment (Anderson and Pratt, 1995; Raven et al., 2016), stable isotope ratios of sulfur were not analysed in sediment.

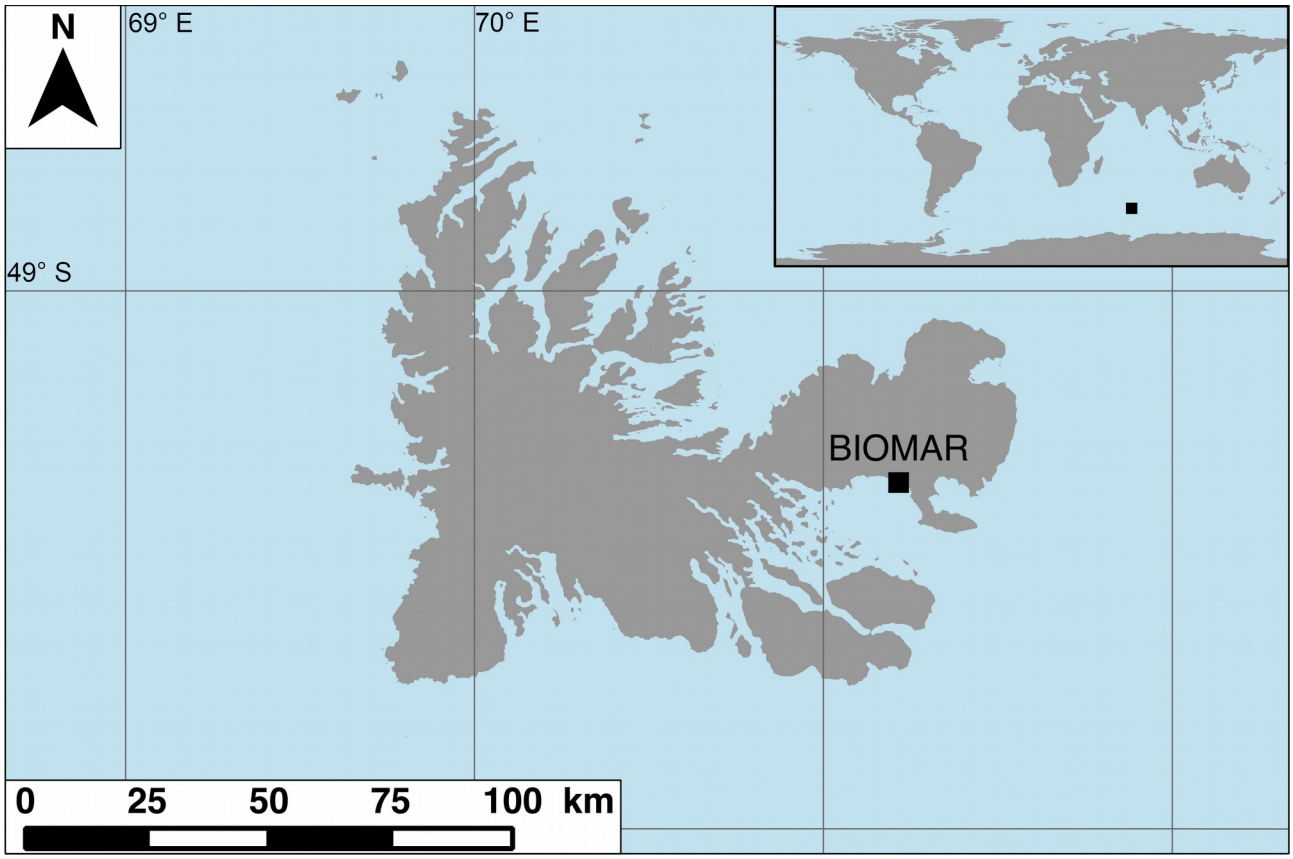


Fig. 4.2. Location of the BIOMAR sampling station in Kerguelen archipelago.

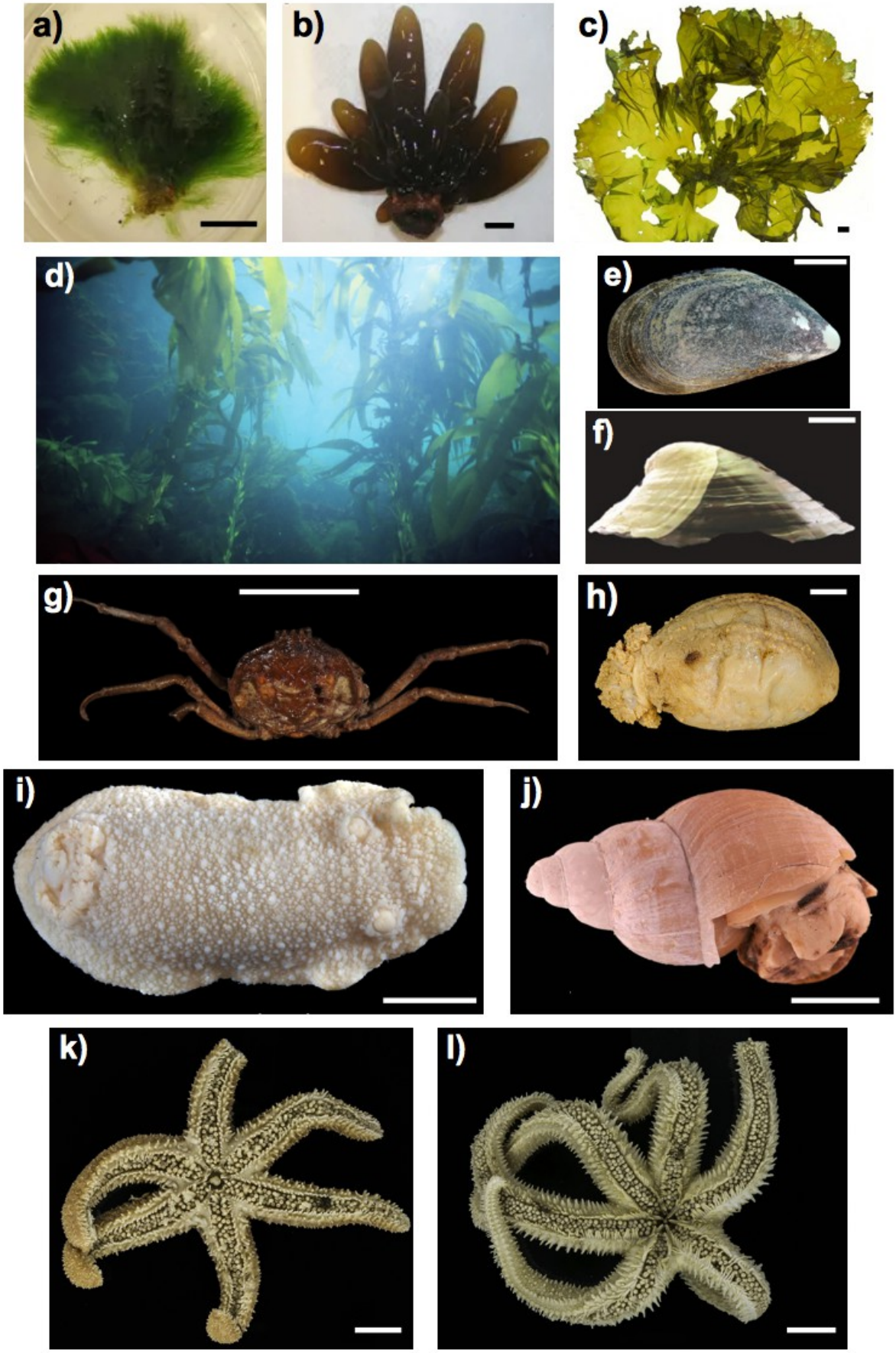

a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)

Fig. 4.3. Examples of organisms sampled from the the subtidal community of Kerguelen Islands. Bar = 1 cm. a) *Acrosiphonia* sp. (picture from Godinho et al., 2013); b) *Adenocystis* sp. (picture from Godinho et al., 2013); c) *Ulva* sp. (picture by Lindeberg M); d) *Macrocystis pyrifera* (picture from Améziane et al., 2011 and by Féral JP); e) *Aulacomya atra* (credit: National Museum of Natural History, Smithsonian Institution; picture by Testa AJ); f) *Nacella* cf. *kerguelenensis* (picture from González-Wevar et al., 2018); g) *Halicarcinus planatus* (credit: RECOLNAT; picture by Mollaret N); h) *Staurocucumis* sp. (credit: National Museum of Natural History, Smithsonian Institution; picture by Nguyen T); i) *Doris* cf. *Kerguelenensis* (credit: Yale Peabody Museum of Natural History; picture by Lazo-Wasem EA); j) *Neobuccinum* cf. *eatoni* (credit: National Museum of Natural History; picture by Testa AJ); k) *Anasterias perrieri* (credit: Université libre de Bruxelles; picture by Pernet P); l) *Diplasterias meridionalis* (credit: Université libre de Bruxelles; picture by Pernet P).

4.2.1 Data analysis

4.2.2.1 Preliminary analyses

Trophic relationships between organism groups were assessed using mixing models (Parnell et al., 2010; 2013; see section 2.3 in chapter 2). However, several preliminary data analyses are necessary before computing mixing models. Preliminary knowledge on the organisms' diets is necessary before computing mixing models (Phillips et al., 2014) to avoid highlighting the consumption of food sources that would not be normally consumed by the organisms. However, not all the organisms included in this study had their diet investigated in detail in previous studies. Consequently, organisms were grouped into four trophic groups based on their potential trophic level and on previous studies on the diet conducted for several species. The first trophic group, i.e. primary producers and/or organic matter sources, contains POM, sediment and all photosynthetic organisms and is thus the lowest trophic level group. To determine which consumers belong to the other trophic groups, differences of $\delta^{15}N$ values between organism groups were assessed with a Kruskal-Wallis test and a post-hoc Dunn test with Benjamini-Hochberg adjustments. The primary consumers included the two groups of organisms with the lowest $\delta^{15}N$ values of organisms highlighted by the post-hoc test. This group is thus the second lowest trophic level group and includes organisms which feed on primary producers and/or on organic matter. By contrast, the secondary consumers, i.e. the highest trophic level group, included the two groups of organisms with the highest $\delta^{15}N$ values of organisms highlighted by the post-hoc test and are organisms which feed on animal matter. The remaining groups highlighted by the post-hoc test were included in an omnivore trophic group, i.e. the second highest trophic level group, whose organisms include both primary producers and/or on organic matter and animal matter in their diet.

Confounding effects of food sources with similar stable isotope values may occur in mixing

models and it is thus recommended to include food sources with isotopically distinct signatures in mixing models (Phillips et al., 2014). Consequently, for each trophic group, organism groups with similar stable isotope values have to be grouped in order to be used as food sources in mixing models. As a result, a Ward hierarchical clustering based on Euclidean distance was performed for each trophic group (except the secondary consumers) on mean stable isotope values of each organism group. The organism groups with similar mean stable isotope (Euclidean distance lower than 2.5) values were then grouped. As the secondary consumers were never used as food sources for the mixing models, the grouping of organism groups with similar stable isotope values was not applied to them.

4.2.2.2 Identification of food sources for each trophic group

Bayesian mixing models with 10^5 iterations were computed to quantify resource use by consumers using the R package simmr (Stable Isotope Mixing Models in R, Parnell et al., 2010; 2013). The models were run for each trophic group with the two lower trophic levels being used as organic matter sources, with the exception of the model for the primary consumers that used only the primary producers and/or organic matter sources. The Rhodophyceae group was also excluded from the baseline food sources in the models because of its extremely low $\delta^{13}C$ values (–31.0 ± 0.9 ‰). Trophic Enrichment Factors (TEF) were investigated in various environments and for several taxa (McCutchan et al., 2003; Caut et al., 2009). Nevertheless, no TEF were assessed for other taxa such as sponges or echinoderms. Consequently, mean ± SD TEF reported for all marine organisms (1.0 ± 1.6 ‰, n = 87 for $\delta^{13}C$, 2.4 ± 1.7 ‰, n = 90 for $\delta^{15}N$, Caut et al., 2009) were used in the models. Similarly, the mean ± SD TEF reported for all organisms was used for $\delta^{34}S$ values (0.5 ± 1.9‰, n = 12) because TEF reported for $\delta^{34}S$ values in aquatic organisms are only limited to a small number of carnivorous species (McCutchan et al., 2003). Two types of models were run: models using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values, and others using only $\delta^{13}C$ and $\delta^{15}N$ values. Gelman-Rubin diagnostics and absolute posterior correlation for all models (mean ± SD absolute correlations for all models: $|r| = 0.21 \pm 0.17$ for the models using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values, $|r| = 0.22 \pm 0.17$ for the models using $\delta^{13}C$ and $\delta^{15}N$ values) indicated similar performance for both types of models. Models using $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were ultimately selected and presented here as a result. Contributions of each food item to the diet of organisms computed by mixing models were presented as modes and 95 % credibility intervals (CI_{95}) of probability density function distributions, i.e. the the range of values in which the contribution of food sources has a 95 %

probability of being included.

4.3 Results

4.3.1 Preliminary analyses

The result of the Kruskal-Wallis test (Chi square = 187.927, $P < 0.001$) and the subsequent post-hoc analysis led to the inclusion of the two bivalves *Aulacomya* cf. *atra* and *Mytilus edulis*, the two limpets *Nacella* cf. *edgari* and *Nacella* cf. *kerguelenensis* and the sponges in the primary consumer trophic group. The secondary consumer trophic group included the sea stars *Anasterias perrieri*, *Anasterias* sp., *Diplasterias meridionalis*, *Leptychaster kerguelenensis* and the Pterasteridae, as well as the gastropod *Neobuccinum* cf. *eatoni*. The omnivore trophic group thus included the remaining consumers (Table 4.1; Fig. 4.4).

In primary producers and/or organic matter sources, *Gigartina* cf. *skottsbergii*, live *Macrocystis pyrifera* and *Macrocystis pyrifera* detritus were combined into a single food source (Table 4.1, Fig. S.4.1.a). Live *Ulva* sp. and *Ulva* sp. detritus were also combined into a single food source. Despite no $\delta^{34}S$ values being available for sediment, POM and sediment were grouped into a food source. In primary consumers, the two bivalves *Aulacomya* cf. *atra* and *Mytilus edulis*, as well as the sponges, were grouped into a suspension feeder trophic group while the two limpets *Nacella* cf. *edgari* and *Nacella* cf. *kerguelenensis* were also grouped together (Table 4.1, Fig. S.4.1.b). In omnivores, sedentary polychaetes, the crab *Halicarcinus planatus* and the Serolidae isopods were grouped into an arthropods and polychaetes group (Table 4.1, Fig. S.4.1.c). The Echinasteridae sea stars and the holoturoid *Staurocucumis* sp. were also combined into an echinoderm group.

Table 4.1. Organism groups and their mean ± SD $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values in the subtidal community grouped by trophic group. Bold organism groups are the organic matter sources resulting from the combination of organism groups with similar stable isotope values according to hierarchical clustering.

Trophic group	Organism group	Analysed Tissue	Acidification	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
Primary producers and/or	***Acrosiphonia* sp.**	Thallus fragment	No	**9**	**–23.4 ± 1.5**	**7.1 ± 0.5**	**17.4 ± 0.7**
organic matter sources	***Adenocystis* sp.**	Thallus	No	**11**	**–6.2 ± 1.7**	**8.0 ± 0.4**	**17.7 ± 0.8**
	Rhodophyceae	Thallus fragment	No	**10**	**–31.0 ± 0.9**	**6.4 ± 0.3**	**17.5 ± 0.8**
	Macrocystis pyrifera* and *Gigartina* cf. *skottsbergii			**34**	**–16.7 ±1.2**	**7.2 ± 1.0**	**17.4 ± 1.6**
	Gigartina cf. *skottsbergii*	Frond fragment	No	13	–16.8 ± 2.3	6.5 ± 0.7	17.3 ± 2.6
	Macrocystis pyrifera	Frond fragment	No	14	–16.7 ± 1.2	7.9 ± 1.1	17.5 ± 0.5
	Macrocystis pyrifera detritus	Frond fragment	No	7	–16.2 ± 2.8	7.3 ± 0.7	17.2 ± 0.7
	POM and Sediment			**20**	**–18.6 ± 1.1**	**4.4 ± 1.2**	**12.4 ± 1.3**
	POM		No	10	–19.5 ± 0.7	5.2 ± 0.8	12.4 ± 1.3
	Sediment		No	10	–17.7 ± 0.4	3.5 ± 1.0	NA
	***Ulva* sp.**			**17**	**–14.2 ± 0.9**	**8.5 ± 0.5**	**17.2 ± 0.8**
	Ulva sp.	Thallus fragment	No	10	–13.8 ± 0.9	8.6 ± 0.4	16.9 ± 0.8
	Ulva sp. detritus	Frond fragment	No	7	–14.8 ± 0.4	8.4 ± 0.6	17.8 ± 0.4
Primary consumers	**Suspension feeders**			**31**	**–16.5 ± 0.6**	**9.0 ± 0.4**	**16.8 ± 1.3**
	Aulacomya cf. *atra*	Adductor muscle	No	11	–16.1 ± 0.6	9.0 ± 0.3	16.9 ± 0.7
	Mytilus edulis	Adductor muscle	No	9	–16.3 ± 0.3	8.9 ± 0.4	18.1 ± 1.2
	Sponges	Body fragment	No	11	–17.1 ± 0.5	9.2 ± 0.5	15.6 ± 0.8
	Grazers			**22**	**–13.3 ± 1.2**	**9.7 ± 0.4**	**19.0 ± 1.7**
	Nacella cf. *edgari*	Foot	No	11	–12.6 ± 1.3	9.6 ± 0.4	18.0 ± 1.4
	Nacella cf. *kerguelenensis*	Foot	No	11	–14.0 ± 0.6	9.8 ± 0.4	20.0 ± 1.3
Omnivores	***Abatus cordatus***	Test	Yes	**10**	**–16.2 ± 0.8**	**11.0 ± 1.2**	**13.4 ± 0.8**
	Doris* cf. *kerguelenensis	Foot	No	**11**	**–12.0 ± 0.9**	**12.1 ± 0.2**	**18.3 ± 0.9**
	Neanthes* cf. *kerguelensis	Whole organism	No	**10**	**–17.8 ± 1.6**	**10.9 ± 1.0**	**17.6 ± 1.2**
	Arthropods and polychaetes			**30**	**–15.5 ± 0.7**	**11.4 ± 0.9**	**15.7 ± 1.2**
	Halicarcinus planatus	Appendage	Yes	10	–15.0 ± 0.8	10.8 ± 1.0	15.7 ± 0.9
	Sedentary polychaetes	Whole organism	No	11	–15.8 ± 0.7	11.5 ± 0.4	15.7 ± 1.6
	Serolidae	Tegument and muscle	Yes	9	–15.6 ± 0.4	12.0 ± 0.7	15.5 ± 0.8
	Echinoderms			**25**	**–13.5 ± 1.2**	**11.2 ± 1.2**	**16.5 ± 1.0**
	Echinasteridae	Tegument	Yes	5	–12.8 ± 1.4	11.5 ± 1.4	16.4 ± 1.6
	Staurocucumis sp.	Tegument	Yes	10	–13.8 ± 1.0	11.0 ± 1.1	16.6 ± 0.7
Secondary consumers	*Anasterias perrieri*	Tegument	Yes	18	–10.8 ± 0.7	14.5 ± 0.3	16.5 ± 1.1
	Anasterias sp.	Tegument	Yes	6	–9.7 ± 0.9	12.8 ± 0.2	15.2 ± 1.4
	Diplasterias meridionalis	Tegument	Yes	34	–12.2 ± 0.9	13.4 ± 1.8	16.5 ± 1.3
	Leptychaster kerguelenensis	Tegument	Yes	27	–11.5 ± 0.7	14.6 ± 0.4	17.1 ± 0.4
	Neobuccinum cf. *eatoni*	Foot	No	11	–13.0 ± 0.8	13.7 ± 0.7	18.2 ± 1.3
	Pterasteridae	Tegument	Yes	6	–13.3 ± 0.6	12.9 ± 0.4	15.8 ± 1.8

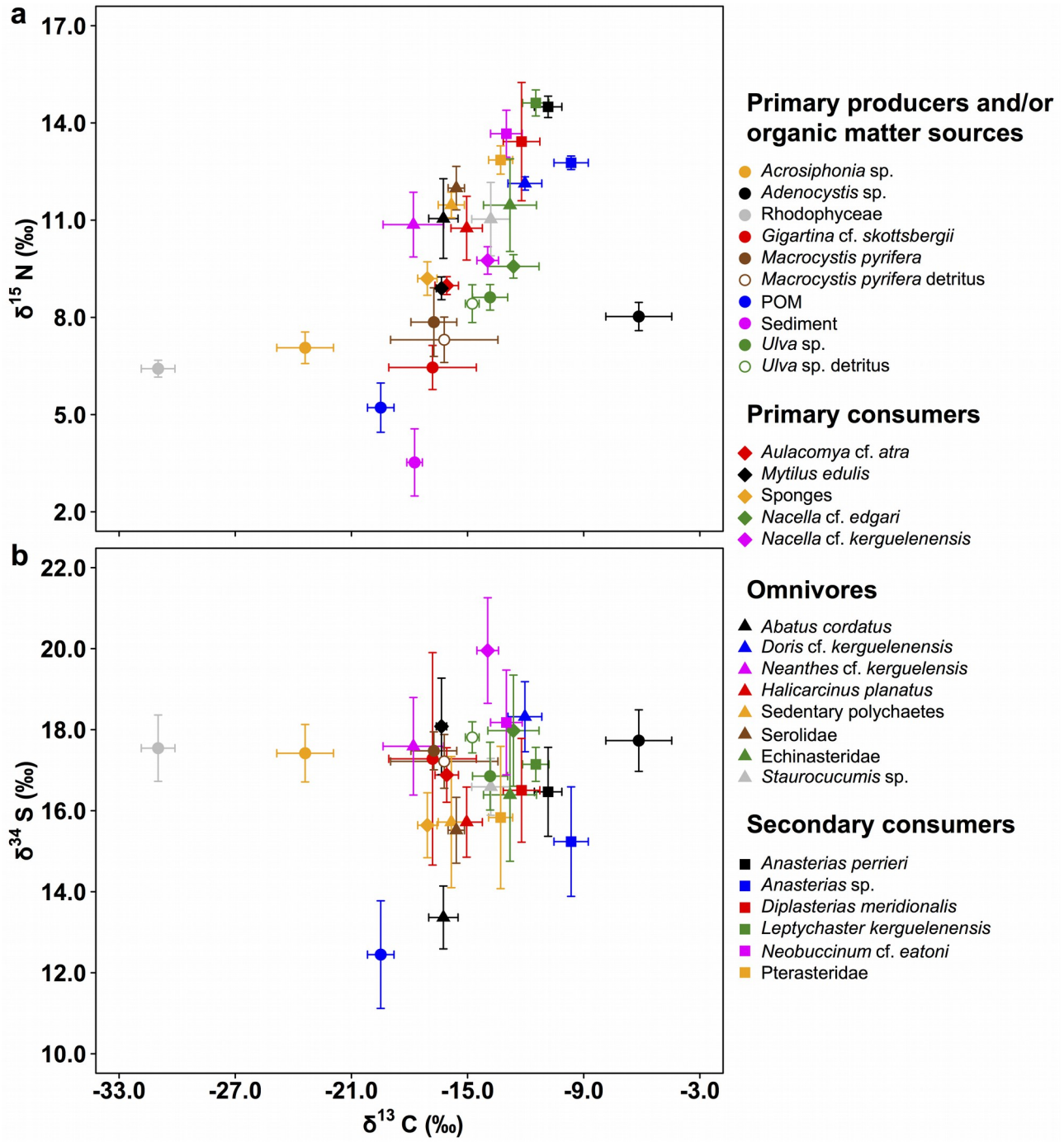


Fig. 4.4. Mean ± SD of a) $\delta^{13}C$ and $\delta^{15}N$ values and b) $\delta^{13}C$ and $\delta^{34}S$ values in the subtidal community at the BIOMAR sampling site, with circles being primary producers and/or organic matter sources, diamonds being primary consumers, triangles being omnivores and squares being secondary consumers.

4.3.2 Identification of food sources for each trophic group

4.3.2.1 Primary consumers

The results of the mixing model for primary consumers (Table 4.2.a, Fig. S.4.2) show that *Acrosiphonia* sp. is an important food source for all three taxa from the suspension feeder group (mode = 26.9 %, CI_{95} = 14.7-38.8 % for *Aulacomya* cf. *atra*, mode = 31.9 %, CI_{95} = 16.3-48.7 % for *Mytilus edulis* and mode = 26.8 %, CI_{95} = 15.9-38.6 % for sponges). The POM and the sediment are also an important food source for *Aulacomya* cf. *atra* (mode = 23.7 %, CI_{95} = 14.2-33.4 %) and the sponges (mode = 33.9 %, CI_{95} = 22.7-45.1 %). By contrast, the grazing limpets appeared to feed on a mixture of macrophytobenthos, with *Nacella* cf. *edgari* feeding mostly on *Adenocystis* sp. (mode = 35.8 %, CI_{95} = 21.4-48.3 %) while *Nacella* cf. *kerguelenensis* had a more diversified diet by feeding on *Adenocystis* sp. (mode = 24.6 %, CI_{95} = 12.3-37.7 %), *Ulva* sp. (mode = 24.2 %, CI_{95} = 5.9-48.3 %) and *Acrosiphonia* sp. (mode = 20.4 %, CI_{95} = 6.6-35.3 %). The modal contribution to the diet of *Macrocystis pyrifera* and *Gigartina* cf. *skottsbergii* never exceeded 20 %. However, the probability that the dietary proportion of *Macrocystis pyrifera* and *Gigartina* cf. *skottsbergii* is lower than that of the primary food sources identified is almost always lower than 95 %. Only the contribution of POM and sediment to the diet of sponges has a 96.8 % probability to be higher than that of *Macrocystis pyrifera*. *Gigartina* cf. *skottsbergii*. *Macrocystis pyrifera* and *Gigartina* cf. *skottsbergii* are also the second most important food source for *Mytilus edulis* (mode = 18.4 %, CI_{95} = 3.8-44.2 %).

4.3.2.2 Omnivores

The results of the mixing model for omnivores (Table 4.2.b, Fig. S.4.3) highlighted three groups of consumers. The first group contained the crab *Halicarcinus planatus*, the sedentary polychaetes and the Serolidae isopods which fed on POM and sediment (mode = 22.0 %, CI_{95} = 4.4-40.4 % for *Halicarcinus planatus*, mode = 34.3 %, CI_{95} = 2.1-46.3 % for sedentary polychaetes) and/or suspension feeders (mode = 30.5 %, CI_{95} = 3.4-58.3 % for *Halicarcinus planatus*, mode = 47.1 %, CI_{95} = 9.4-69.9 % for the Serolidae). The second group contained only *Doris* cf. *kerguelenensis* which appeared to feed on limpets (mode = 39.9 %, CI_{95} = 11.6-61.0 %) and *Adenocystis* sp. (mode = 20.0 %, CI_{95} = 8.1-33.3 %). The third group contained only *Neanthes* cf. *kerguelensis* which fed on *Acrosiphonia* sp. (mode = 42.7 %, CI_{95} = 17.3-57.1 %). However, the mixing model did not highlight major food sources contributing to the diet of the Echinasteridae sea stars and the holoturoid *Staurocucumis* sp., as none of the food source had a modal contribution to their diet

higher than 20 %. Nevertheless, several food sources had a modal contribution higher than 10 %, such as *Adenocystis* sp. (mode = 17.4 %, CI_{95} = 2.1-39.3 % for the Echinasteridae, mode = 13.7 %, CI_{95} = 3.0-26.7 % for *Staurocucumis* sp.), as well as the POM and the sediment (mode = 12.0 %, CI_{95} = 2.4-28.4 %) and the suspension feeders (mode = 11.1 %, CI_{95} = 2.5-52.2 %) for *Staurocucumis* sp. Similarly, no major food sources were highlighted by the mixing model for the sea urchin *Abatus cordatus* (no food sources with a modal contribution higher than 20 %) but *Acrosiphonia* sp. had a modal contribution higher than 10 %, (mode = 17.2 %, CI_{95} = 1.8-35.4 %). Furthermore, it should be noted that 95 % confidence intervals were high for many food sources in several consumers.

Table 4.2. Percentages of relative contributions (mode and limits of the 95 % confidence interval) of food sources to the diet of each consumer group estimated by Bayesian mixing models for a) primary consumers, b) omnivores and c) secondary consumers. Bold organism groups are the food sources resulting from the combination of organism groups with similar stable isotope values according to hierarchical clustering.

a)

Trophic group	Organism group	*Acrosiphonia* sp.	*Adenocystis* sp.	*Macrocystis pyrifera* and *Gigartina* cf. *skottsbergii*	POM and sediment	*Ulva* sp.
Primary consumers	**Suspension feeders**					
	Aulacomya cf. *altra*	26.9 (14.7-38.8)	13.7 (4.5-23.2)	16.3 (4.1-34.0)	23.7 (14.2-33.4)	17.2 (4.4-35.2)
	Mytilus edulis	31.9 (16.3-48.7)	13.2 (3.3-25.4)	18.4 (3.8-44.2)	13.9 (3.8-32.3)	13.0 (2.8-37.5)
	Sponges	26.8 (15.9-38.6)	5.3 (1.6-15.8)	10.4 (2.6-30.0)	33.9 (22.7-45.1)	17.6 (4.2-32.7)
	Grazers					
	Nacella cf. *edgari*	14.1 (3.1-31.0)	35.8 (21.4-48.3)	16.2 (3.2-42.9)	8.8 (2.3-21.5)	11.9 (2.9-42.9)
	Nacella cf. *kerguelenensis*	20.4 (6.6-35.3)	24.6 (12.3-37.7)	17.0 (3.8-39.5)	7.2 (2.0-21.6)	24.2 (5.9-48.3)

b)

Trophic group	Organism group	*Acrosiphonia* sp.	*Adenocystis* sp.	*Macrocystis pyrifera* and *Gigartina* cf. *skottsbergii*	POM and sediment	*Ulva* sp.	Suspension feeders	Grazers
Omnivores	***Abatus cordatus***	17.2 (1.8-35.4)	2.9 (0.8-13.2)	4.1 (1.1-28.9)	4.2 (1.7-67.4)	4.4 (1.2-32.7)	7.0 (2.2-63.8)	3.5 (1.0-28.3)
	Doris* cf. *kerguelenensis	2.2 (0.7-12.2)	20.0 (8.1-33.3)	2.4 (0.8-17.1)	1.8 (0.6-8.3)	6.8 (1.6-38.8)	6.1 (1.7-34.2)	39.9 (11.6-61.0)
	Neanthes* cf. *kerguelensis	42.7 (17.3-57.1)	2.5 (0.8-14.1)	2.9 (1.0-30.0)	3.1 (0.8-14.3)	3.7 (1.1-31.6)	6.5 (1.7-49.3)	3.6 (1.3-29.6)
	Arthropods and polychaetes							
	Halicarcinus planatus	3.2 (1.1-20.2)	4.9 (1.2-16.7)	4.1 (1.1-25.9)	22.0 (4.4-40.4)	5.9 (1.6-42.9)	30.5 (3.4-58.3)	4.3 (1.3-30.4)
	Sedentary polychaetes	6.2 (1.4-23.8)	3.2 (1.0-15)	3.5 (1.1-25.5)	34.3 (2.1-46.3)	4.9 (1.5-34.1)	15.7 (3.1-69.5)	3.3 (1.2-26.3)
	Serolidae	13.9 (2.5-28.3)	2.1 (0.7-11.2)	3.8 (1.0-22.4)	2.9 (1.1-24.3)	3.6 (1.3-32.6)	47.1 (9.4-69.9)	5.0 (1.3-32.4)
	Echinoderms							
	Echinasteridae	2.7 (0.9-21.6)	17.4 (2.1-39.3)	2.8 (1.1-36.1)	3.8 (1.1-29.5)	4.7 (1.5-66.7)	4.3 (1.4-52.6)	3.7 (1.4-59.8)
	Staurocumis sp.	3.4 (1.1-17.3)	13.7 (3.0-26.7)	3.0 (1.2-27)	12.0 (2.4-28.4)	5.7 (2.0-55.9)	11.1 (2.5-52.2)	4.5 (1.5-37.4)

c)

Trophic group	Organism group	Suspension feeders	Grazers	Abatus cordatus	Arthropods and polychaetes	*Doris* cf. *kerguelenensis*	Echinoderms	*Neanthes* cf. *kerguelensis*
Secondary consumers	*Anasterias perrieri*	1.6 (0.5-7.9)	1.7 (0.6-11.5)	4.2 (1.1-30.9)	2.6 (0.8-26.3)	60.8 (28.3-76.7)	3.9 (1.4-41.5)	1.1 (0.4-8.1)
	Anasterias sp.	4.7 (1.6-40.2)	4.0 (1.5-41.6)	7.0 (2.0-53.7)	5.8 (1.5-44.3)	4.1 (1.4-36.4)	4.5 (1.6-46.3)	3.5 (1.2-31.1)
	Diplasterias meridionalis	1.9 (0.5-9.6)	2.4 (0.7-15.2)	9.0 (1.8-30.7)	2.3 (0.7-17.3)	16.7 (3.5-54.2)	56.8 (3.9-72.1)	1.5 (0.4-6.2)
	Leptychaster kerguelenensis	1.1 (0.4-6.3)	2.1 (0.7-10.4)	7.5 (1.6-19.4)	4.1 (1.2-20.5)	52.6 (39.5-63.9)	21.2 (5.4-38.3)	1.4 (0.4-6.2)
	Neobuccinum cf. *eatoni*	4.6 (1.3-22.3)	9.9 (2.1-35.5)	3.7 (1.2-18.7)	6.0 (1.5-29.2)	36.2 (13.0-52.2)	5.5 (1.7-36.0)	5.8 (1.5-22.9)
	Pterasteridae	6.6 (1.7-33.7)	7.2 (2.0-39.4)	9.3 (2.0-40.0)	5.1 (1.7-40.1)	8.5 (2.0-35.3)	7.7 (2.0-43.0)	4.4 (1.2-22.5)

4.3.2.3 Secondary consumers

Half of the secondary consumers fed on the nudibranch *Doris* cf. *kerguelenensis* (Table 4.2.c, Fig. S.4.4). Indeed, it appeared as the main prey for *Anasterias perrieri* (mode = 60.8 %, CI_{95} = 28.3-76.7 %), *Leptychaster kerguelenensis* (mode = 52.6 %, CI_{95} = 39.5-63.9 %) and *Neobuccinum* cf. *eatoni* (mode = 36.2 %, CI_{95} = 13.0-52.2 %). Furthermore, although the modal contribution of *Doris* cf. *kerguelenensis* to the diet of *Diplasterias meridionalis* did not exceed 20 % (mode = 16.7 %, CI_{95} = 3.5-54.2 %), it could still be considered as a secondary food source as its contribution is higher than those of food sources with modal contribution lower than 10 %.

The main prey of *Diplasterias meridionalis* appeared to be echinoderms (mode = 56.8 %, CI_{95} = 3.9-72.1 %) . Echinoderms also appeared as a secondary food source for *Leptychaster kerguelenensis* (mode = 21.2 %, CI_{95} = 5.4-38.3 %). Finally, the mixing model did not highlight major food sources for *Anasterias* sp. and the Pterasteridae, as no food source had a modal contribution to the diet higher than 10 % for these two species.

4.4 Discussion

4.4.1 How faithfully does the mixing models represent the Kerguelen Islands coastal food web?

The mixing model outputs showed that multiple organic matter sources support the subtidal food web of Kerguelen Islands. However, interpretation of results was complicated by two phenomena. First, 95 % confidence intervals were large in several instances. This was notably the case for contributions of primary producers and/or organic matter sources and primary consumers to the diet of omnivores. Second, for some consumers (*Abatus cordatus*, the Echinasteridae, *Staurocucumis* sp., *Anasterias* sp. and the Pterasteridae), models suggested that many food items had similar and low contributions to the animals' diets, without highlighting clear dietary preferences. In both cases, these hard-to-interpret outputs might be the reflection of a complex food web featuring multiple trophic interactions that stable isotopes are not sufficient to depict accurately. They could also be linked with technical limitations. Firstly, for each element, we used the same TEF for all consumer and food items. In the absence of more suitable TEF, we resorted to use general values, supposedly widely applicable (i.e. mean estimates taken from meta-analyses; Caut et al., 2009; McCutchan et al., 2003). However, TEF can be organism- and diet-dependent, and use of a single TEF can reduce mixing model performance (Caut et al., 2009; Remy et al., 2017). Secondly, in some cases, organisms could feed on items that were not included in the model. This could occur either because those items were simply not sampled, or because consumers selectively subsample the sampled

food items and rely on fractions of them for their nutrition. This is probably the case for the sea star *Anasterias* sp. Indeed, this consumer species had the highest $\delta^{13}C$ values reported in this study, and was thus outside the mixing polygon delimited by the sampled food items. In such situations, mixing models can perform poorly and sometimes have limited utility (Phillips et al., 2014).

4.4.2 Food web structure of the nearshore kelp forests of Kerguelen Islands

Despite above-mentioned limitations, mixing models highlighted the presence of two major food chains in the kelp forests of Kerguelen Islands (Fig. 4.5). The first food chain seems to be based on the consumption of both benthic and pelagic organic matter sources, while the second one is primarily based on phytobenthos. Furthermore, although mixing models did not highlight major food sources for several organisms, it is still possible to emit hypotheses regarding their role in the food web functioning thanks to knowledge about their ecology obtained in previous studies.

The kelp species *Macrocystis pyrifera* did not appear to be a major organic matter source in the observed food chains. In particular, it appeared as a secondary or tertiary food source for primary consumers. Kaehler et al. (2000; 2006) suggested the importance of kelp-derived detritus in communities associated to kelp forests. However, contrary to this study, Kaehler et al. (2000; 2006) did not sample any other macrophytobenthos species than *Macrocystis pyrifera* and thus not only could not take into account the potential importance of these other species in the functioning of coastal food webs, but may also have overestimated the importance of *Macrocystis pyrifera*.

4.4.2.1 Bentho-pelagic food chain

The first mixing model on the primary consumers separated two groups of organisms. The first one contained the suspension feeding primary consumers which consumed POM, sediment and *Acrosiphonia* sp. It is unlikely that *Acrosiphonia* sp. is directly consumed by bivalves and sponges and it is thus more probably consumed as detritus. Indeed, consumption, selection and assimilation of macrophytobenthos-derived particles, including kelp, by bivalves has been observed (Stuart et al., 1982; Cranford and Grant, 1990; Cabanellas-Reboredo et al., 2010; Renaud et al., 2015). Another hypothesis to explain the apparent consumption of *Acrosiphonia* sp. by suspension feeders would be the selection of specific elements from POM with more depleted stable isotope values than those of the sampled surface POM. Indeed, *Acrosiphonia* sp. had the lowest $\delta^{13}C$ values among the food sources used in mixing models. Without using mixing models, low $\delta^{13}C$ values would usually suggest consumption of organic matter from pelagic origin in suspension feeders.

Differences of stable isotope values between sampled POM and POM consumed by suspension feeders could be due to temporal and/or depth variation of POM composition. A variant of this hypothesis would be that suspension feeders may specifically select phytoplankton (Levinton et al., 2002) that may have different stable isotope values from other POM components. Indeed, stable isotope values of bulk POM are usually used as proxies of those of phytoplankton because of the inherent difficulty to separate phytoplankton from bulk POM. However, phytoplankton may have different stable isotope values from those of bulk POM (Harmelin-Vivien et al., 2008; Hansman and Sessions, 2016) as other components such as phytobenthos detritus, resuspended sediments or terrestrial inputs will also contribute to the stable isotope values of POM.

In the second mixing model on omnivores, POM and sediment also appeared to be important food sources for *Halicarcinus planatus* and sedentary polychaetes. Furthermore, the suspension feeders appeared as important food sources for *Halicarcinus planatus* and the Serolidae isopods. *Halicarcinus planatus* is known to consume a mixture of phytobenthos, copepods and polychaetes (ref. in Vinuesa et al., 2011) while the Serolidae isopods consume amphipods and polychaetes (Luxmoore, 1985). *Neanthes* cf. *kerguelensis* may also be considered as a component of the bentho-pelagic food chain as it appeared to feed mostly on *Acrosiphonia* sp. which is mostly associated with the bentho-pelagic food chain. Indeed, Nereididae are known to display various feeding behaviours, including deposit feeding (Tsuchiya and Kurihara, 1979; Fong, 1987) and predation (Costa et al., 2006) but also suspension feeding by trapping particles in a mucous net (Costa et al., 2006; Toba and Sato, 2013). Only a small contribution of *Acrosiphonia* sp. to the diet of the sea urchin *Abatus cordatus* was highlighted by the mixing model. However, the deposit feeder diet reported in its Antarctic congeners (McClintock, 1994; Michel et al., 2016), its distribution on medium to fine sediments (Poulin and Féral, 1995) and its narrow ecological niche (Saucède et al., 2017) suggest that *Abatus cordatus* has a specialised deposit feeding strategy. In particular, this species would select specific organic particles from the sediment with specific stable isotope values. This would explain why the trophic pathway between sediments and *Abatus cordatus* was not highlighted by the mixing models as stable isotopes were analysed in bulk sediments.

None of the predators appeared to directly exploit this mostly pelagic food chain as none of the suspension feeders, the arthropods or the polychaetes were highlighted as major food sources by the third mixing model, suggesting that this may be a short length food chain. Nevertheless, the bentho-pelagic food chain may still provide food sources to several predators as some secondary consumers may consume prey that may potentially exploit both the bentho-pelagic food chain described here

and the second food chain based on phytobenthos (see section 4.4.2.3).

4.4.2.2 Phytobenthos-based food chain

The second group highlighted by the first mixing model on the primary consumers contained both limpet species, with *Nacella* cf. *edgari* feeding on the Phaeophyceae *Adenocystis* sp. while *Nacella* cf. *kerguelenensis* fed on a mixture of phytobenthos including *Adenocystis* sp. and the Chlorophyceae *Ulva* sp. and *Acrosiphonia* sp. While consumption of *Adenocystis* sp. has been observed for *Nacella* species, it is a minor contributor to their diet (Rosenfeld et al., 2018). Indeed, *Nacella* species are generalist grazers that consume the most common resources available, which are a mixture of micro and macrophytobenthos (Blankley and Branch, 1985; Andrade and Brey, 2014; Rosenfeld et al., 2018). Similarly, results from Antarctic indicate that microphytobenthos is a key food source for limpets, with the high $\delta^{13}C$ values of limpets being close to those of microphytobenthos which also had some of the highest $\delta^{13}C$ values among primary producers (Dunton, 2001; Corbisier et al., 2004), like *Adenocystis* sp. in this study. Furthermore, periods of body mass increase in limpets correspond to periods of high standing stock of microphytobenthos (Brêthes et al., 1994). Consequently, it is sensible to consider that microphytobenthos is an important food source for both *Nacella* cf. *edgari* and *Nacella* cf. *kerguelenensis* in Kerguelen Islands. However, these two species may still have well differentiated trophic niches as suggested by the mixing model highlighting higher reliance on *Ulva* sp. and *Acrosiphonia* sp. for *Nacella* cf. *kerguelenensis* than for *Nacella* cf. *edgari*.

Doris cf. *kerguelenensis* appeared as the single major consumer of limpets in the mixing model on intermediate consumers and also appeared to feed on *Adenocystis* sp. This result is surprising as *Doris* cf. *kerguelenensis* is known as a sponge consumer (McDonald and Nybakken, 1997) and that its feeding parts do not seem compatible with limpet predation. A possible explanation would be that *Doris* cf. *kerguelensis* actually rely on other organisms, not sampled here but whose feeding habits (and therefore isotopic composition) resemble the ones of the two limpet species. They could include sessile fauna that does not rely on pelagic sources for its nutrition. Indeed, sessile and suspension feeding epifauna of macrophytobenthos, such as bryozoans, may rely on resuspended epiphytic microphytobenthos (Lepoint et al., 2014) or on host macrophytobenthos exudates (De Burgh and Fankboner, 1978; Manríquez and Cancino, 1996) and then be a pathway of matter between the benthic primary producers and subsequent trophic levels.

Predators appeared as an important component of the phytobenthos-based food chain. Indeed,

the sea stars *Anasterias perrieri*, *Leptychaster kerguelenensis* and the gastropod *Neobuccinum* cf. *eatoni* appeared to feed mostly on *Doris* cf. *kerguelenensis* but they probably also consume other consumers depending more on benthic compartment than on pelagic one. Previous studies on the ecology of sea stars from the *Anasterias* genus have shown that these species are important predators in the system, consuming, among others, limpets, the crab *Halicarcinus planatus*, polychaetes and isopods (Blankley, 1984; Blankley and Branch, 1984; McClintock, 1985). These earlier results suggest their importance as predators in the phytobenthos-based food chain.

4.4.2.3 Potential trophic link between the two food chains

No major food sources were highlighted by mixing models for both omnivore echinoderms, i.e. the Echinasteridae sea stars and the holoturoid *Staurocucumis* sp. However, it is still possible to propose hypotheses regarding their role in the food web functioning, thanks to knowledge about their ecology obtained in previous studies and a cautionary interpretation of their respective mixing model outputs. Indeed, several food sources had a modal contribution higher than 10 % such as *Adenocystis* sp. for both organism groups, as well as the POM and the sediment and the suspension feeders for *Staurocucumis* sp. The known diet of several Echinasteridae species includes sponges, bryozoans, POM and biofilms (Mauzey et al., 1968; Jangoux, 1982), which would explain why this group appeared as an omnivore instead of a secondary consumer like other sea stars. Similarly, the diet of Subantarctic holoturoids includes a mixture of diatoms, sponges, copepods, amphipods, ostracods, bryozoans and foraminifera (McClintock, 1994). Consequently, the Echinasteridae and *Staurocucumis* sp. would be supported by both the bentho-pelagic food chain by feeding on POM and sponges and the phytobenthos-based food chain by feeding on epiphytes and epifauna and thus would trophically link the two food chains. This trophic link between the two food chains would also be reinforced by the inclusion of omnivore echinoderms in the diet of *Leptychaster kerguelenensis* that mostly exploit the phytobenthos-based food chain by consuming *Doris* cf. *kerguelenensis*, and by being the main prey of *Diplasterias meridionalis* that may also consume *Doris* cf. *kerguelenensis* as a supplementary food source.

4.4.3 Summary and conclusions

Two major food chains were identified in this study by using mixing models in the nearshore subtidal Kerguelen ecosystem (Fig. 4.5). The bentho-pelagic food chain appeared to be characterised by suspension feeders exploiting both pelagic POM and maybe resuspended

macrophytobenthos detritus as a secondary food source. Omnivores were also being present in this food chain but no major predators were identified. It is also possible to hypothesise that *Abatus cordatus* belongs to a this food chain by consuming sedimentary detritus. The phytobenthos-based food chain is characterised by micro and macrophytobenthos supporting grazers or epifauna. Those primary consumers are then consumed by mesopredators (*Doris* cf. *kerguelenensis* in this study) which are then consumed by higher trophic level predators. It is possible that omnivore echinoderms are supported by both the bentho-pelagic and phytobenthos-based food chains and thus they may be the main trophic link between the two food chains, as they are an important prey for two predatory sea star species that also exploit the phytobenthos-based food chain. A similar food web was hypothesised in Patagonia (Castilla, 1985; Adami and Gordillo, 1999) although tighter links appeared to occur between suspension feeders, herbivores and detritivores thanks to predation on all these trophic guilds by sea stars.

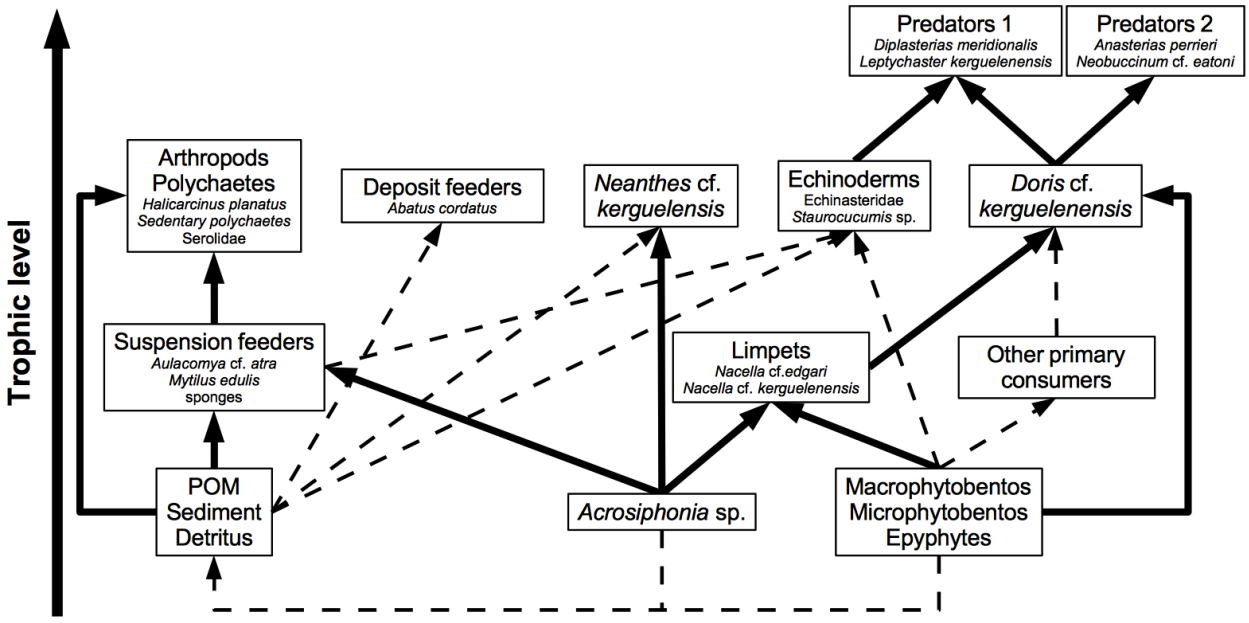


Fig. 4.5. Conceptual food web of the shallow subtidal benthic community of Kerguelen Islands. Each arrow indicates a carbon transfer between two organism groups. Full arrows indicate trophic transfers highlighted by the mixing models while dotted arrows indicate hypothetical carbon transfers.

The kelp *Macrocystis pyrifera* did not appear as a major food source for any of the investigated consumers in the subtidal food web of Kerguelen Islands. Consequently, none of the investigated consumers may have a major direct impact on large kelp densities and abundance in Kerguelen Islands. In Patagonia, although overgrazing of live kelp may locally occur (Dayton, 1985), drifting

kelp seems to be rather preferentially consumed by urchins (Castilla, 1985). Overall, overgrazing of *Macrocystis pyrifera* seems unlikely in Kerguelen Islands, because of the lack of major kelp grazers. Furthermore, sea stars mostly preyed upon omnivore organisms that do not include *Macrocystis pyrifera* in their diet. Earlier studies on the ecology of Subantarctic sea stars from the *Anasterias* genus have shown that their diet includes, among others, limpets, *Halicarcinus planatus*, polychaetes and isopods (Blankley, 1984; Blankley and Branch, 1984; McClintock, 1985). Although these prey are different from those highlighted by the mixing model in this study, they are unlikely major consumers of large *Macrocystis pyrifera*. Consequently, sea stars may not have the same "protective" function for large kelp in Kerguelen kelp forests than in temperate (Schultz et al., 2016; Burt et al., 2018) or Patagonian kelp forests (Dayton, 1985). However, their consumption of limpets may ease the settlement and growing of kelp as limpets may limit the growth of phytobenthos by feeding on spores and sporelings (Blankley and Branch, 1985). Sea stars may display a higher functional diversity than previously thought. Indeed, studies focusing on the impact of sea stars on kelp abundance were actually limited to one species (*Meyenaster gelatinosus* for Dayton, 1985 and *Pycnopodia helianthoides* for Schultz et al., 2016 and for Burt et al., 2018) and food web studies including several species of sea stars considered most sea stars as apex predators relying on multiple production pathways (Castilla, 1985; Adami and Gordillo, 1999). By contrast, in this study, at least one group of sea stars, i.e. the Echinasteridae, appeared to have a lower trophic level than other sea stars. Furthermore, sea stars appeared to exploit different trophic pathways with *Anasterias perrieri* being more dependent on the phytobenthos-based food chain by feeding mostly on the nudibranch *Doris* cf. *kerguelenensis*, while *Diplasterias meridionalis* and *Leptychaster kerguelenensis* may variably feed on both the bentho-pelagic and phytobenthos-based food chains by including different proportions of *Doris* cf. *kerguelenensis* and lower trophic level echinoderms in their diet. Finally, while no food sources were highlighted by mixing models for *Anasterias* sp. and the Echinasteridae and the Pterasteridae, their distinct stable isotope values may indicate that they exploit other trophic pathways than the two ones highlighted by this study.

Recent changes in kelp populations, communities and ecosystems have been observed worldwide and linked to recent climatic trends (Smale, 2020). *Macrocystis pyrifera* populations appeared to be sensitive to heatwaves or climate-driven oceanographic changes (Johnson et al., 2011; Arafeh-Dalmau et al., 2019) although resilience was also observed (Reed et al., 2016). Consequently, impacts of climate change on Kerguelen populations have to be expected. Other important kelp species from the Southern Ocean may also be impacted by climate change. For

example, a heatwave resulted in the local extinction of *Durvillaea* species in New Zealand (Thomsen et al., 2019). Conversely, invasive kelp species such as *Undaria pinnatifida* may replace the local kelp species after their extinction (Arafeh-Dalmau et al., 2019; Thomsen et al., 2019). Finally, kelp species may colonise new areas in the future thanks to their capacity of dispersion. For example, *Durvillaea antarctica* may be able to settle in more southern islands as suggested by the observation of two reproductively viable specimens originating from Kerguelen and South Georgia Islands being able to reach King George Island in the region of the Western Antarctic Peninsula (WAP) by being transported eastward by the ACC (Fraser et al., 2018). In particular, tidewater glacier retreat in WAP (Braun and Gossmann, 2002; Cook et al., 2005) may open new areas for colonisation for kelp, although the concurrent increases in turbidity (Sahade et al., 2015) and sedimentation rates (Boldt et al., 2013) may initially limit the expansion of kelp populations and their associated organisms in this region. Indeed, high turbidity is a chronic disturbance for the benthos as it may reduce light transmission to kelp and other phytobenthos species, but also impacts other benthic organisms (Thrush et al., 2004) and influence the benthos characteristics and its food web functioning.

Chapter 4 – Supplementary material: Food web structure of a Subantarctic nearshore community: main food chains and trophic role of sea stars

Examples of sea star taxa investigated in the chapter 4. From left to right: *Anasterias* sp., *Leptychaster kerguelenensis* and Pterasteridae (pictures by Le Bourg B).

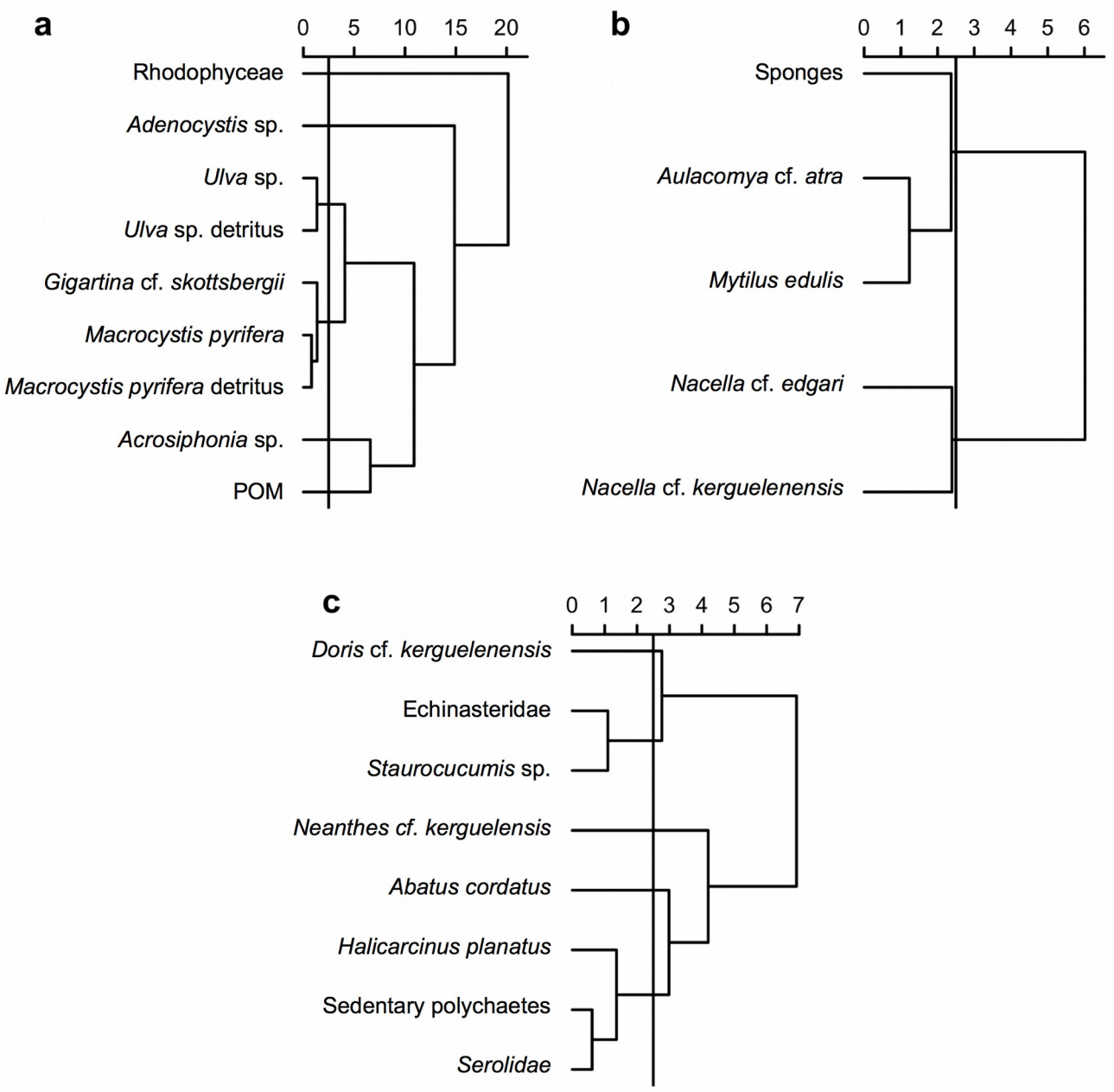


Fig. S.4.1. Results of hierarchical clusterings on the averages of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values (Euclidean distance, Ward method) for each trophic group. Organisms groups with similar isotopic values (Euclidean distance < 2.5) were combined into food sources following these clusterings prior to being used in Bayesian mixing models. Results for a) primary producers and/or organic matter sources (sediment was not included in this clustering as no $\delta^{34}S$ values were available for this source), b) primary consumers and c) omnivores.

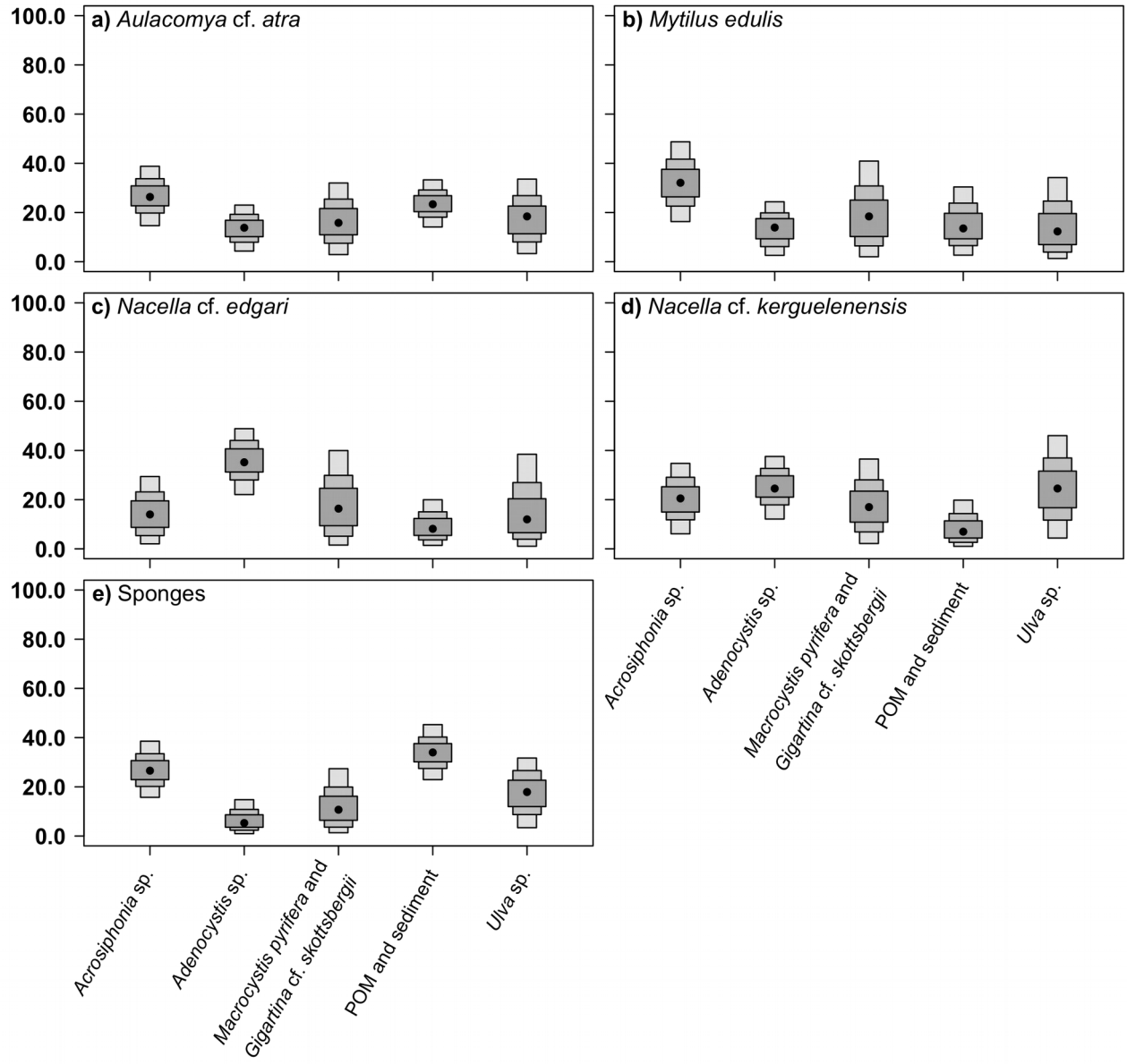


Fig. S.4.2. Percentages of the relative contributions of primary producers and/or organic matter sources to the diet of each primary consumer group determined by a Bayesian mixing model. Black dots are the modes. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals, from dark to light grey.

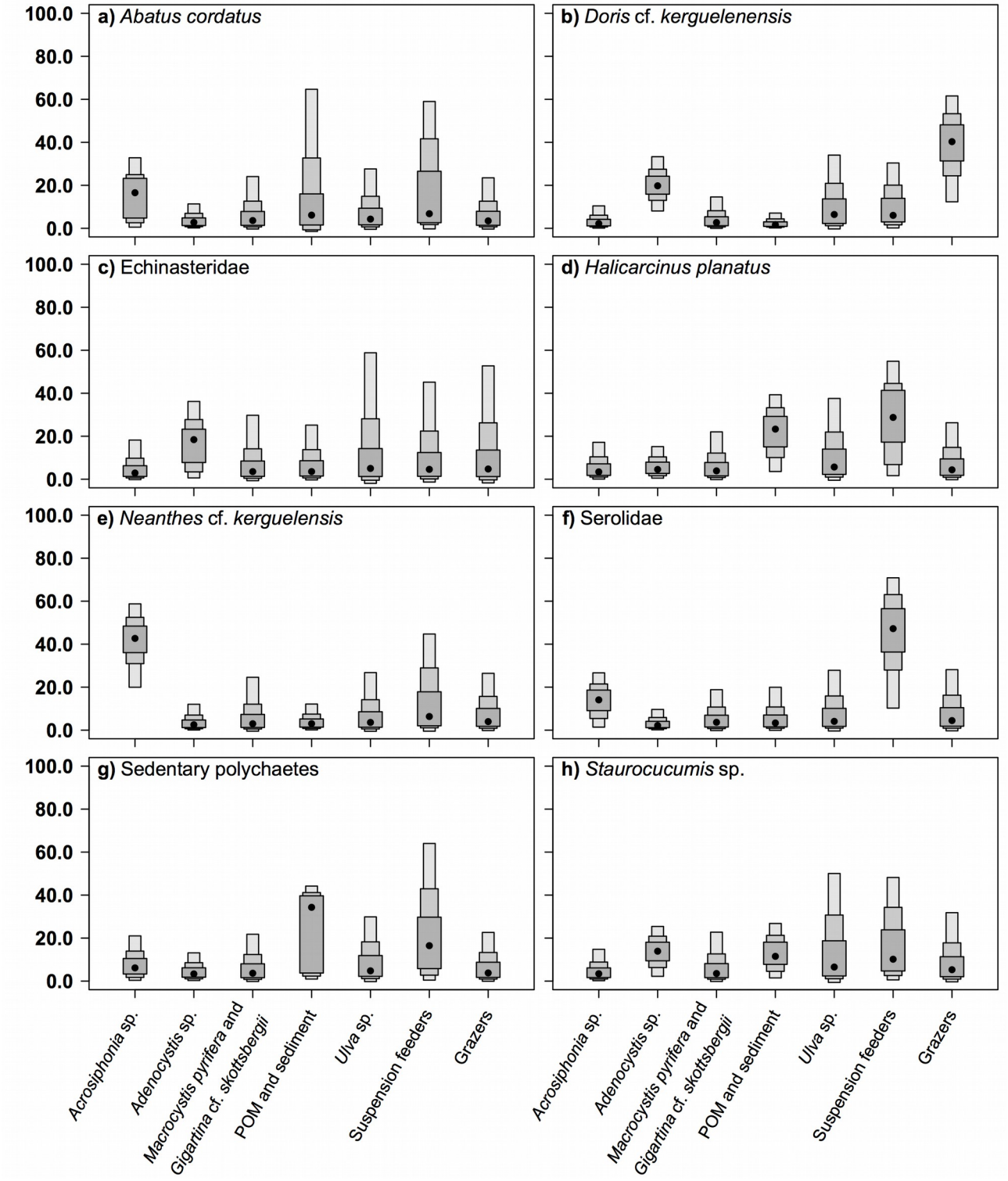


Fig. S.4.3. Percentages of the relative contributions of primary producers and/or organic matter sources and primary consumers to the diet of each omnivore group determined by a Bayesian mixing model. Black dots are the modes. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals, from dark to light grey.

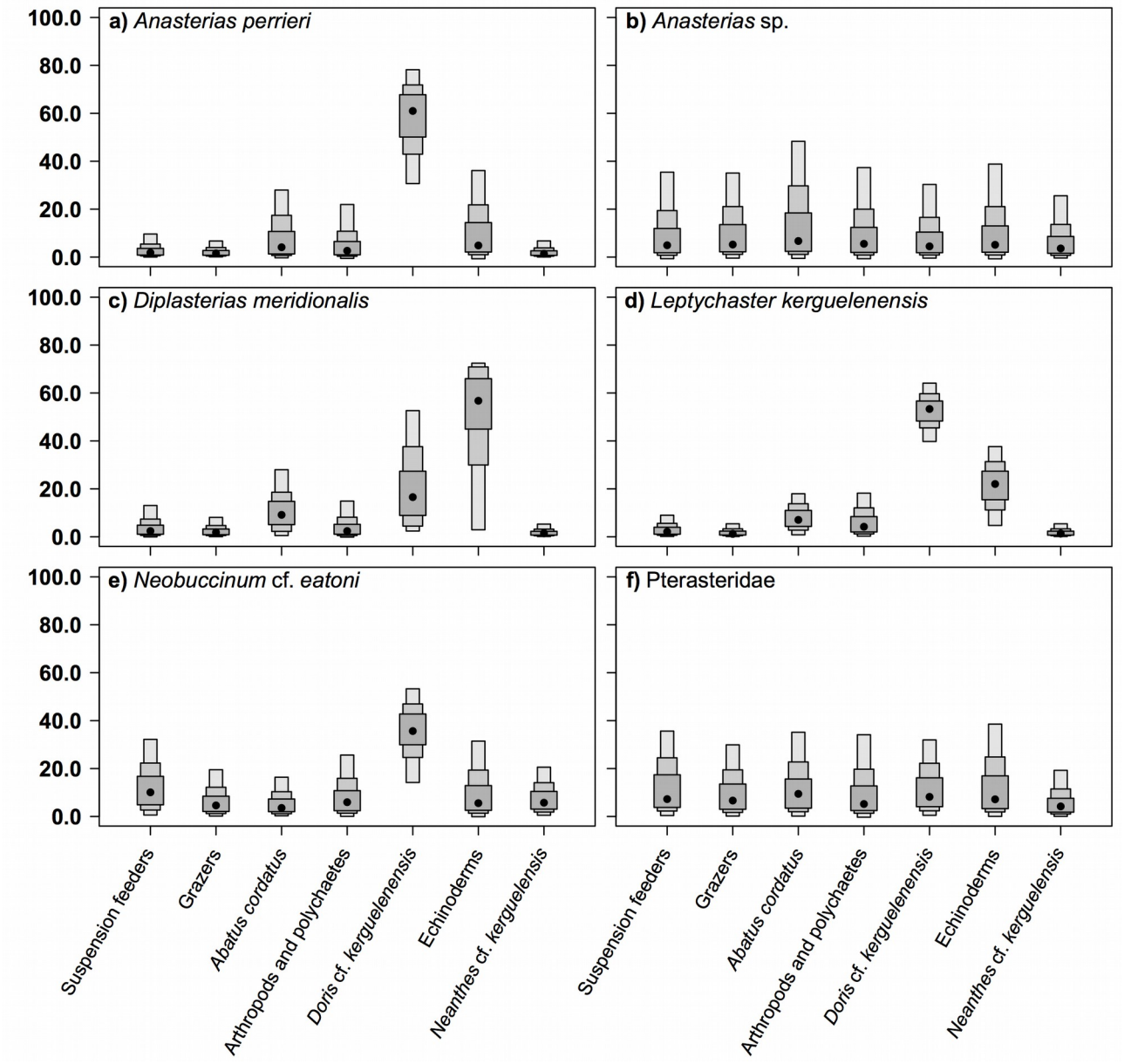


Fig. S.4.4. Percentages of the relative contributions of primary consumers omnivores to the diet of each secondary consumer group determined by a Bayesian mixing model. Black dots are the modes. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals, from dark to light grey.

Chapter 5: Trophic ecology of sea stars in an Antarctic fjord: size-related and spatial variations

View of Ezcurra Inlet in King George Island (South Shetland Islands; picture by Rozycki O).

5.1 Introduction

Trophic ecology of organisms is the result of both environmental constraints and of intrinsic biological features of these organisms (Hayden et al., 2019), notably ontogenetic changes. Indeed, ontogenetic changes of dietary habits, and thus of trophic niche width, frequently occur during the life history of organisms, in conjunction with ontogenetic changes of morphological features (e.g. size; Luczkovich et al., 1995; Scharf et al., 2000) or of habitat (Sánchez-Hernández et al., 2019). Ontogenetic changes of trophic ecology can be assessed using stable isotopes, as relationships between stable isotope ratios and size are of a common occurrence within organism groups (e.g. Hussey et al., 2011; Polito et al., 2013; Linzmaier et al., 2018), including sea stars (Nadon and Himmelman, 2010). On the one hand, relationships between body size and $\delta^{13}C$ values may be linked to a change of habitat use or prey selection by the organisms (e.g. from pelagic to benthic based food web, Dittel et al., 2006, or from benthic to pelagic based food web, Rossi et al., 2004; Frédérich et al., 2010). On the other hand, relationships between body size and $\delta^{15}N$ values may highlight a change of trophic level, as larger predators may feed on a higher size range of prey (Scharf et al., 2000; Baeta and Ramón, 2013; Fernandez et al., 2017) and/or on higher trophic level prey while growing (e.g. Viherluoto et al., 2000; Dittel et al., 2006; Hussey et al., 2011; Polito et al., 2013). Change of habitat use and higher diversity of prey has been observed in larger sea stars (Manzur et al., 2010) and changes of prey size in larger sea stars have been observed both experimentally (Sommer et al., 1999; Gooding and Harley, 2015) and in field studies (Baeta and Ramón, 2013; Fernandez et al., 2017), highlighting the potential existence of ontogenetic shifts in the trophic ecology of sea star species from the Southern Ocean.

Habitat characteristics and its modifications may also have an impact on the trophic ecology of organisms. These impacts can notably be observed by assessing spatial differences of trophic ecology of organisms and food web structure between locations with different characteristics (e.g. Norkko et al., 2007; Coll et al., 2011; Gosch et al., 2019). This can also be done using stable isotopes. Indeed, stable isotope ratios of organisms may differ between sampling locations (Veit-Köhler et al., 2013) as stable isotope values of the marine food web baselines can vary spatially at larger (Harmelin-Vivien et al., 2008; McMahon et al., 2013; Espinasse et al., 2019) and smaller scales (Wyatt et al., 2013; Tu et al., 2015).

Spatial variation in isotopic baseline (i.e. isotopic composition of primary producers and/or organic matter pools at the basis of the food web) is linked to spatial changes in the nature of primary production, but also to primary production process itself (i.e. change of isotopic

composition without a change of the nature of primary production). In marine environments, this can be explained by different factors such as change in nutrient availability and phytoplankton growth rates (McMahon et al., 2013), different importance of terrestrial and river inputs (Harmelin-Vivien et al., 2008; McMahon et al., 2013) or differences in inputs of allochthonous and autochthonous matter in the food web (Wyatt et al., 2013). Consequently, studying spatial variations of organisms' stable isotope composition may be useful to highlight different resource use, especially in sedentary or poorly motile organisms such as sea stars which could be dependent on the closest or most easily available carbon sources. Both aspects of baseline changes (i.e. source nature-related *versus* process-related) must nevertheless be taken into account to interpret the data. Other environmental features that may impact the trophic ecology of organisms include the prey availability and the presence of other organisms with similar trophic ecology. While sufficient prey availability may result in the consumption of the same prey by all organisms without competitive interaction (Costa-Pereira et al., 2019), limited prey availability may induce changes of trophic behaviours such as adding new prey items to the diet and thus increasing the trophic niche width (optimal foraging; Stephen and Krebs, 1986; e.g. Svanbäck and Bolnick, 2007; Costa-Pereira et al., 2019) or specialising on prey not consumed by other organisms (niche partitioning; Schoener, 1974; e.g. Mason et al., 2008; Juncos et al., 2015). Ultimately, trophic competition between organisms can lead to trophic niche width reduction (Tran et al., 2015; Jackson et al., 2016; Costa-Pereira et al., 2019) or even to exclusion of some consumers from the food web (competitive exclusion; Hardin, 1960; e.g. Bøhn et al., 2008).

Differences of stable isotope values or isotopic niche overlap between organism groups would provide indications about trophic interactions between potentially competing organisms, with similar stable isotopes values and high isotopic niche overlap indicating similar trophic ecology, while different stable isotopes values and low isotopic niche overlap would indicate resource partitioning.

In this study, we aimed to assess 1) the influence of sea star size on their trophic ecology and 2) how small-scale variation in environmental conditions can influence feeding habits, including interspecific trophic interactions. To do so, we used sea stars sampled in Ezcurra Inlet, a fjord of the Admiralty Bay in King George Island (South Shetland Islands), by the Institute of Oceanology of the Polish Academy of Sciences (IO PAN) in December 2010. Ezcurra Inlet is characterised by spatially variable environmental conditions, and notably, by a decreasing gradient of turbidity from the inner to the outer fjord (Pęcherzewski et al., 1980; Jonasz, 1983) that spatially shape the benthos

characteristics. Furtheremore, this sampling provided a large number of specimens spread over several sampling stations. In addition, the species *Diplasterias brandti* and *Odontaster validus* were frequently sampled together, allowing to study the spatial variations of their trophic interactions in Ezcurra Inlet and thus to preliminary assess the possibility of the variability of competition for food along an environmental gradient. As a result, this sampling offered an opportunity to assess both the influence of sea star size on their trophic ecology and the potential variations of their trophic ecology at small spatial scale in relation to environmental conditions

Therefore, this work proposes to assess the ontogenetic and spatial variations of the trophic ecology of sea stars in the spatially variable Ezcurra Inlet in two steps. First, we aim to assess the differences of stable isotope values between sea star species and sampling stations and the relationship between the sea stars size and their stable isotope values. This first approach was done in order to reach the following objectives: 1) to obtain general information of the trophic ecology of the sampled species, 2) to determine if ontogenetic changes (i.e. size) of the trophic ecology occur in sea stars and 3) to assess spatial variation inside the Ezcurra Inlet. Secondly, the stable isotopes data of *Diplasterias brandti* and *Odontaster validus*, the most abundant species, were compared to further determine if changes of stable isotope values and variability occur at small spatial scales and how this influence their trophic interactions.

For both approaches, spatial changes of stable isotope values were linked to the spatial variations of environmental characteristics, and notably the turbidity gradient in Ezcurra Inlet, which determine the benthos characteristics and could influence the trophic ecology of sea star as a result.

5.2 Material and methods

5.2.1 Study site

Ezcurra Inlet is part of the Admiralty bay in King George Island (South Shetland Islands, *ca* 62° 10’ S and 58° 33’ W, Fig. 5.1). Environmental conditions in Ezcurra Inlet are spatially driven from the inside to the outside of the fjord, especially in its deepest parts (> 50 m). Indeed, more internal areas of the Ezcurra Inlet are characterised by high quantities of mostly inorganic suspended matter originating from terrestrial ice run-off provided by melting tidewater glaciers (Pęcherzewski et al., 1980; Jonasz, 1983). These inputs of inorganic matter in the inner parts of Ezcurra Inlet are a chronic disturbance for the benthos. High concentration of suspended sediments (i.e. turbidity) may indeed reduce light transmission, dilute organic matter, and clog feeding structures of suspension feeders (Thrush et al., 2004; Donohue and Garcia Molinos, 2009; Bell et al., 2015), and thus

influence the bottom sediment and benthos characteristics. As a result, the inner parts of Ezcurra Inlet, bottoms are characterised by silt, clay and mud (Rodrigues et al., 2010; Berbel and Braga, 2014) and are devoid of phytobenthos (Zieliński, 1990). In addition, their zoobenthos shows low diversity and is abundance- and biomass-dominated by polychaetes (Pabis et al., 2011; Siciński et al., 2011; Krzeminska and Kuklinski, 2018). By contrast, the outer fjord is characterised by lower turbidity (Pęcherzewski et al., 1980), coarser sediment (Rodrigues et al., 2010; Brebel and Barga, 2014), phytobenthos presence (Zieliński, 1990) and higher zoobenthic diversity and biomass, with suspension feeders being a main component of the benthos (Pabis et al., 2011; Siciński et al., 2011; Krzeminska and Kuklinski, 2018). Depth zonation of communities also occurs, with shallow subtidal areas (10-40 m deep) characterised by heterogenous sediment (Pabis et al., 2011; Siciński et al., 2011), by a phytobenthos community dominated by the Phaeophyceae in term of biomass (Zieliński, 1990), and being occupied by echinoderms and amphipods distributed along the coastline in the fjord (Pabis et al., 2011; Siciński et al., 2011). These shallow subtidal areas are also characterised by higher diversity and abundance of sessile encrusting fauna in the outer part of Ezcurra Inlet than in the inner part (Krzeminska and Kuklinski, 2018).

5.2.2 Sampling and stable isotope analysis

Sea star individuals were collected (n = 286, 8 species in total, Table 5.1) by a scuba diver from December 6th to 23rd 2010 in 8 stations in Ezcurra Inlet (Fig. 5.1), during the ZA campaign (ZA standing for Zatoka Admiralicji, i.e. Admiralty Bay in Polish). However, five individuals from the species *Labidiaster annulatus*, *Odontaster meridionalis* and *Psilaster charcoti* were discarded from the data analysis because of their low number per species (n < 5 individuals per species). Consequently, the data for these three species were not presented in this study but are provided in the table S.5.1. Sampling was repeated in each station 2 to 7 times, between 6 and 30 m. These replicates were pooled in their respective stations (Table 5.1). Sampled sea stars were fixed with formaldehyde and then stored in ethanol and brought back at the IO PAN in Sopot (Poland).

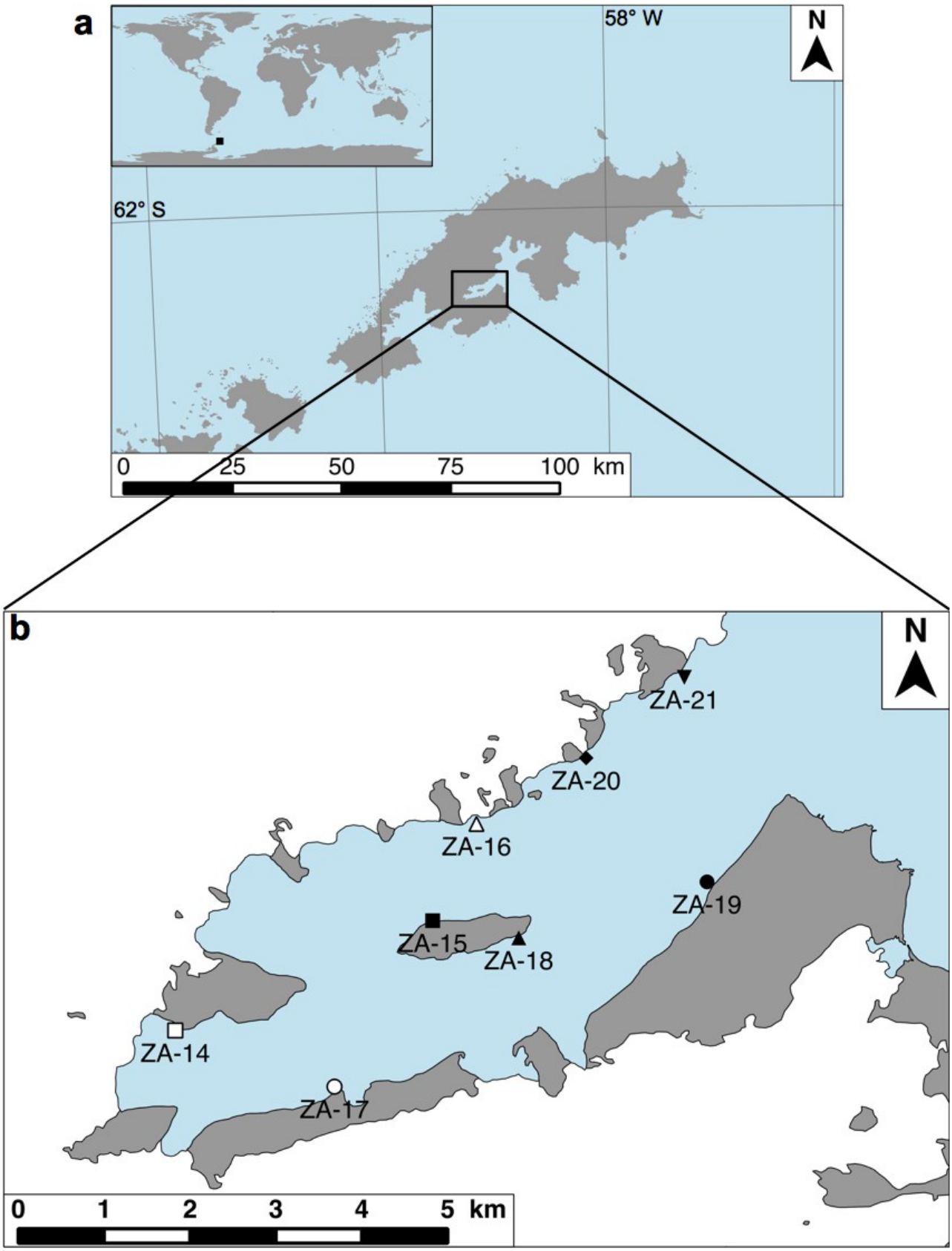


Fig. 5.1. Location of a) Ezcurra Inlet in King George Island and of b) sampling stations in the Ezcurra Inlet with ice sheets (white) covering the landmasses (grey) surrounding Ezcurra Inlet.

In the laboratory, sea stars were identified to the lowest taxonomic level possible (i.e. species). For each individual sea star, the arm length (distance from the mouth to the tip of the longest arm) and the disc radius (distance from the mouth to the interradial margin, i.e. the point separating two arms) were recorded and one or several arms were separated from the central disc. Internal organs and podia were removed in each arm. Arms were then washed and oven-dried at 50°C during 48 hours before being brought to the University of Liège for stable isotope analysis (SIA). Sample preparation (grinding, removal of carbonates) and SIA were carried out in accordance with the procedure described in the section 2.2 of the chapter 2. Correction factors were added to the $\delta^{13}C$ and $\delta^{34}S$ values of sea stars to take into account the effects of preservative fluids on stable isotope ratios (see chapter 2 and 3 and Le Bourg et al., 2020).

5.2.3 Data analysis

5.2.3.1. Spatial and ontogenetic changes of stable isotope values in sea stars

This analysis focused on all sufficiently sampled sea star species ($n \geq 5$ individuals per species) sampled in Ezcurra Inlet. The influences of the sea star species, the sampling station and of the two covariates (disc radius and arm length) on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were assessed with linear models type III ANCOVAs. First order interactions between the factor species and the two covariates were included in the model. However, first order interactions of the sampling station with the species and the two covariates were not included in the model as not all species were sampled in every station. Non-significant interactions were progressively removed from the model and a post-hoc Scheffé analysis was performed on the species factor.

Whenever disc radius, arm length, and/or their interaction with the factor species had a significant influence on stable isotope ratios of sea stars, the links between these variables were further assessed for each species with correlation tests. As the effect of the sampling station on stable isotope values and the covariates may bias the relationship, and because the relationship between the stable isotope values and the covariates is analysed in each species, the effect of the sampling station on stable isotope values and the covariates was preliminary corrected for each species separately.

Consequently, in each species, the stable isotope values and its covariate were mean-corrected for each station according to the procedure described in the section 2.4 of the chapter 2. Pearson correlation tests between the mean-corrected variables were then computed for each species.

5.2.3.2. Data analysis of stable isotope values in Diplasterias brandti *and* Odontaster validus

This analysis aimed to highlight potential interactive effects between the species and sampling stations. It was conducted on the species *Diplasterias brandti* and *Odontaster validus* only. These species were the more abundant and had the best spatial coverage. The analysis was also conducted only on stations ZA-15, ZA-18, ZA-19, ZA-20 and ZA-21 as a low number ($n < 5$) of *Diplasterias brandti* and/or *Odontaster validus* was available in stations ZA-14, ZA-16 and ZA-17 (Table 5.1). The influences of the sampling stations, of the two sea star species, of the disc radius and the arm length, on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were assessed with linear models type III ANCOVAs. The interaction between the two factors were also included in the model. Non-significant interactions were progressively removed from the model and a post-hoc Scheffé analysis was performed on the sampling stations factor.

Furthermore, for each station and each species, sample-size corrected (SEA_C) and Bayesian (based on 10^5 successive iterations; SEA_B) estimates of standard ellipse area (SEA) were computed with the SIBER package (Jackson et al., 2011) by using the $\delta^{13}C$ and $\delta^{15}N$ values ($SEA_{C.CN}$ and $SEA_{B.CN}$), or the $\delta^{13}C$ and $\delta^{34}S$ ($SEA_{C.CS}$ and $SEA_{B.CS}$, see chapter 2 for description of isotopic metrics). Pairwise comparisons of SEA_B between species for each station and between stations for each species were performed by calculating the percentage of the estimated SEA that differed between each pair of standard ellipse. This percentage indicates the probability that a given standard ellipse has larger or smaller SEA than the other. If the percentage of higher or lower SEA exceeded 95 %, the difference between compared SEA_B was considered as meaningful. Pairwise relative ellipse overlap between *Diplasterias brandti* and *Odontaster validus* were calculated in each station as a measure of isotopic niche partitioning between both species. In each pairwise computation, the percentage of overlap (%Ov) between the ellipses of *Diplasterias brandti* (DB) and *Odontaster validus* (OV) is the proportion of the area of overlap between both ellipses (Ov) relative to the SEA_C of both ellipses.

$$\%Ov = \frac{Ov}{SEA_{C\,DB} + SEA_{C\,OV} - Ov} \quad (1)$$

5.3 Results

5.3.1 Stable isotope values in the whole sea star assemblage

The ANCOVA results indicated that $\delta^{13}C$ values differed between species ($F_{4,263} = 6.751$, $P < 0.001$), with *Notasterias bongraini* having the lowest $\delta^{13}C$ values (–23.0 ± 1.0 ‰; mean ± SD),

followed by both *Perknaster sladeni* (–18.7 ± 1.7 ‰) and *Odontaster validus* (–17.6 ± 1.8 ‰). The highest $\delta^{13}C$ values were recorded in *Diplasterias brandti* (–16.6 ± 1.7 ‰) and *Bathybiaster loripes* (–15.5 ± 1.1 ‰, Table 5.1 and Fig. 5.2). $\delta^{13}C$ values also differed between sampling stations ($F_{7,263}$ 15.932, $P < 0.001$). The post-hoc analysis highlighted three groups of stations. The first group contained the five inner stations with the highest $\delta^{13}C$ values (ZA-14, ZA-15, ZA-16, ZA-17 and ZA-18). The second group had intermediate $\delta^{13}C$ values and contained two northern outer stations (ZA-20 and ZA-21) and the two southern stations from the previous group (ZA-17 and ZA-18). The last group contained the southern outer station (ZA-19) as well as one of the northern outer stations from the previous groups (ZA-20) and had the lowest $\delta^{13}C$ values. To summarise, $\delta^{13}C$ values in sea stars tended to decrease from the interior to the exterior of Ezcurra Inlet. A significant interaction between the species and the disc radius was also observed ($F_{4,263} = 10.265$, $P < 0.001$). Indeed, after correcting the potential influence of the sampling station on $\delta^{13}C$ values and on the disc radius values, the corrected $\delta^{13}C$ values increased with the corrected disc radius for *Diplasterias brandti* (1.1 ‰ìcm^{-1}; Fig. 5.3.b) and *Odontaster validus* (1.7 ‰ìcm^{-1}; Fig. 5.3.d). Conversely, they decreased for *Perknaster sladeni* (-3.4 ‰ìcm^{-1}; Fig. 5.3.e). No relation was found for *Bathybiaster loripes* (Fig. 5.3.a), or *Notasterias bongraini* (Fig. 5.3.c).

$\delta^{15}N$ values also differed between species ($F_{4,263} = 7.310$, $P < 0.001$). *Notasterias bongraini* had the lowest $\delta^{15}N$ values (7.1 ± 0.6 ‰) and *Bathybiaster loripes* had the highest ones (11.6 ± 0.8 ‰). *Diplasterias brandti* (9.2 ± 0.5 ‰), *Odontaster validus* (9.3 ± 0.7 ‰) and *Perknaster sladeni* (9.2 ± 1.3 ‰) had similar intermediate $\delta^{15}N$ values (Table 5.1 and Fig. 5.2.a). $\delta^{15}N$ values also differed between sampling stations ($F_{7,263}$ 3.904, $P < 0.001$). The post-hoc analysis highlighted three groups of stations. The first group contained the two inner stations with the highest $\delta^{15}N$ values (ZA-14 and ZA-17). The second group had intermediate $\delta^{15}N$ values and contains five stations distributed in the rest of Ezcurra Inlet (ZA-15, ZA-16, ZA-18, ZA-19 and ZA-21). The lowest $\delta^{15}N$ values were observed in the outer station ZA-20, although it was not significantly different from the $\delta^{15}N$ values in sea stars from the inner stations ZA-15 and ZA-18 from the previous group. Consequently, the spatial gradient of $\delta^{15}N$ values was less pronounced than for $\delta^{13}C$ values. A significant interaction between the species and the disc radius was also observed ($F_{4,263} = 4.278$, $P = 0.002$). Station-corrected $\delta^{15}N$ values increased with the station-corrected disc radius for *Bathybiaster loripes* (2.5 ‰ìcm^{-1}; Fig. 5.4.a), *Diplasterias brandti* (0.7 ‰ìcm^{-1}; Fig. 5.4.b) and *Odontaster validus* (0.7 ‰ìcm^{-1}; Fig. 5.4.d) but no relation was found for *Notasterias bongraini* (Fig. 5.4.c) or *Perknaster sladeni* (Fig. 5.4.e).

$\delta^{34}S$ values also differed between species ($F_{4,256}$ = 4.721, P < 0.001) with *Bathybiaster loripes* having lower $\delta^{34}S$ values than the other species (16.0 ± 1.0 ‰; Table 5.1 and Fig. 5.2.b). The sampling station had no effect on $\delta^{34}S$ values ($F_{7,256}$ = 1.163, P = 0.324). The arm length had a significant effect on $\delta^{34}S$ values ($F_{1,256}$ = 9.729, P = 0.002), with the correlation tests between station-corrected $\delta^{34}S$ values and station-corrected arm length being significant for *Diplasterias brandti* (0.1 ‰ìcm^{-1}; Fig. 5.5.b) and *Notasterias bongraini* (0.3 ‰ìcm^{-1}; Fig. 5.5.c).

Table 5.1. Sea star species in each station of Ezcurra Inlet with the collected number, the ranges of the arm length and of the disc radius and the means ± SD $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values for each species as well as for each whole station (bold lines).

Station	Species	n	Range arm length (cm)	Range disc radius (cm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
ZA-14	*Bathybiaster loripes*	8	5.3-8.1	1.4-1.9	–15.2 ± 1.0	11.7 ± 0.6	15.8 ± 0.9
	Total	**8**	**5.3-8.1**	**1.4-1.9**	**–15.2 ± 1.0**	**11.7 ± 0.6**	**15.8 ± 0.9**
ZA-15	*Diplasterias brandti*	16	0.7-10.5	0.1-1.4	–15.1 ± 1.2	9.0 ± 0.5	17.3 ± 0.8
	Odontaster validus	19	0.8-3.9	0.2-1.7	–17.0 ± 0.9	9.0 ± 0.4	17.7 ± 0.8
	Total	**35**	**0.7-10.5**	**0.1-1.7**	**–16.2 ± 1.4**	**9.0 ± 0.5**	**17.5 ± 0.8**
ZA-16	*Bathybiaster loripes*	1	8.4	2.1	–14.4	11.5	15.2
	Diplasterias brandti	21	1.2-10.8	0.1-0.8	–15.4 ± 0.8	9.3 ± 0.4	17.4 ± 0.8
	Odontaster validus	1	1.2	0.4	–20.5	8.2	16.3
	Total	**23**	**1.2-10.8**	**0.1-2.1**	**–15.6 ± 1.3**	**9.3 ± 0.7**	**17.2 ± 1.0**
ZA-17	*Bathybiaster loripes*	3	5.4-6.6	1.3-1.6	–16.5 ± 1.3	11.2 ± 1.4	17.0 ± 0.6
	Notasterias bongraini	1	10.2	1.9	–22.1	8.4	18.9
	Odontaster validus	3	2.7-3.6	1.1-1.7	–14.4 ± 1.0	10.6 ± 0.9	17.6 ± 0.6
	Total	**7**	**2.7-10.2**	**1.1-1.9**	**–16.4 ± 2.9**	**10.5 ± 1.4**	**17.5 ± 0.8**
ZA-18	*Diplasterias brandti*	6	1.4-8.0	0.1-1.6	–15.5 ± 1.5	8.9 ± 0.5	17.4 ± 0.8
	Notasterias bongraini	1	8.9	0.9	–22.8	6.6	16.4
	Odontaster validus	11	1.2-4.3	0.4-1.8	–17.1 ± 1.0	9.1 ± 0.5	18.1 ± 0.6
	Total	**18**	**1.2-8.9**	**0.1-1.8**	**–16.9 ± 2.0**	**8.9 ± 0.7**	**17.8 ± 0.8**
ZA-19	*Diplasterias brandti*	30	0.9-12.8	0.1-1.4	–17.8 ± 1.3	9.4 ± 0.5	17.3 ± 0.6
	Notasterias bongraini	13	1.2-8.1	0.2-1.2	–23.3 ± 1.1	7.3 ± 0.6	17.8 ± 1.2
	Odontaster validus	62	0.3-3.9	0.1-1.9	–18.3 ± 1.7	9.4 ± 0.7	17.4 ± 1.2
	Total	**105**	**0.3-12.8**	**0.1-1.9**	**–18.8 ± 2.3**	**9.1 ± 1.0**	**17.4 ± 1.0**
ZA-20	*Diplasterias brandti*	11	1.1-8.7	0.1-1.2	–17.5 ± 1.7	9.3 ± 0.4	17.1 ± 0.6
	Notasterias bongraini	6	5.1-6.8	0.6-1	–22.6 ± 0.5	6.8 ± 0.4	18.0 ± 0.5
	Odontaster validus	9	1.4-2.7	0.6-1.4	–16.1 ± 2.0	8.8 ± 0.7	17.2 ± 0.8
	Perknaster sladeni	2	1.1-7.5	0.3-1.9	–19.3 ± 3.6	9.4 ± 1.1	17.8 ± 0.8
	Total	**28**	**1.1-8.7**	**0.1-1.9**	**–18.2 ± 3.0**	**8.6 ± 1.1**	**17.4 ± 0.7**
ZA-21	*Diplasterias brandti*	18	0.7-5.7	0.1-0.9	–17.4 ± 1.4	9.0 ± 0.6	17.0 ± 0.9
	Odontaster validus	24	0.8-4.6	0.2-1.6	–17.3 ± 1.9	9.3 ± 0.7	17.3 ± 1.3
	Perknaster sladeni	15	0.6-3.9	0.1-1.2	–18.6 ± 1.5	9.2 ± 1.4	17.1 ± 1.4
	Total	**57**	**0.6-5.7**	**0.1-1.6**	**–17.6 ± 1.7**	**9.2 ± 0.9**	**17.1 ± 1.2**

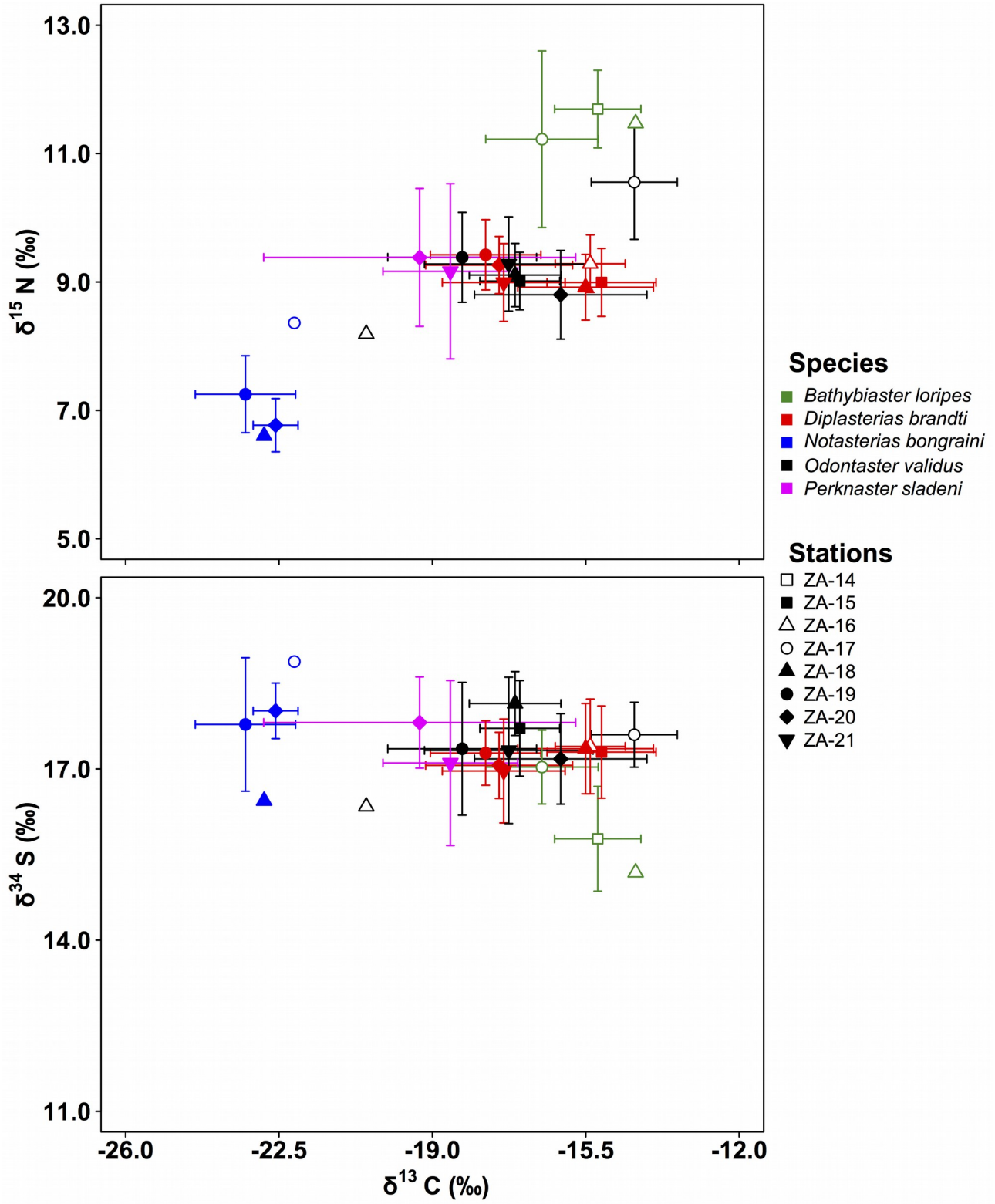


Fig. 5.2. Mean ± SD of a) $\delta^{13}C$ and $\delta^{15}N$ values and b) $\delta^{13}C$ and $\delta^{34}S$ values for each sea star species (colour) in each sampling station (symbol) of the Ezcurra inlet.

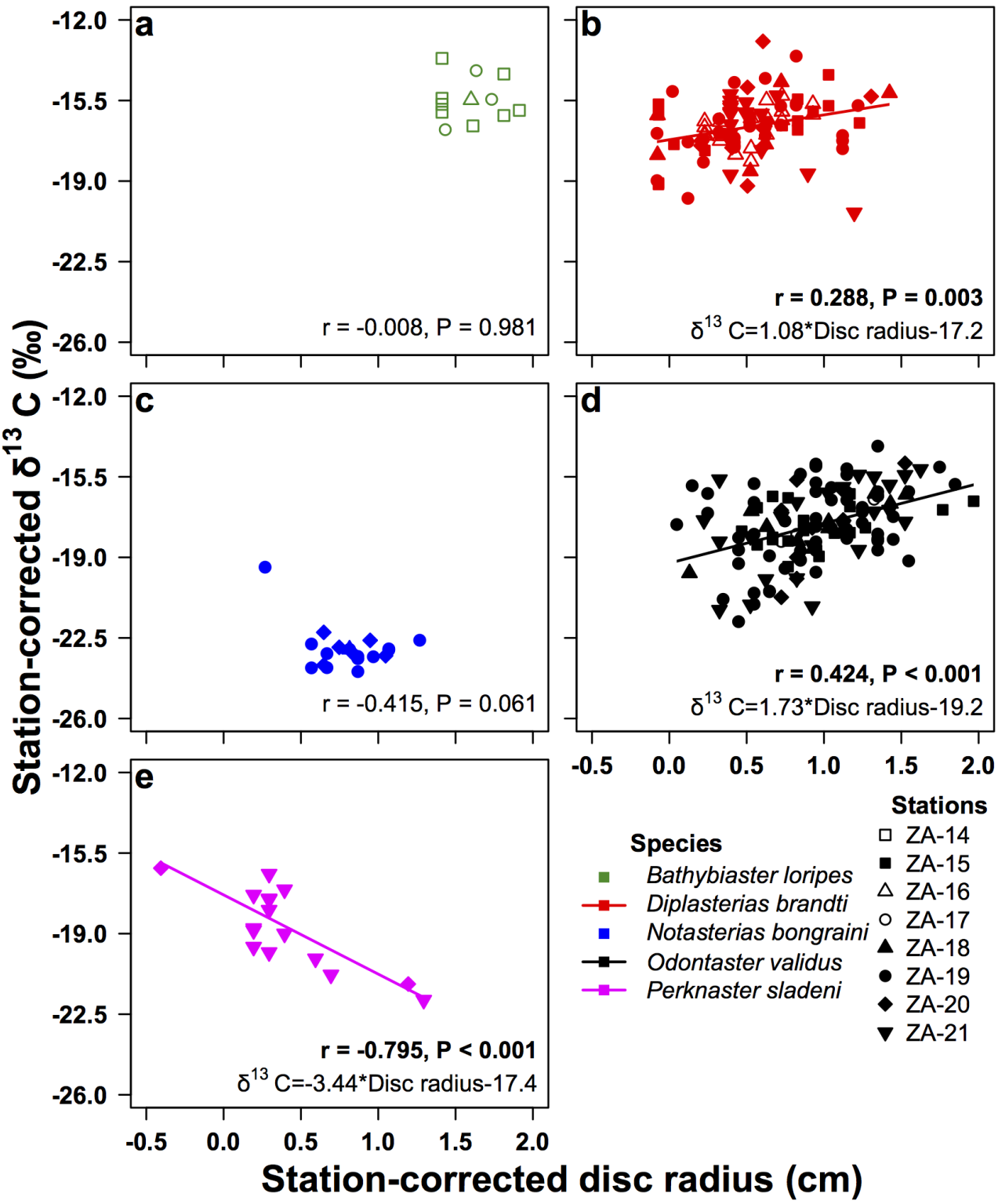


Fig. 5.3. Correlation coefficients between the station-corrected disc radius and $\delta^{13}C$ values in a) *Bathybiaster loripes*, b) *Diplasterias brandti*, c) *Notasterias bongraini*, d) *Odontaster validus* and e) *Perknaster sladeni* from Ezcurra Inlet.

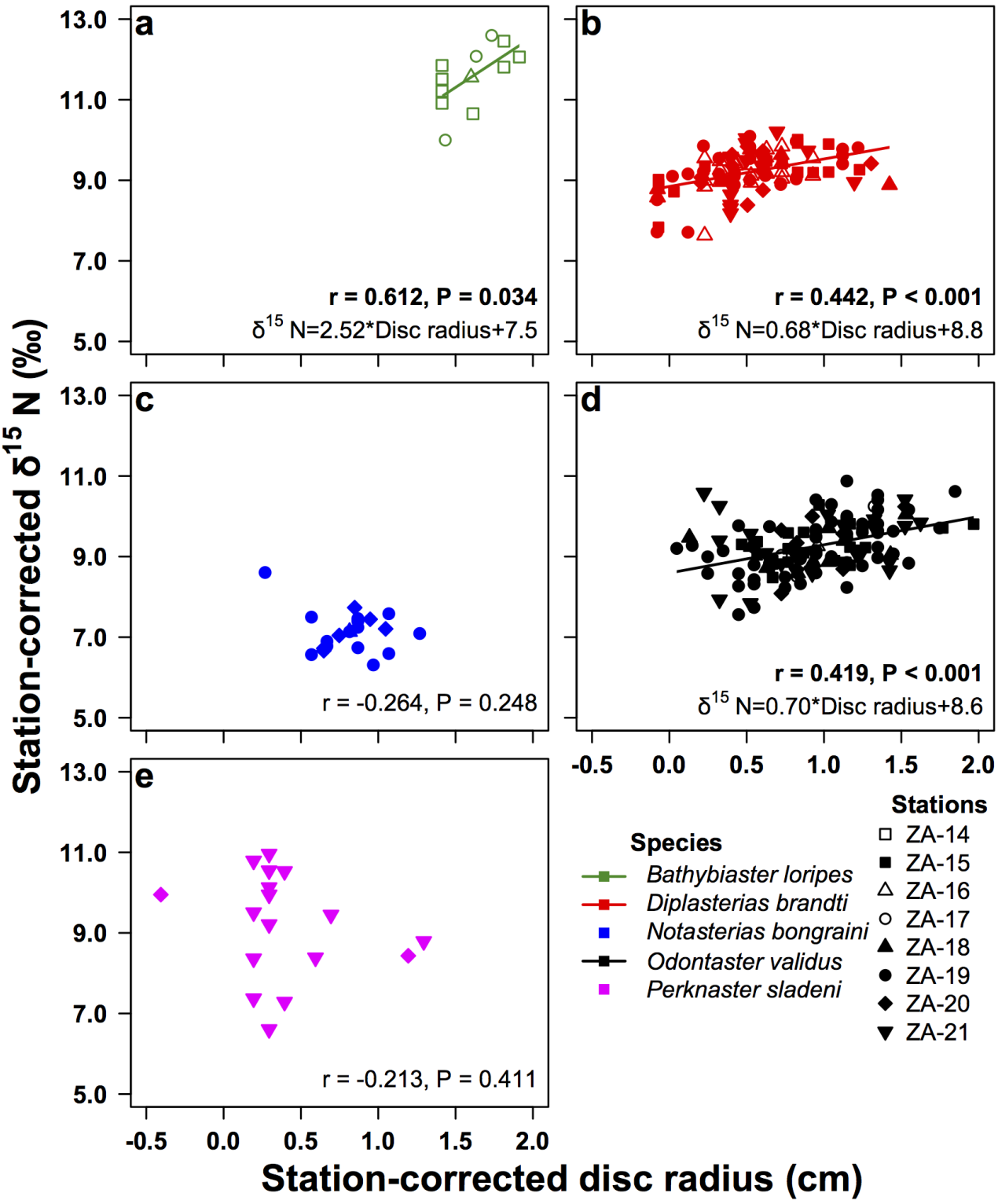


Fig. 5.4. Correlation coefficients between the station-corrected disc radius and δ^{15}N values in a) *Bathybiaster loripes*, b) *Diplasterias brandti*, c) *Notasterias bongraini*, d) *Odontaster validus* and e) *Perknaster sladeni* from Ezcurra Inlet.

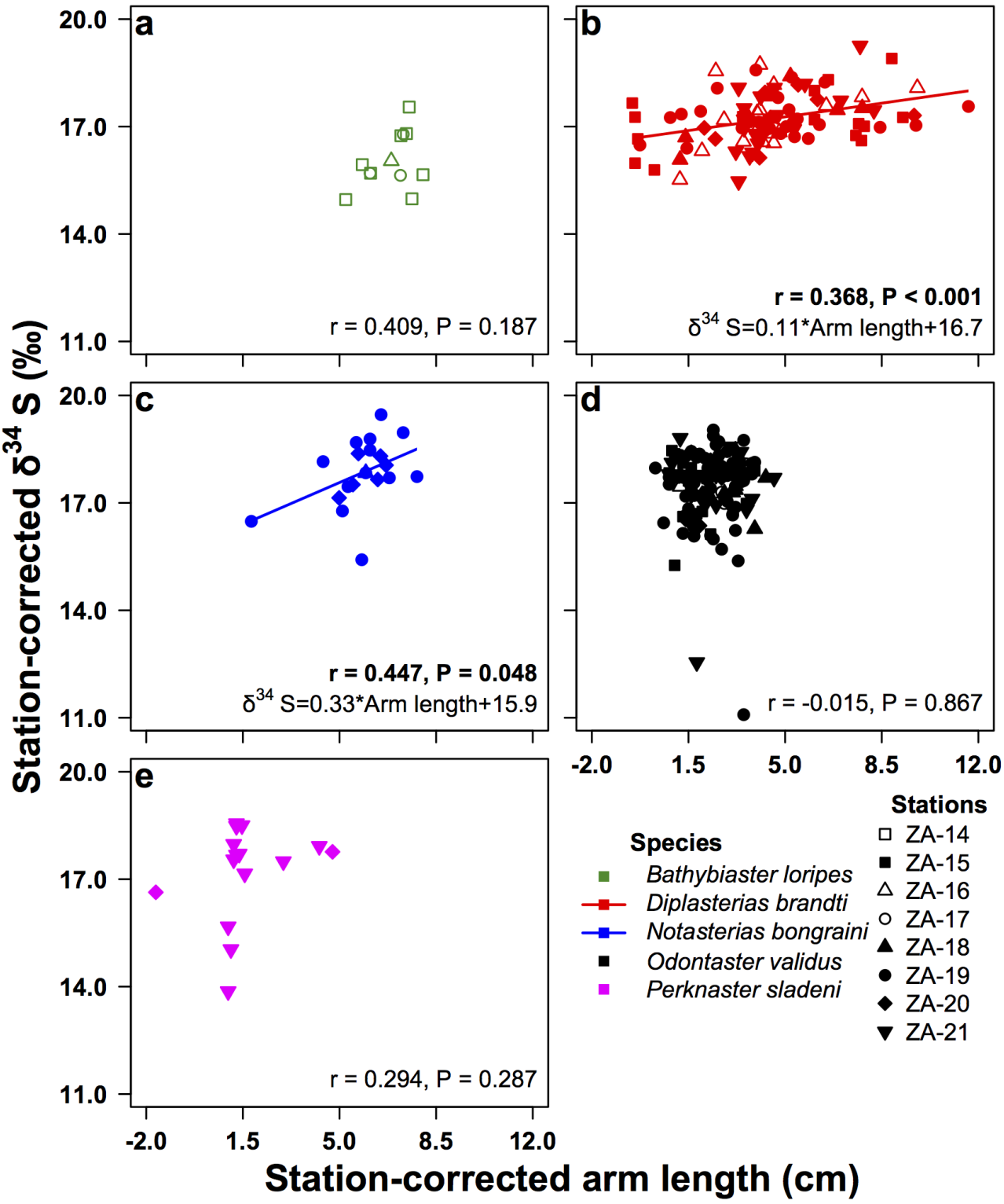


Fig. 5.5. Correlation coefficients between the station-corrected arm length and $\delta^{34}S$ values in a) *Bathybiaster loripes*, b) *Diplasterias brandti*, c) *Notasterias bongraini*, d) *Odontaster validus* and e) *Perknaster sladeni* from Ezcurra Inlet.

5.3.2 Stable isotope values in Diplasterias brandti and Odontaster validus

The ANCOVA results computed only with *Diplasterias brandti* and *Odontaster validus* tended to confirm the results of the previous ANCOVAs with *Diplasterias brandti* and *Odontaster validus* having similar $\delta^{15}N$ values ($F_{1,196} = 0.000$, $P = 0.996$). Similarly, $\delta^{13}C$ ($F_{4,196} = 12.624$, $P < 0.001$) and $\delta^{15}N$ values ($F_{4,196} = 3.914$, $P = 0.004$) varied between sampling stations while $\delta^{34}S$ values did not change between sampling stations ($F_{4,191} = 0.589$, $P = 0.671$). Contrary to the previous analysis, differences of $\delta^{13}C$ and $\delta^{34}S$ values between *Diplasterias brandti* and *Odontaster validus* became marginally significant ($F_{1,196} = 3.655$, $P = 0.057$) and significant ($F_{1,196} = 4.610$, $P = 0.033$), respectively. The ANCOVA results also notably highlighted an influence of the interaction between the species and the sampling station on the $\delta^{13}C$ values ($F_{4,196} = 4.559$, $P = 0.002$). Indeed, $\delta^{13}C$ values in *Diplasterias brandti* appeared to be higher than those of *Odontaster validus* in the inner stations but became more similar in the outer stations (Fig. 5.6 and 5.7).

Estimation of $SEA_{B.CN}$ for *Diplasterias brandti* and *Odontaster validus* (Fig. 5.8.a) showed that *Odontaster validus* had a larger isotopic niche than *Diplasterias brandti* in the two outer stations ZA-19 and ZA-21 (Fig. 5.6.c and e). *Diplasterias brandti* had a significantly larger $SEA_{B.CS}$ than *Odontaster validus* in the station ZA-18 (Fig. 5.7.b) while *Odontaster validus* had a significantly larger isotopic niche than *Diplasterias brandti* only in the station ZA-19 (Fig. 5.7.c, Fig. 5.8.b). Furthermore, both $SEA_{B.CN}$ and $SEA_{B.CS}$ increased from the inner to the outer stations for *Odontaster validus* (Fig. 5.8). Isotopic niche overlap varied between stations. When computed with $\delta^{13}C$ and $\delta^{15}N$ values, the overlap was low in the inner stations of the Ezcurra inlet (3.4 % for ZA-15, 14.7 % for ZA-18 and 9.7 % for ZA-20) but high in the two outer stations (55.8 % for ZA-19 and 51.0 % for ZA-21; Fig. 5.6). A similar pattern occurred when niches were computed with $\delta^{13}C$ and $\delta^{34}S$ values, with lower overlap in inner stations (3.5 % for ZA-15 and 9.5 % in ZA-18) than in outer stations (36.1 % for ZA-19 and 48.9 % for ZA-21), although a more important overlap was observed in the intermediate station ZA-20 than when the overlap was computed with $\delta^{13}C$ and $\delta^{15}N$ values (30.5 %; Fig. 5.7).

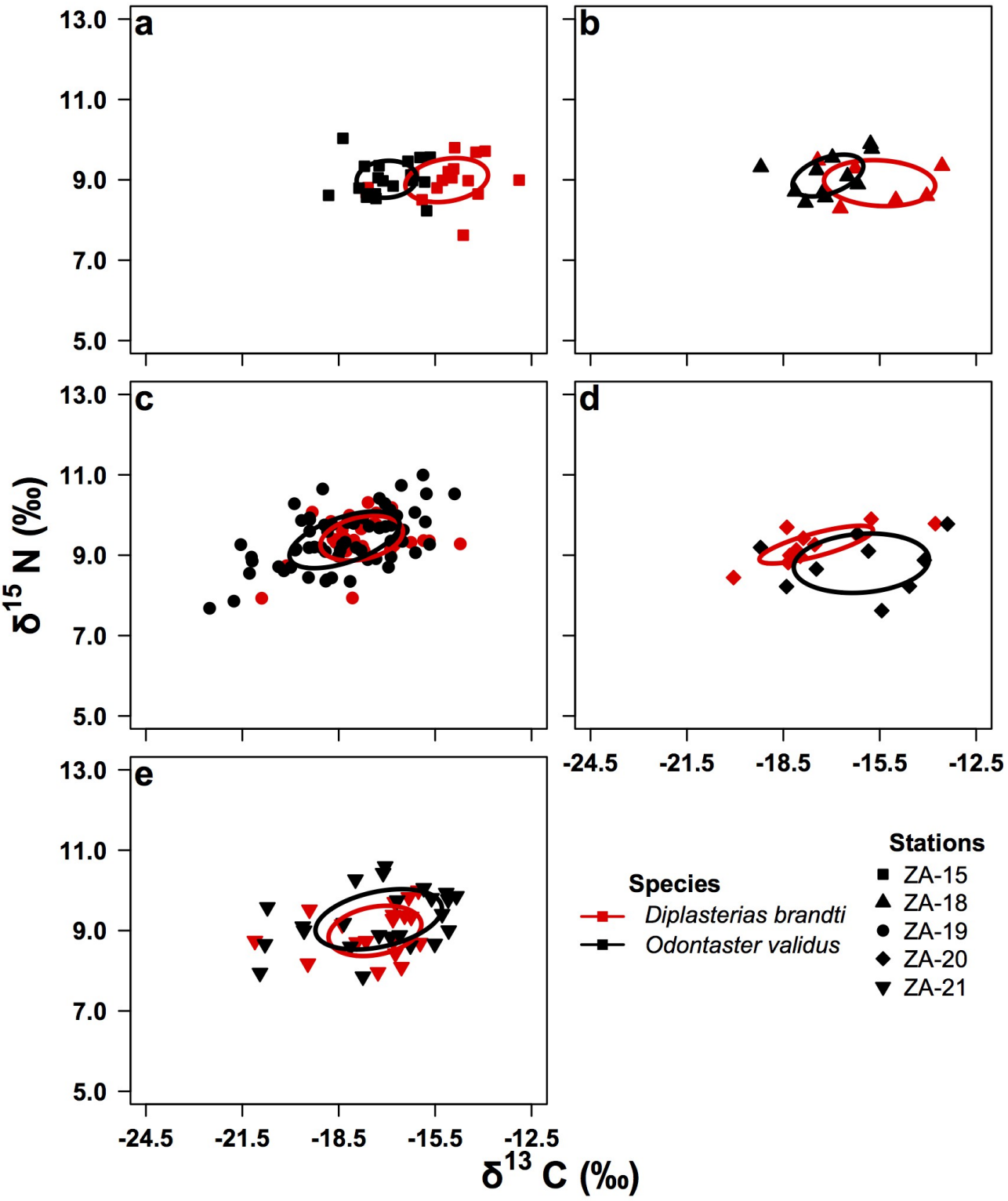


Fig. 5.6. Individual stable isotope values and resulting isotopic niches computed with $\delta^{13}C$ and $\delta^{15}N$ values of *Diplasterias brandti* and *Odontaster validus* in the sampling stations a) ZA-15, b) ZA-18, c) ZA-19, d) ZA-20 and e) ZA-21 in Ezcurra Inlet.

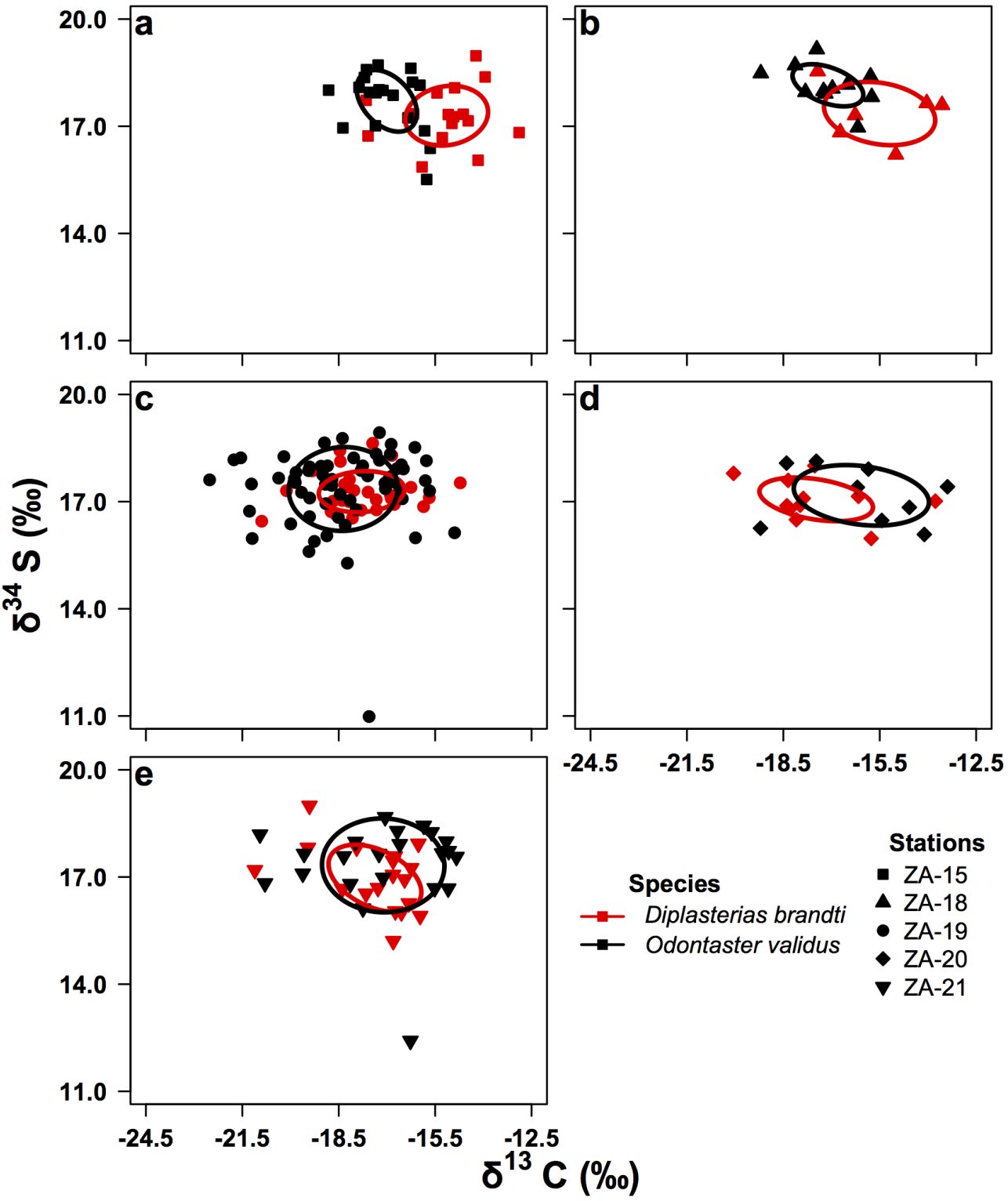


Fig. 5.7. Individual stable isotope values and resulting isotopic niches computed with $\delta^{13}C$ and $\delta^{34}S$ values of *Diplasterias brandti* and *Odontaster validus* in the sampling stations a) ZA-15, b) ZA-18, c) ZA-19, d) ZA-20 and e) ZA-21 in Ezcurra Inlet.

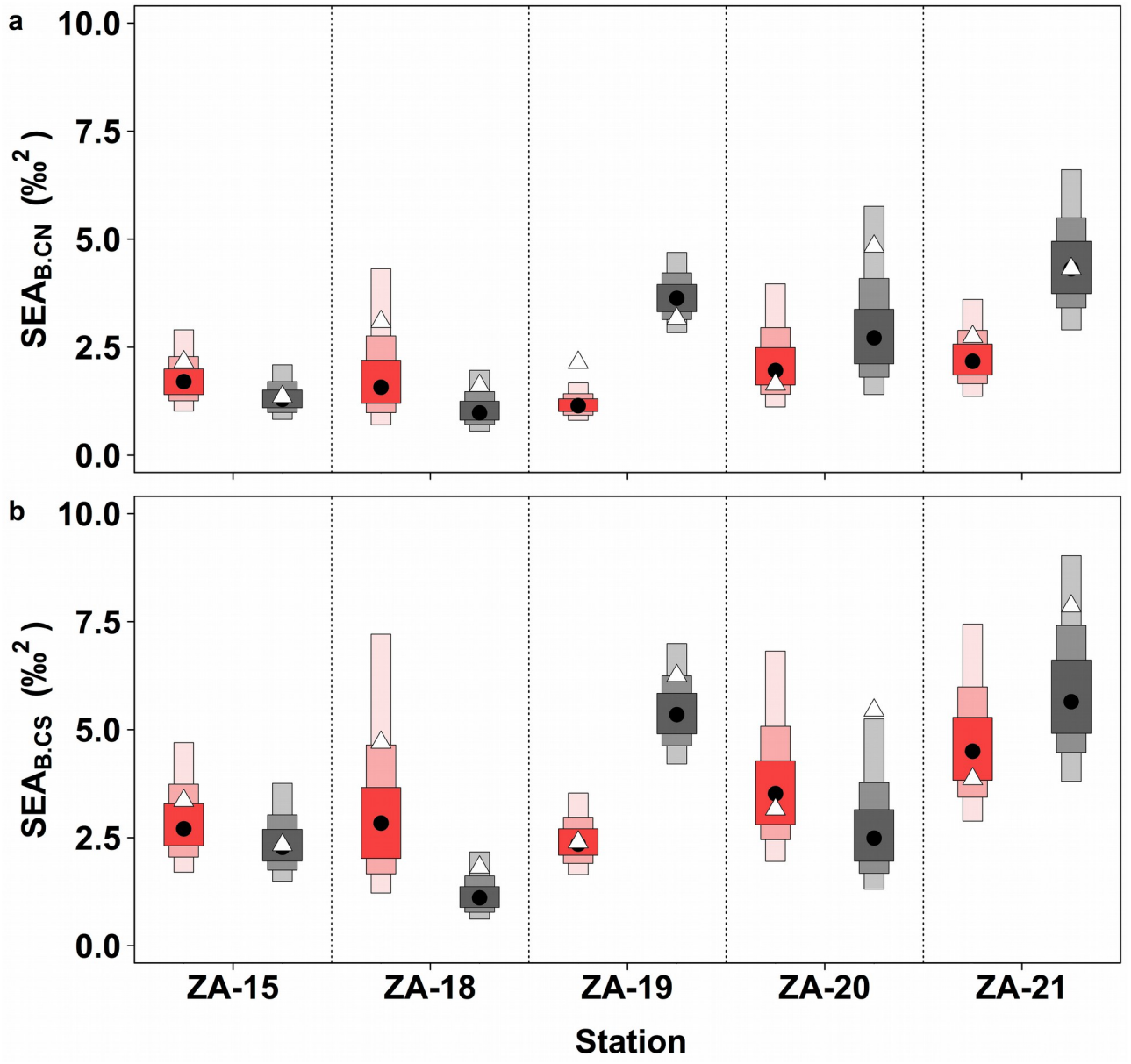


Fig. 5.8. SIBER density plots depicting the standard ellipse areas for *Diplasterias brandti* (red) and *Odontaster validus* (black) in each sampling station in Ezcurra Inlet and computed with a) $\delta^{13}C$ and $\delta^{15}N$ values and b) $\delta^{13}C$ and $\delta^{34}S$ values. Black dots are the modes. Shaded boxes represent the 50 %, 75 % and 95 % confidence intervals. White triangles are standard ellipse areas corrected for sample size (SEA_C).

5.4 Discussion

5.4.1 Size-related variations of the trophic ecology of sea stars

Size influenced stable isotope composition of sea stars from Ezcurra Inlet. However, not all species were equally subject to the change of stable isotope values with size. Furthermore, $\delta^{13}C$ and $\delta^{15}N$ values appeared to be linked to the disc radius, while the arm length had no influence on these stable isotope compositions once the effect of the disc radius had been taken into account. The better relationship between the disc radius and $\delta^{13}C$ and $\delta^{15}N$ values could be explained by the importance of the disc in sea star feeding, as direct contact between the food and the stomach is necessary whether the food is ingested or not (Jangoux, 1982). Furthermore, as stomach never extends beyond the edge of the disc for species everting their stomach, a larger disc allows sea stars to extend their stomach over a larger area, resulting in a capacity to feed on larger prey or on larger surfaces when consuming biofilms or encrusting organisms (Lawrence, 2012).

$\delta^{13}C$ is generally used to determine the baseline sources of carbon in food webs or feeding areas (Hobson, 1999; Michener and Kaufman, 2007) and notably discriminate pelagic (lower $\delta^{13}C$ values) and benthic primary producers (higher $\delta^{13}C$ values; France, 1995). Consequently, ontogenetic changes of $\delta^{13}C$ values may indicate the inclusion of previously unexploited carbon pathways in the diet of sea stars. $\delta^{13}C$ values increased with the disc radius in *Diplasterias brandti* and *Odontaster validus* while they decreased in *Perknaster sladeni* and remained stable in *Bathybiaster loripes* and *Notasterias bongraini*. The constricted range of disc size in *Bathybiaster loripes* could explain the absence of relationship between the $\delta^{13}C$ values and the disc radius in this species. Increasing of $\delta^{13}C$ values with disc size in *Diplasterias brandti* and *Odontaster validus* may indicate a progressive inclusion of more benthic prey in their diet (or prey relying more on benthic food web). *Notasterias bongraini* appears to strictly feed on pelagic carbon pathways throughout its growth, as this species had the lowest reported $\delta^{13}C$ and showed no relationship between its stable isotope values and disc radius. The ontogenetic decrease of $\delta^{13}C$ values observed in *Perknaster sladeni* suggests increasing reliance on pelagic carbon pathways while growing, although caution is needed for this interpretation because of the skewed distribution toward small disc radius sizes for this species.

Nitrogen isotopic compositions (^{15}N:^{14}N; $\delta^{15}N$) are generally used to assess nitrogen sources and to estimate the trophic level of consumers (Michener and Kauffman, 2007). Larger prey may occupy higher trophic levels, which is reflected in their higher $\delta^{15}N$ values. This is a common observation in teleosts for example (e.g. Frédérich et al., 2010; Linzmaier et al., 2018). As a result, consumption of larger prey in the diet of growing organisms would result in the increase of their $\delta^{15}N$

values. In sea stars, $\delta^{15}N$ values increased with the disc radius in *Bathybiaster loripes*, *Diplasterias brandti* and *Odontaster validus*, but not in *Notasterias bongraini* or *Perknaster sladeni*. Nadon and Himmelman (2010) observed a similar pattern of ontogenetic changes of $\delta^{15}N$ values in the Saint Lawrence Gulf, with the increase of $\delta^{15}N$ values with body size occurring in two sea star species (*Leptasterias polaris*, *Solaster endeca*) but not in two others (*Asterias vulgaris*, *Crossaster papposus*). In particular, the increase of $\delta^{15}N$ values in *Leptasterias polaris* was linked to the inclusion of predatory gastropods in the diet of larger individuals (Himmelman and Dutil, 1991). Caution is necessary regarding the interpretation of the increasing of $\delta^{15}N$ values with the disc radius in *Bathybiaster loripes*, as this increase was fast but occurred on a constricted disc radius range. However, potentially slow growth rates may explain ontogenetic changes of $\delta^{15}N$ values on a constricted disc radius range. Similarly, the absence of ontogenetic change of $\delta^{15}N$ values in *Perknaster sladeni* suggest no major ontogenetic shift in the trophic level of this species, but has to be interpreted with caution as the disc size of *Perknaster sladeni* was mostly constricted between 0.1 and 0.6 cm and only two individuals were larger than 0.6 cm. By contrast, the increase of $\delta^{15}N$ values with the disc radius was rather slow for *Diplasterias brandti* and *Odontaster validus*. Slow increase of $\delta^{15}N$ values with disc size may indicate a progressive rise in these two species' trophic positions during their growth, by progressively integrating larger (Sommer et al., 1999; Baeta and Ramón, 2013; Gooding and Harley, 2015; Fernandez et al., 2017) and/or more carnivorous (Himmelman and Dutil, 1991) prey in their diet. In particular, *Odontaster validus* is known to consume a wide range of prey, including diatoms, sponges, crustaceans, bivalves and other echinoderms (Pearse, 1965; Dayton et al., 1974; reviewed in Dearborn, 1977 and McClintock, 1994) and may progressively add the largest of these prey items to its diet throughout its growth. By contrast, *Notasterias bongraini* does not appear to include larger and/or higher trophic level prey in its diet while growing, as no ontogenetic changes of $\delta^{15}N$ values occurred for this species.

Actually, by taking into account both $\delta^{13}C$ and $\delta^{15}N$ values and their relationships with the disc radius, it is possible to make hypotheses on the trophic ecology of sea stars. High mean $\delta^{13}C$ and $\delta^{15}N$ values may indicate that *Bathybiaster loripes* feed on benthic prey and degraded organic matter, as suggested by stomachs retrieved from this species being filled with mud (Dearborn, 1977). For *Diplasterias brandti* and *Odontaster validus*, it can be hypothesised that young sea stars partly rely on suspended particulate organic matter (including phytoplankton and/or zooplankton) sedimenting from the water column, and progressively add larger benthic prey to their diet while growing. However, *Diplasterias brandti* may overall have a more benthic diet than *Odontaster validus* as

suggested by its higher $\delta^{13}C$ values. By contrast, *Notasterias bongraini* appears to strictly depend on pelagic items throughout its growth as highlighted by this species having the lowest reported $\delta^{13}C$ and $\delta^{15}N$ values and the absence of relationship between the stable isotope values and the disc radius. Its congener, *Notasterias armata*, was observed feeding on bivalves (Dearborn, 1977; Brueggeman, 1998), suggesting that this species may consume suspension feeding organisms. However, these species also possess large pedicellariae that were hypothesised to play some role in food capture (Dearborn, 1977). Indeed, although the range of functions of the pedicellariae is not yet fully known, their usage for food capture was observed (Chia and Amerongen, 1975; Dearborn et al., 1991) notably in specialised suspension feeders such as Brisingida (Emson and Young, 1994). Consequently, pedicellariae may allow the capture of pelagic food items such as zooplankton by *Notasterias bongraini* throughout its life. *Perknaster sladeni* had $\delta^{13}C$ and $\delta^{15}N$ values similar to those of *Odontaster validus*. Most of the sampled specimens were small individuals that were likely juveniles, and the lower $\delta^{13}C$ values in larger individuals suggested an increasing reliance on pelagic food webs with size. Its congener, *Perknaster fuscus*, is known to feed on sponges (Dayton et al., 1974). Therefore, small juvenile *Perknaster sladeni* could feed on small benthic organisms before becoming spongivores. These changes could also reflect a shift from prey relying on benthic producers towards prey relying more on the water column, regardless of the identity of this prey.

Contrary to previous results, $\delta^{34}S$ values were linked to the arm length in two species, while the disc radius had no influence on this parameter once the effect of the arm length has been taken into account. $\delta^{34}S$ are usually used in studies on marine food webs to refine the discrimination between primary producers or between benthic and pelagic sources (Fry et al., 1982; Machás and Santos, 1999; Connolly et al., 2004) as pelagic sulfates with high $\delta^{34}S$ values are the main source of inorganic sulfur for both phytoplankton and phytobenthos at the baseline of food webs (Giordano and Raven, 2014) while sulfides with low $\delta^{34}S$ values are present in sediment as a result of the activity of sulfate reducing bacteria (Fry et al., 1982). Consequently, the presence or absence of ontogenetic shifts of $\delta^{34}S$ values may indicate a change or a lack of change of feeding habitat. They remained stable in *Bathybiaster loripes*, *Odontaster validus* and *Perknaster sladeni* suggesting no drastic shift during their life. By contrast, $\delta^{34}S$ values increased with the arm length in *Diplasterias brandti* and *Notasterias bongraini*. The increase of $\delta^{34}S$ values with the arm length in *Notasterias bongraini* may further highlight the importance of pelagic food webs for this species through a suspension feeding behaviour or the consumption of suspension feeding organism. However, the increasing $\delta^{34}S$ values with the arm length for *Displasterias brandti* would indicate that this species

has a more pelagic diet while growing, which contradicts the previous interpretation done with $\delta^{13}C$ and $\delta^{15}N$ values which concluded that this species feeds more often on benthic prey while growing. Nevertheless, it should be noted that the increase of $\delta^{34}S$ values with the arm length in *Diplasterias brandti* was very slow compared to those observed in the relationships between the disc radius and $\delta^{13}C$ and $\delta^{15}N$ values, probably as a result of the higher size range provided by the arm length measurements. Furthermore, $\delta^{34}S$ values of all sea star species remained close to the $\delta^{34}S$ values of seawater sulfates instead of those of sediment sulfides (Fry et al., 1982) showing that, while living on the sediment and several species consuming benthic prey, all sea star species depend on pelagic environments, directly (i.e. suspension feeding) or indirectly (deposit feeding or predation on suspensivore), although the lower $\delta^{34}S$ values measured in *Bathybiaster loripes* may indicate a higher contribution of degraded sedimentary matter in the diet of this species.

5.4.2 Spatial variations of the trophic ecology of sea stars and their link to habitat characteristics

The results highlighted the existence of spatial variations of the trophic ecology of sea stars in Ezcurra Inlet. Indeed, $\delta^{13}C$ and $\delta^{15}N$ values differed between sampling stations, with $\delta^{13}C$ values decreasing from the inner to the outer stations and $\delta^{15}N$ values being higher in the two innermost stations. The pattern of decreasing $\delta^{13}C$ values from the inner to the outer Ezcurra Inlet was also observed in the organic carbon from surface sediment (Deflandre et al., 2013) and may be linked to the higher importance of matter of terrestrial origin provided by glacier meltwater in inner stations and the autochthonous production in outer stations (Pęcherzewski et al., 1980; Jonasz, 1983). The differentiation of sampling stations by $\delta^{13}C$ values in sea stars and their link with the pattern of $\delta^{13}C$ values in the organic carbon of sediment (Deflandre et al., 2013) may suggest limited mobility of sea stars between stations, as they would have to stay in a station long enough for their tissue turnover to reflect differences $\delta^{13}C$ values between stations.

Terrestrial ice run-offs in the inner stations also induce differences of mostly mineral suspended matter concentration, and thus of turbidity between the inner (i.e. high turbidity) and the outer of Ezcurra Inlet (i.e. low turbidity; Pęcherzewski et al., 1980). Furthermore, sediment characteristics differ between the inner (i.e. muddy) and the outer of Ezcurra Inlet (i.e. coarser sediement; Rodrigues et al., 2010; Deflandre et al., 2013; Berbel and Braga, 2014). Those habitat characteristics impact the benthos characteristics, diversity, abundance and biomass with absence of phytobenthos (Zieliński, 1990) and low benthic diversity and biomass occurring in the inner areas (Pabis et al., 2011; Siciński et al., 2011; Krzeminska and Kuklinski, 2018) while phytobenthos is

present (Zieliński, 1990) and animal diversity and biomass are higher in the outer areas (Pabis et al., 2011; Siciński et al., 2011; Krzeminska et Kuklinski, 2018). Negative relationships between mineral turbidity and benthos specific and functional diversity and biomass are a common phenomenon that was also observed in other types of environment such as lakes (Donohue and Garcia Molinos, 2009), estuaries (Giberto et al., 2004; Thrush et al., 2004), coral reefs (Kleypas, 1996; Jordán-Garza et al., 2017) and notably Arctic fjords (Wlodarska-Kowalczuk and Pearson, 2004; Wlodarska-Kowalczuk et al., 2005, 2019; Meyer et al., 2015) and Potter Cove in King George Island (Pasotti et al., 2015a; Sahade et al., 2015). Nevertheless, higher biomass may also occur in more turbid waters if organic matter supplies are sufficient, like in estuaries (Giberto et al., 2004). By contrast, more limited terrestrial inputs in other inner Antarctic fjords (Eidam et al., 2019) may explain the higher diversity recorded in these areas when compared to inner Arctic fjords (Grange and Smith, 2013). However, increased turbidity is not associated with reduced trophic diversity in areas affected by ice disturbance. Indeed, similar trophic diversity was observed in areas affected or not by ice disturbance (Pasotti et al., 2015b; Włodarska-Kowalczuk et al., 2019). Higher diversity and biomass of organisms in the outer area of Ezcurra Inlet and other less disturbed areas may induce higher prey availability in this area, allowing the exploitation of the same prey by several species, as well as a higher diversity of prey being consumed by each species. By contrast, lower diversity and biomass of organisms in the inner area of Ezcurra Inlet and other disturbed areas would induce lower prey availability. As a result, niche constriction would occur within species, inducing niche segregation between species to avoid competition, resulting in the similar trophic diversity observed within communities affected by ice disturbance when compared to undisturbed areas (Pasotti et al., 2015b; Włodarska-Kowalczuk et al., 2019). This hypothesis would explain the observed trophic interaction spatial pattern for *Diplasterias brandti* and *Odontaster validus*. Indeed, the isotopic niche size of *Odontaster validus* increased from the inner to the outer stations, suggesting trophic niche constriction in the inner stations and higher diversity of prey towards the opening of Ezcurra inlet. Similarly, the isotopic niche overlap between these two species was low in the inner stations, indicating potential resource partitioning, and became more important in the outer stations, suggesting similar trophic ecology for both species in this area where prey are more abundant. Detailed investigations of the diet by using stomach content analysis have been done for *Odontaster validus*, which appeared as a highly generalist omnivore feeding on various prey including diatoms, sponges, crustaceans, bivalves and other echinoderms, as well as displaying an active scavenging behaviour (Pearse, 1965; Dayton et al., 1974; reviewed in Dearborn, 1977 and McClintock, 1994).

Consequently, trophic plasticity would be expected for this species depending of environmental conditions. That could explain the expansion of its isotopic niche in the outer Ezcurra Inlet, as all individuals do not necessarily feed on the same items. That could also explain its segregation from the isotopic niche of *Diplasterias brandti* in the inner Ezcurra Inlet, to avoid competition. More limited investigations were conducted on the diet of *Diplasterias* species. Early studies concluded that *Diplasterias brucei* is mostly a bivalve specialist although it may also feed on gastropods and display necrophagous behaviour (Dayton et al., 1974; reviewed in Dearborn, 1977 and McClintock, 1994). However, a low trophic level was computed for *Diplasterias brucei* in Terre Adélie following the lack of sea ice break-up in the region, suggesting a more direct consumption of the sea ice-derived production (Michel et al., 2019), and this species was also observed feeding on prey such as large isopods and limpets (Rauschert, 1986a; 1986b) that were not reported in the last review on its diet (McClintock, 1994). This suggests that *Diplasterias* sea stars may have more diverse feeding habits than previously thought, and may feed on prey similar to those of *Odontaster validus*, as suggested by the overlap of the isotopic niches of both species in the outer Ezcurra inlet. Nevertheless, the isotopic niche size of *Diplasterias brandti* did not change from the inner to the outer Ezcurra Inlet, suggesting on one hand more limited trophic plasticity for this species than for *Odontaster validus*. On the other hand, it may also suggest that *Diplasterias brandti* is able to maintain higher trophic diversity than *Odontaster validus* in areas with higher turbidity, and thus in more stressful environmental conditions.

5.4.3 Summary and conclusion

The results presented here highlighted both the occurrence of ontogenetic variations of trophic ecology and the influence of morphological features on the trophic ecology of Antarctic sea stars. Ontogenetic variations were highlighted by the change of stable isotope values with increasing size. For $\delta^{13}C$ and $\delta^{15}N$ values, i.e. the two mostly used isotope systems in trophic ecology studies, the disc radius of sea stars rather than the arm length influenced stable isotope values, indicating that this specific morphological feature has more impact than the whole sea star size on trophic ecology.

Spatial variations of trophic ecology linked to a gradient of environmental conditions appeared to occur for sea stars from Ezcurra Inlet. In particular, these spatial variations may be linked to the decrease of the importance of terrestrial inputs provided by glacier meltwater from the inner to the outer of Ezcurra Inlet. Inner stations of Ezcurra Inlet are thus more subjected to disturbance, which could reduce prey availability in these areas and induce trophic niche constriction and segregation

between sea stars to reduce competition risks. By contrast, higher prey availability could occur in the outer stations of Ezcurra Inlet thanks to limited terrestrial inputs and, thus, overlap of sea stars' trophic niches with more limited risk of competition could occur in these areas.

Terrestrial glaciers, ice shelves and sea ice from King George Island and of the Western Antarctic Peninsula are receding because of climate change (Braun and Gossmann, 2002; Cook et al., 2005; Stammerjohn et al., 2008a; Rückamp et al., 2011). This melting causes short-term increases of turbidity because of terrestrial run-off (Sahade et al., 2015) and, thus, increases of sedimentation rates (Boldt et al., 2013) and of mud contribution to the bottom sediment (Munoz and Wellner, 2016). Other expected impacts of glacier retreat may include increasing freshwater pulses (Dierssen et al., 2002) and iceberg scouring (Barnes and Souster, 2011). Considering the impact of elevated turbidity on the benthos (Wilber and Clarke, 2001; Thrush et al., 2004; Donohue and Garcia Molinos, 2009; Bell et al., 2015), glacier retreat and increasing terrestrial inputs may thus further contribute to a reduction of the diversity and abundance of the benthic communities already impacted by turbidity (Sahade et al., 2015) in the short term. As a result, modifications of the trophic ecology of sea stars living in this area are expected to occur. However, in the long term, reduced glacier surface could diminish terrestrial inputs and open new areas for benthic colonisation, leading to more diverse benthic assemblages (Pasotti et al., 2015a) and subsequent modifications of the trophic ecology of sea stars. In this context, the results from this study demonstrated that dominant species like *Odontaster validus* can adapt their diet to environmental variations, suggesting they may cope with environment-induced changes in resource availability.

Chapter 5 – Supplementary material: Trophic ecology of sea stars in an Antarctic fjord: size-related and spatial variations

Sea star species investigated in the chapter 5. From left to right, first row: *Bathybiaster loripes* (credit: Université libre de Bruxelles; picture by Pernet P) ; *Diplasterias brandti* (picture by Arntz WE). Second row: *Notasterias bongraini* (credit: National Museum of Natural History, Smithsonian Institution; picture by Testa AJ); *Odontaster validus* (picture by Jossart Q); *Perknaster sladeni* (credit: National Museum of Natural History, Smithsonian Institution; picture by Testa AJ).

Table S.5.1. Individual sea star collected in each station of Ezcurra Inlet with the depth of sampling, the arm length and the disc radius and the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values for each species as well as for each whole station (bold lines).

Sample ID	Station	Species	Depth (m)	Replicate	Arm length (cm)	Disc radius (cm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{34}S$ (‰)
ZA-14-10-A-Bat lorl 1	ZA-14	*Bathybiaster loripes*	10.0	A	8.1	1.9	-15.7	12.2	15.4
ZA-14-10-A-Bat lorl 2	ZA-14	*Bathybiaster loripes*	10.0	A	7.3	1.4	-15.2	12.0	16.5
ZA-14-10-A-Bat lorl 3	ZA-14	*Bathybiaster loripes*	10.0	A	5.3	1.4	-15.8	11.6	14.7
ZA-14-10-A-Bat lorl 4	ZA-14	*Bathybiaster loripes*	10.0	A	7.6	1.6	-16.4	10.8	17.3
ZA-14-10-B-Bat lorl 1	ZA-14	*Bathybiaster loripes*	10.0	B	7.5	1.8	-15.9	11.9	16.5
ZA-14-10-C-Bat lorl 1	ZA-14	*Bathybiaster loripes*	10.0	C	5.9	1.4	-13.4	11.3	15.7
ZA-14-10-C-Bat lorl 2	ZA-14	*Bathybiaster loripes*	10.0	C	7.7	1.8	-14.1	12.6	14.7
ZA-14-10-C-Bat lorl 3	ZA-14	*Bathybiaster loripes*	10.0	C	6.2	1.4	-15.4	11.0	15.4
ZA-15-20-A-Dipla sp 1	ZA-15	*Diplasterias brandti*	20.0	A	7.8	1.0	-13.9	9.7	18.4
ZA-15-20-A-Dipla sp 2	ZA-15	*Diplasterias brandti*	20.0	A	7.3	1.0	-14.9	9.8	18.1
ZA-15-20-A-Odo val 1	ZA-15	*Odontaster validus*	20.0	A	3.9	1.7	-16.0	9.6	18.1
ZA-15-20-A-Odo val 2	ZA-15	*Odontaster validus*	20.0	A	1.5	0.6	-16.8	8.8	17.9
ZA-15-20-A-Odo val 3	ZA-15	*Odontaster validus*	20.0	A	3.6	1.5	-16.3	9.5	17.2
ZA-15-20-A-Odo val 4	ZA-15	*Odontaster validus*	20.0	A	2.4	1.0	-17.1	9.0	18.0
ZA-15-20-A-Odo val 5	ZA-15	*Odontaster validus*	20.0	A	2.3	0.9	-15.7	9.6	16.4
ZA-15-20-A-Odo val 6	ZA-15	*Odontaster validus*	20.0	A	2.0	0.8	-17.4	8.7	17.0
ZA-15-20-A-Odo val 7	ZA-15	*Odontaster validus*	20.0	A	1.0	0.4	-15.8	8.2	15.5
ZA-15-20-A-Odo val 8	ZA-15	*Odontaster validus*	20.0	A	1.3	0.5	-15.8	8.9	16.9
ZA-15-20-A-Odo val 9	ZA-15	*Odontaster validus*	20.0	A	1.0	0.3	-16.3	9.1	18.6
ZA-15-Dipla sp 1	ZA-15	*Diplasterias brandti*	27.0		10.1	1.2	-14.2	9.7	19.0
ZA-15-Dipla sp 10	ZA-15	*Diplasterias brandti*	27.0		1.5	0.2	-15.9	8.5	15.9
ZA-15-Dipla sp 11	ZA-15	*Diplasterias brandti*	27.0		0.8	0.1	-14.6	7.6	17.3
ZA-15-Dipla sp 12	ZA-15	*Diplasterias brandti*	27.0		0.8	0.1	-14.2	8.6	16.0
ZA-15-Dipla sp 13	ZA-15	*Diplasterias brandti*	27.0		0.9	0.1	-17.6	8.8	16.7
ZA-15-Dipla sp 14	ZA-15	*Diplasterias brandti*	27.0		0.7	0.1	-17.6	8.7	17.7
ZA-15-Dipla sp 2	ZA-15	*Diplasterias brandti*	27.0		9.1	1.4	-15.0	9.1	17.1
ZA-15-Dipla sp 3	ZA-15	*Diplasterias brandti*	27.0		8.8	1.2	-12.9	9.0	16.8
ZA-15-Dipla sp 4	ZA-15	*Diplasterias brandti*	27.0		10.5	0.9	-15.1	9.2	17.3
ZA-15-Dipla sp 5	ZA-15	*Diplasterias brandti*	27.0		7.3	0.8	-14.9	9.3	17.3
ZA-15-Dipla sp 6	ZA-15	*Diplasterias brandti*	27.0		8.9	1.1	-14.5	9.0	17.2
ZA-15-Dipla sp 7	ZA-15	*Diplasterias brandti*	27.0		4.7	0.4	-16.2	9.1	17.3
ZA-15-Dipla sp 8	ZA-15	*Diplasterias brandti*	27.0		5.6	0.5	-15.4	8.8	17.9
ZA-15-Dipla sp 9	ZA-15	*Diplasterias brandti*	27.0		9.0	1.0	-15.3	9.0	16.7
ZA-15-Odo val 1	ZA-15	*Odontaster validus*	27.0		1.8	0.7	-18.4	10.0	17.0
ZA-15-Odo val 10	ZA-15	*Odontaster validus*	27.0		0.9	0.2	-17.3	9.1	18.7
ZA-15-Odo val 2	ZA-15	*Odontaster validus*	27.0		1.4	0.5	-18.8	8.6	18.0
ZA-15-Odo val 3	ZA-15	*Odontaster validus*	27.0		2.2	0.9	-17.3	8.5	17.9
ZA-15-Odo val 4	ZA-15	*Odontaster validus*	27.0		1.3	0.5	-17.7	9.3	18.4
ZA-15-Odo val 5	ZA-15	*Odontaster validus*	27.0		1.5	0.6	-17.2	9.4	18.0
ZA-15-Odo val 6	ZA-15	*Odontaster validus*	27.0		1.6	0.9	-16.2	9.0	18.2
ZA-15-Odo val 7	ZA-15	*Odontaster validus*	27.0		0.8	0.3	-17.9	8.8	18.1
ZA-15-Odo val 8	ZA-15	*Odontaster validus*	27.0		1.1	0.4	-17.6	8.6	18.6
ZA-15-Odo val 9	ZA-15	*Odontaster validus*	27.0		1.0	0.4	-17.5	8.7	17.9
ZA-16-17m-Dipla sp 1	ZA-16	*Diplasterias brandti*	17.0		1.2	0.1	-15.2	7.7	15.7
ZA-16-17m-Dipla sp 10	ZA-16	*Diplasterias brandti*	17.0		6.5	0.6	-14.0	9.3	17.8
ZA-16-17m-Dipla sp 11	ZA-16	*Diplasterias brandti*	17.0		4.0	0.2	-15.2	9.0	17.1
ZA-16-17m-Dipla sp 12	ZA-16	*Diplasterias brandti*	17.0		9.8	0.8	-14.9	9.6	18.3
ZA-16-17m-Dipla sp 13	ZA-16	*Diplasterias brandti*	17.0		7.8	0.6	-15.1	9.1	18.0
ZA-16-17m-Dipla sp 14	ZA-16	*Diplasterias brandti*	17.0		4.1	0.3	-16.6	9.4	17.6
ZA-16-17m-Dipla sp 15	ZA-16	*Diplasterias brandti*	17.0		5.2	0.5	-15.0	9.9	NA
ZA-16-17m-Dipla sp 16	ZA-16	*Diplasterias brandti*	17.0		2.8	0.2	-15.8	9.6	17.4
ZA-16-17m-Dipla sp 17	ZA-16	*Diplasterias brandti*	17.0		4.2	0.5	-14.2	9.2	16.7
ZA-16-17m-Dipla sp 18	ZA-16	*Diplasterias brandti*	17.0		4.1	0.6	-14.7	9.9	18.9
ZA-16-17m-Dipla sp 19	ZA-16	*Diplasterias brandti*	17.0		3.5	0.4	-16.3	9.2	16.8
ZA-16-17m-Dipla sp 2	ZA-16	*Diplasterias brandti*	17.0		2.0	0.1	-15.7	8.9	16.5
ZA-16-17m-Dipla sp 20	ZA-16	*Diplasterias brandti*	17.0		4.2	0.4	-16.9	9.0	17.1

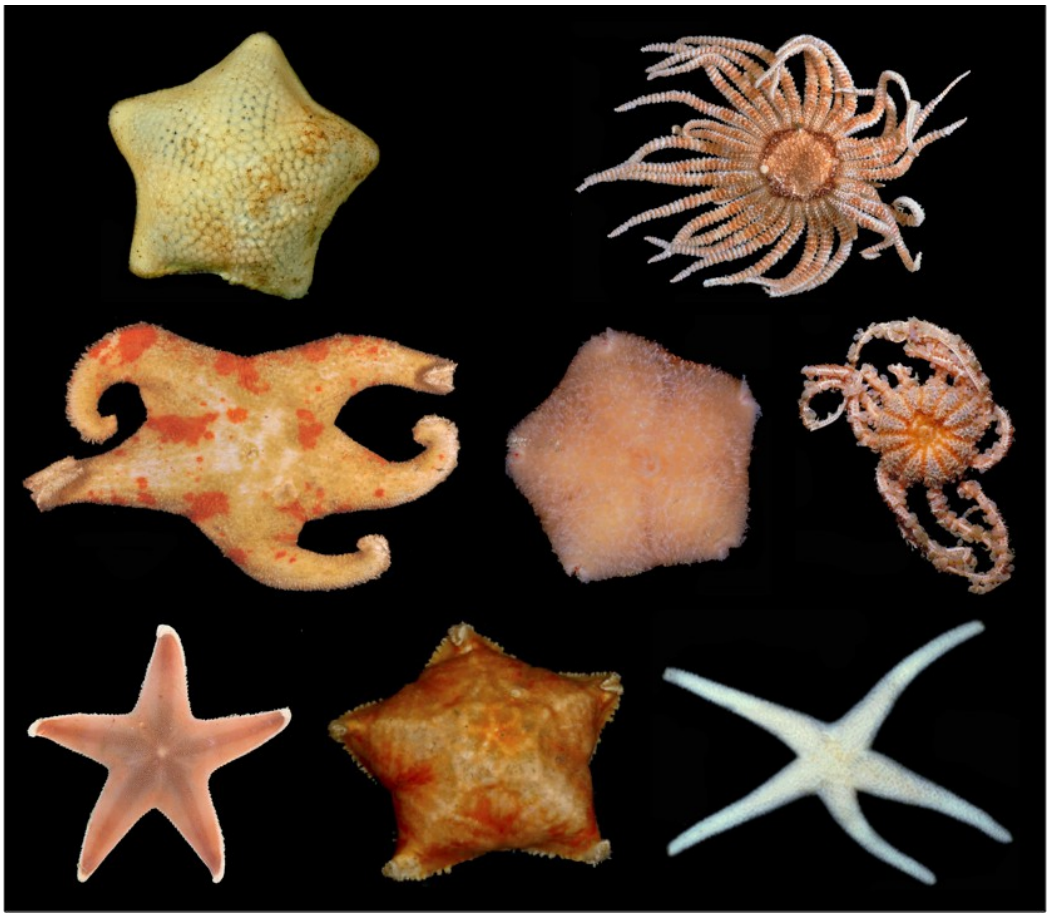
ZA-16-17m-Dipla sp 3	ZA-16	*Diplasterias brandti*	17.0		4.0	0.3	-16.6	9.5	17.6
ZA-16-17m-Dipla sp 4	ZA-16	*Diplasterias brandti*	17.0		4.8	0.5	-15.7	9.3	17.0
ZA-16-17m-Dipla sp 5	ZA-16	*Diplasterias brandti*	17.0		4.4	0.4	-15.0	9.5	17.0
ZA-16-17m-Dipla sp 6	ZA-16	*Diplasterias brandti*	17.0		2.5	0.1	-15.4	9.6	18.7
ZA-16-17m-Dipla sp 7	ZA-16	*Diplasterias brandti*	17.0		10.8	0.8	-14.4	9.2	NA
ZA-16-17m-Dipla sp 8	ZA-16	*Diplasterias brandti*	17.0		4.6	0.2	-16.0	9.3	18.3
ZA-16-17m-Dipla sp 9	ZA-16	*Diplasterias brandti*	17.0		2.3	0.1	-15.8	9.1	NA
ZA-16-17m-Odo val 1	ZA-16	*Odontaster validus*	17.0		1.2	0.4	-20.5	8.2	16.3
ZA-16-20-A-Psi char 1	ZA-16	*Psilaster charcoti*	20.0	A	7.0	1.7	-17.7	10.5	16.8
ZA-16-20-C-Bat lor 1	ZA-16	*Bathybiaster loripes*	20.0	C	8.4	2.1	-14.4	11.5	15.2
ZA-16-20-C-Dipla sp 1	ZA-16	*Diplasterias brandti*	20.0	C	4.6	0.6	-14.7	9.5	16.7
ZA-17-17m-Odo val 1	ZA-17	*Odontaster validus*	17.0		3.6	1.7	-13.3	11.5	18.2
ZA-17-17m-Odo val 2	ZA-17	*Odontaster validus*	17.0		2.8	1.1	-15.1	10.3	17.1
ZA-17-17m-Odo val 3	ZA-17	*Odontaster validus*	17.0		2.7	1.2	-14.8	9.8	17.4
ZA-17-30-B-Bat lor 1	ZA-17	*Bathybiaster loripes*	30.0	B	6.5	1.5	-15.2	11.7	16.6
ZA-17-30-C-Bat lor 1	ZA-17	*Bathybiaster loripes*	30.0	C	6.6	1.6	-16.5	12.3	17.8
ZA-17-30-C-Bat lor 2	ZA-17	*Bathybiaster loripes*	30.0	C	5.4	1.3	-17.8	9.7	16.7
ZA-17-30-C-ND 1	ZA-17	*Notasterias bongraini*	30.0	C	10.2	1.9	-22.1	8.4	18.9
ZA-18-10-B-Odo val 1	ZA-18	*Odontaster validus*	10.0	B	1.2	0.4	-19.2	9.3	18.5
ZA-18-10-B-Odo val 2	ZA-18	*Odontaster validus*	10.0	B	3.2	0.8	-16.5	9.1	18.2
ZA-18-10-B-Odo val 3	ZA-18	*Odontaster meridionalis*	10.0	B	2.1	0.9	-22.2	10.3	19.9
ZA-18-10-B-Odo val 5	ZA-18	*Odontaster validus*	10.0	B	2.0	0.9	-17.2	8.6	17.9
ZA-18-20-B-Dipla sp 1	ZA-18	*Diplasterias brandti*	20.0	B	5.4	0.7	-17.4	9.5	18.5
ZA-18-20-B-Dipla sp 2	ZA-18	*Diplasterias brandti*	20.0	B	5.5	0.8	-16.3	9.3	17.3
ZA-18-20-B-Dipla sp 3	ZA-18	*Diplasterias brandti*	20.0	B	1.4	0.1	-15.0	8.5	16.2
ZA-18-20-B-Odo val 1	ZA-18	*Odontaster validus*	20.0	B	3.1	1.2	-18.1	8.7	18.7
ZA-18-20-B-Odo val 2	ZA-18	*Odontaster validus*	20.0	B	4.3	1.8	-15.8	9.9	18.4
ZA-18-20-B-Odo val 3	ZA-18	*Odontaster validus*	20.0	B	2.8	1.1	-17.8	8.4	18.0
ZA-18-20-B-Odo val 4	ZA-18	*Odontaster validus*	20.0	B	3.9	1.7	-16.2	8.9	17.0
ZA-18-20-B-Odo val 5	ZA-18	*Odontaster validus*	20.0	B	2.3	1.6	-15.7	9.8	17.8
ZA-18-20-B-Odo val 6	ZA-18	*Odontaster validus*	20.0	B	3.1	1.3	-17.2	8.7	18.0
ZA-18-20-C-Dipla sp 1	ZA-18	*Diplasterias brandti*	20.0	C	1.6	0.1	-16.7	8.3	16.8
ZA-18-20-C-Dipla sp 2	ZA-18	*Diplasterias brandti*	20.0	C	8.0	1.6	-14.0	8.6	17.6
ZA-18-20-C-Dipla sp 3	ZA-18	*Diplasterias brandti*	20.0	C	7.1	0.9	-13.6	9.3	17.6
ZA-18-20-C-Nota sp 1	ZA-18	*Notasterias bongraini*	20.0	C	8.9	0.9	-22.8	6.6	16.4
ZA-18-20-C-Odo val 1	ZA-18	*Odontaster meridionalis*	20.0	C	3.6	1.4	-20.0	8.7	17.3
ZA-18-20-C-Odo val 2	ZA-18	*Odontaster validus*	20.0	C	3.2	1.3	-17.0	9.6	18.1
ZA-18-20-C-Odo val 3	ZA-18	*Odontaster validus*	20.0	C	3.2	1.4	-17.5	9.2	19.2
ZA-19-10-B-Odo val 1	ZA-19	*Odontaster validus*	10.0	B	2.3	1.0	-15.7	9.3	17.3
ZA-19-10-B-Odo val 2	ZA-19	*Odontaster validus*	10.0	B	0.8	0.2	-16.6	9.4	17.4
ZA-19-10-B-Odo val 3	ZA-19	*Odontaster validus*	10.0	B	0.3	0.3	-17.8	9.1	17.9
ZA-19-10-C-Odo val 1	ZA-19	*Odontaster validus*	10.0	C	3.9	1.9	-16.6	10.7	18.0
ZA-19-10-C-Odo val 2	ZA-19	*Odontaster validus*	10.0	C	1.3	0.5	-18.9	8.4	16.0
ZA-19-10-C-Odo val 3	ZA-19	*Odontaster validus*	10.0	C	0.6	0.1	-18.3	9.3	16.3
ZA-19-10-C-Odo val 4	ZA-19	*Odontaster validus*	10.0	C	2.2	0.9	-19.4	8.4	17.9
ZA-19-10-C-Odo val 5	ZA-19	*Odontaster validus*	10.0	C	1.4	0.6	-16.5	9.3	17.1
ZA-19-10-C-Odo val 6	ZA-19	*Odontaster validus*	10.0	C	0.8	0.3	-17.0	8.7	17.6
ZA-19-2-Dipla sp 1	ZA-19	*Diplasterias brandti*	13.0		6.3	1.0	-14.7	9.3	17.5
ZA-19-2-Dipla sp 2	ZA-19	*Diplasterias brandti*	13.0		5.2	0.9	-16.9	9.1	17.2
ZA-19-2-Dipla sp 3	ZA-19	*Diplasterias brandti*	13.0		5.4	1.0	-16.8	9.3	16.9
ZA-19-2-Dipla sp 4	ZA-19	*Diplasterias brandti*	13.0		2.4	0.2	-16.3	9.3	17.4
ZA-19-2-Dipla sp 5	ZA-19	*Diplasterias brandti*	13.0		0.9	0.1	-18.1	7.9	16.5
ZA-19-2-Odo val 1	ZA-19	*Odontaster validus*	13.0		3.3	1.2	-17.2	9.7	18.2
ZA-19-2-Odo val 10	ZA-19	*Odontaster validus*	13.0		1.6	0.7	-19.7	9.9	17.3
ZA-19-2-Odo val 11	ZA-19	*Odontaster validus*	13.0		3.5	1.4	-16.9	9.4	17.5
ZA-19-2-Odo val 12	ZA-19	*Odontaster validus*	13.0		3.1	1.2	-18.5	9.0	16.6
ZA-19-2-Odo val 13	ZA-19	*Odontaster validus*	13.0		1.7	0.6	-18.7	8.4	17.5
ZA-19-2-Odo val 14	ZA-19	*Odontaster validus*	13.0		3.4	1.8	-15.8	9.8	17.6
ZA-19-2-Odo val 15	ZA-19	*Odontaster validus*	13.0		2.8	0.8	-18.1	8.3	17.0
ZA-19-2-Odo val 16	ZA-19	*Odontaster validus*	13.0		1.9	0.8	-20.2	8.6	18.3
ZA-19-2-Odo val 17	ZA-19	*Odontaster validus*	13.0		3.4	1.4	-18.9	9.1	17.5
ZA-19-2-Odo val 18	ZA-19	*Odontaster validus*	13.0		2.3	0.9	-19.8	9.2	17.8
ZA-19-2-Odo val 19	ZA-19	*Odontaster validus*	13.0		3.2	1.4	-17.0	9.7	17.4

ZA-19-2-Odo val 2	ZA-19	*Odontaster validus*	13.0	1.7	0.7	-21.2	9.0	17.5
ZA-19-2-Odo val 20	ZA-19	*Odontaster validus*	13.0	1.7	0.5	-19.4	9.9	17.1
ZA-19-2-Odo val 21	ZA-19	*Odontaster validus*	13.0	2.4	1.0	-19.3	9.2	15.9
ZA-19-2-Odo val 22	ZA-19	*Odontaster validus*	13.0	3.8	1.6	-16.9	9.0	17.7
ZA-19-2-Odo val 23	ZA-19	*Odontaster validus*	13.0	2.3	0.9	-16.1	9.1	16.0
ZA-19-2-Odo val 24	ZA-19	*Odontaster validus*	13.0	2.7	1.4	-18.7	9.8	17.6
ZA-19-2-Odo val 25	ZA-19	*Odontaster validus*	13.0	2.4	1.1	-17.2	10.4	18.9
ZA-19-2-Odo val 26	ZA-19	*Odontaster validus*	13.0	2.5	1.2	-15.9	11.0	NA
ZA-19-2-Odo val 27	ZA-19	*Odontaster validus*	13.0	2.6	1.0	-16.9	9.7	18.6
ZA-19-2-Odo val 28	ZA-19	*Odontaster validus*	13.0	3.2	1.4	-14.9	10.5	16.1
ZA-19-2-Odo val 29	ZA-19	*Odontaster validus*	13.0	2.3	1.1	-16.7	10.0	17.9
ZA-19-2-Odo val 3	ZA-19	*Odontaster validus*	13.0	2.1	1.0	-15.8	10.5	18.1
ZA-19-2-Odo val 30	ZA-19	*Odontaster validus*	13.0	3.1	1.4	-19.4	9.9	16.6
ZA-19-2-Odo val 31	ZA-19	*Odontaster validus*	13.0	2.5	1.2	-16.1	10.1	18.5
ZA-19-2-Odo val 32	ZA-19	*Odontaster validus*	13.0	2.7	1.0	-16.5	9.6	17.9
ZA-19-2-Odo val 33	ZA-19	*Odontaster validus*	13.0	3.2	1.3	-17.6	8.9	17.7
ZA-19-2-Odo val 34	ZA-19	*Odontaster validus*	13.0	2.9	1.2	-16.9	10.1	18.3
ZA-19-2-Odo val 35	ZA-19	*Odontaster validus*	13.0	3.2	1.5	-18.0	9.2	16.8
ZA-19-2-Odo val 36	ZA-19	*Odontaster validus*	13.0	3.8	1.3	-17.8	9.9	18.0
ZA-19-2-Odo val 37	ZA-19	*Odontaster validus*	13.0	3.5	1.5	-18.9	9.8	18.6
ZA-19-2-Odo val 38	ZA-19	*Odontaster validus*	13.0	2.7	1.0	-19.4	9.2	15.6
ZA-19-2-Odo val 39	ZA-19	*Odontaster validus*	13.0	2.4	1.0	-18.4	9.3	18.8
ZA-19-2-Odo val 4	ZA-19	*Odontaster validus*	13.0	3.3	1.3	-18.2	9.8	15.3
ZA-19-2-Odo val 5	ZA-19	*Odontaster validus*	13.0	1.7	0.5	-20.0	8.7	16.4
ZA-19-2-Odo val 6	ZA-19	*Odontaster validus*	13.0	3.5	1.4	-17.1	10.3	17.5
ZA-19-2-Odo val 7	ZA-19	*Odontaster validus*	13.0	1.6	0.6	-17.3	8.9	18.3
ZA-19-2-Odo val 8	ZA-19	*Odontaster validus*	13.0	2.5	1.0	-19.1	9.2	18.0
ZA-19-2-Odo val 9	ZA-19	*Odontaster validus*	13.0	1.2	0.4	-21.5	9.3	18.2
ZA-19-27m-Dipla sp 1	ZA-19	*Diplasterias brandti*	27.0	12.8	1.3	-18.2	10.0	17.6
ZA-19-27m-Dipla sp 10	ZA-19	*Diplasterias brandti*	27.0	6.4	0.7	-17.8	9.2	NA
ZA-19-27m-Dipla sp 11	ZA-19	*Diplasterias brandti*	27.0	6.5	0.9	-17.7	9.1	NA
ZA-19-27m-Dipla sp 2	ZA-19	*Diplasterias brandti*	27.0	5.2	0.8	-17.8	9.7	16.8
ZA-19-27m-Dipla sp 3	ZA-19	*Diplasterias brandti*	27.0	5.1	0.5	-17.4	9.8	18.6
ZA-19-27m-Dipla sp 4	ZA-19	*Diplasterias brandti*	27.0	6.0	0.6	-15.9	9.4	16.9
ZA-19-27m-Dipla sp 5	ZA-19	*Diplasterias brandti*	27.0	2.6	0.3	-20.9	7.9	16.5
ZA-19-27m-Dipla sp 6	ZA-19	*Diplasterias brandti*	27.0	4.7	0.6	-18.3	9.1	17.4
ZA-19-27m-Dipla sp 7	ZA-19	*Diplasterias brandti*	27.0	7.4	0.8	-15.7	9.4	17.1
ZA-19-27m-Dipla sp 8	ZA-19	*Diplasterias brandti*	27.0	5.8	0.5	-18.0	9.4	17.3
ZA-19-27m-Dipla sp 9	ZA-19	*Diplasterias brandti*	27.0	6.4	0.6	-18.5	9.4	18.4
ZA-19-27m-Lab anu 1	ZA-19	*Labidiaster annulatus*	27.0	21.2	2.9	-22.8	11.1	17.9
ZA-19-27m-Nota sp 1	ZA-19	*Notasterias bongraini*	27.0	5.0	0.8	-23.7	7.6	18.6
ZA-19-27m-Nota sp 2	ZA-19	*Notasterias bongraini*	27.0	5.5	0.8	-24.2	6.9	18.7
ZA-19-27m-Nota sp 3	ZA-19	*Notasterias bongraini*	27.0	3.8	0.6	-23.5	7.0	18.1
ZA-19-27m-Nota sp 4	ZA-19	*Notasterias bongraini*	27.0	6.7	0.8	-23.7	7.4	18.9
ZA-19-27m-Nota sp 5	ZA-19	*Notasterias bongraini*	27.0	5.9	0.5	-24.1	7.6	19.4
ZA-19-27m-Nota sp 6	ZA-19	*Notasterias bongraini*	27.0	8.1	0.9	-23.6	6.4	NA
ZA-19-27m-Nota sp 7	ZA-19	*Notasterias bongraini*	27.0	4.7	0.5	-23.0	6.7	17.4
ZA-19-27m-Nota sp 8	ZA-19	*Notasterias bongraini*	27.0	5.2	1.2	-22.9	7.2	15.4
ZA-19-27m-Nota sp 9	ZA-19	*Notasterias bongraini*	27.0	5.5	0.6	-24.1	6.9	18.4
ZA-19-27m-Odo val 1	ZA-19	*Odontaster validus*	27.0	2.1	1.1	-18.5	9.1	17.2
ZA-19-27m-Odo val 2	ZA-19	*Odontaster validus*	27.0	2.9	1.2	-18.9	8.4	16.9
ZA-19-27m-Odo val 3	ZA-19	*Odontaster validus*	27.0	1.3	0.5	-22.5	7.7	17.6
ZA-19-Dipla sp 1	ZA-19	*Diplasterias brandti*	23.0	10.9	1.4	-16.9	10.0	17.1
ZA-19-Dipla sp 10	ZA-19	*Diplasterias brandti*	23.0	3.7	0.3	-18.4	9.4	18.1
ZA-19-Dipla sp 11	ZA-19	*Diplasterias brandti*	23.0	6.6	0.7	-17.6	10.3	17.3
ZA-19-Dipla sp 12	ZA-19	*Diplasterias brandti*	23.0	7.6	1.0	-16.8	10.2	18.3
ZA-19-Dipla sp 13	ZA-19	*Diplasterias brandti*	23.0	6.5	0.7	-17.3	9.8	16.8
ZA-19-Dipla sp 14	ZA-19	*Diplasterias brandti*	23.0	5.9	0.4	-19.3	10.1	17.9
ZA-19-Dipla sp 15	ZA-19	*Diplasterias brandti*	23.0	2.0	0.1	-20.1	8.7	17.3
ZA-19-Dipla sp 2	ZA-19	*Diplasterias brandti*	23.0	5.6	0.8	-18.2	9.3	17.0
ZA-19-Dipla sp 3	ZA-19	*Diplasterias brandti*	23.0	4.6	0.6	-18.7	9.4	17.0
ZA-19-Dipla sp 4	ZA-19	*Diplasterias brandti*	23.0	9.6	1.3	-18.4	9.6	17.0
ZA-19-Dipla sp 5	ZA-19	*Diplasterias brandti*	23.0	7.0	1.3	-18.7	9.8	16.7

ZA-19-Dipla sp 6	ZA-19	*Diplasterias brandti*	23.0		3.1	0.4	-18.3	9.4	17.5
ZA-19-Dipla sp 7	ZA-19	*Diplasterias brandti*	23.0		5.2	0.6	-18.6	9.3	16.6
ZA-19-Dipla sp 8	ZA-19	*Diplasterias brandti*	23.0		6.2	0.7	-17.3	10.1	17.1
ZA-19-Lab anu 1	ZA-19	*Labidiaster annulatus*	23.0		NA	NA	-19.5	13.4	16.8
ZA-19-Nota sp 1	ZA-19	*Notasterias bongraini*	23.0		4.5	1.0	-23.3	6.7	16.7
ZA-19-Nota sp 2	ZA-19	*Notasterias bongraini*	23.0		6.2	0.8	-23.6	7.5	17.6
ZA-19-Nota sp 3	ZA-19	*Notasterias bongraini*	23.0		7.2	1.0	-23.2	7.7	17.7
ZA-19-Nota sp 4	ZA-19	*Notasterias bongraini*	23.0		1.2	0.2	-19.7	8.7	16.4
ZA-19-Odo val 1	ZA-19	*Odontaster validus*	23.0		3.2	1.6	-19.9	10.3	17.6
ZA-19-Odo val 10	ZA-19	*Odontaster validus*	23.0		2.9	1.0	-20.4	8.7	17.7
ZA-19-Odo val 11	ZA-19	*Odontaster validus*	23.0		1.7	0.7	-21.2	8.9	16.0
ZA-19-Odo val 12	ZA-19	*Odontaster validus*	23.0		1.5	0.6	-21.3	8.5	16.7
ZA-19-Odo val 2	ZA-19	*Odontaster validus*	23.0		2.2	0.9	-19.9	9.1	17.5
ZA-19-Odo val 3	ZA-19	*Odontaster validus*	23.0		3.5	1.3	-17.6	9.7	11.0
ZA-19-Odo val 4	ZA-19	*Odontaster validus*	23.0		3.4	1.4	-19.0	10.6	17.7
ZA-19-Odo val 5	ZA-19	*Odontaster validus*	23.0		1.8	0.6	-21.8	7.9	18.2
ZA-19-Odo val 6	ZA-19	*Odontaster validus*	23.0		3.1	1.2	-18.8	9.6	18.0
ZA-19-Odo val 7	ZA-19	*Odontaster validus*	23.0		2.6	1.0	-19.4	9.6	18.0
ZA-19-Odo val 9	ZA-19	*Odontaster validus*	23.0		2.6	1.0	-18.0	9.8	18.2
ZA-20-20-A-Dipla sp 1	ZA-20	*Diplasterias brandti*	20.0	A	3.2	0.3	-18.4	9.7	16.9
ZA-20-20-A-Dipla sp 2	ZA-20	*Diplasterias brandti*	20.0	A	5.2	0.5	-18.3	8.8	17.6
ZA-20-20-A-Dipla sp 3	ZA-20	*Diplasterias brandti*	20.0	A	1.5	0.1	-18.1	9.1	16.5
ZA-20-20-A-Dipla sp 4	ZA-20	*Diplasterias brandti*	20.0	A	1.1	0.1	-18.3	9.0	16.8
ZA-20-20-A-Nota sp 1	ZA-20	*Notasterias bongraini*	20.0	A	5.6	0.6	-23.3	6.3	17.7
ZA-20-20-A-Nota sp 2	ZA-20	*Notasterias bongraini*	20.0	A	6.8	1.0	-22.9	6.8	18.2
ZA-20-20-B-Dipla sp 1	ZA-20	*Diplasterias brandti*	20.0	B	3.3	0.4	-20.0	8.4	17.8
ZA-20-20-B-Dipla sp 2	ZA-20	*Diplasterias brandti*	20.0	B	4.5	0.5	-17.5	9.3	18.0
ZA-20-20-B-Odo val 1	ZA-20	*Odontaster validus*	20.0	B	1.5	0.7	-18.4	8.2	18.1
ZA-20-20-B-Odo val 3	ZA-20	*Odontaster validus*	20.0	B	1.6	0.7	-17.5	8.7	18.1
ZA-20-20-B-Perkna sp 1	ZA-20	*Perknaster sladeni*	20.0	B	1.1	0.3	-16.8	10.1	17.2
ZA-20-20-C-Aco sp 1	ZA-20	*Perknaster sladeni*	20.0	C	7.5	1.9	-21.8	8.6	18.4
ZA-20-20-C-Dipla sp 1	ZA-20	*Diplasterias brandti*	20.0	C	8.7	1.2	-16.2	9.5	17.1
ZA-20-20-C-Dipla sp 2	ZA-20	*Diplasterias brandti*	20.0	C	3.3	0.3	-18.0	9.0	16.9
ZA-20-20-C-Dipla sp 3	ZA-20	*Diplasterias brandti*	20.0	C	3.5	0.3	-17.9	9.4	17.1
ZA-20-20-C-Dipla sp 4	ZA-20	*Diplasterias brandti*	20.0	C	3.1	0.4	-15.8	9.9	16.0
ZA-20-20-C-Odo val 1	ZA-20	*Odontaster validus*	20.0	C	1.4	0.6	-19.2	9.2	16.3
ZA-20-30-A-Nota sp 1	ZA-20	*Notasterias bongraini*	30.0	A	6.5	0.6	-21.8	6.4	17.8
ZA-20-30-B-Notas sp 1	ZA-20	*Notasterias bongraini*	30.0	B	5.8	0.9	-22.2	7.1	18.6
ZA-20-30-B-Notas sp 2	ZA-20	*Notasterias bongraini*	30.0	B	6.6	0.8	-22.8	7.4	18.5
ZA-20-30-B-Notas sp 3	ZA-20	*Notasterias bongraini*	30.0	B	5.1	0.7	-22.5	6.7	17.3
ZA-20-6-A-Dipla sp 1	ZA-20	*Diplasterias brandti*	6.0	A	2.8	0.5	-13.8	9.8	17.0
ZA-20-6-A-Odo val 1	ZA-20	*Odontaster validus*	6.0	A	1.7	0.8	-16.2	9.5	17.4
ZA-20-6-A-Odo val 2	ZA-20	*Odontaster validus*	6.0	A	2.0	1.0	-14.6	8.2	16.8
ZA-20-6-A-Odo val 3	ZA-20	*Odontaster validus*	6.0	A	1.5	0.6	-15.4	7.6	16.5
ZA-20-6-A-Odo val 4	ZA-20	*Odontaster validus*	6.0	A	2.3	1.0	-15.9	9.1	17.9
ZA-20-6-A-Odo val 5	ZA-20	*Odontaster validus*	6.0	A	1.9	0.7	-14.1	8.9	16.1
ZA-20-6-B-Odo val 1	ZA-20	*Odontaster validus*	6.0	B	2.7	1.4	-13.4	9.8	17.4
ZA-21-10-A-Dipla sp 1	ZA-21	*Diplasterias brandti*	10.0	A	1.0	0.1	-16.2	9.3	17.2
ZA-21-10-A-Odo val 1	ZA-21	*Odontaster validus*	10.0	A	1.7	0.5	-17.7	7.9	16.1
ZA-21-10-A-Odo val 10	ZA-21	*Odontaster validus*	10.0	A	2.5	1.1	-17.2	8.9	17.6
ZA-21-10-A-Odo val 11	ZA-21	*Odontaster validus*	10.0	A	2.0	0.8	-19.6	9.0	17.6
ZA-21-10-A-Odo val 12	ZA-21	*Odontaster validus*	10.0	A	1.6	0.7	-16.9	8.8	NA
ZA-21-10-A-Odo val 2	ZA-21	*Odontaster validus*	10.0	A	4.6	1.6	-14.8	9.9	17.6
ZA-21-10-A-Odo val 3	ZA-21	*Odontaster validus*	10.0	A	1.6	0.5	-20.7	9.6	NA
ZA-21-10-A-Odo val 4	ZA-21	*Odontaster validus*	10.0	A	3.3	1.3	-15.2	9.9	18.0
ZA-21-10-A-Odo val 5	ZA-21	*Odontaster validus*	10.0	A	0.9	0.3	-18.0	10.3	18.0
ZA-21-10-A-Odo val 6	ZA-21	*Odontaster validus*	10.0	A	3.3	1.1	-15.6	9.8	18.3
ZA-21-10-A-Odo val 7	ZA-21	*Odontaster validus*	10.0	A	3.6	1.5	-15.1	9.8	16.7
ZA-21-10-A-Odo val 8	ZA-21	*Odontaster validus*	10.0	A	2.5	0.9	-18.1	8.6	16.8
ZA-21-10-A-Odo val 9	ZA-21	*Odontaster validus*	10.0	A	3.1	1.4	-15.5	8.7	16.7
ZA-21-10-A-Perkna sp 1	ZA-21	*Perknaster sladeni*	10.0	A	2.6	0.6	-20.7	9.4	17.4
ZA-21-10-A-Perkna sp 10	ZA-21	*Perknaster sladeni*	10.0	A	0.7	0.3	-18.9	7.3	NA
ZA-21-10-A-Perkna sp 12	ZA-21	*Perknaster sladeni*	10.0	A	1.1	0.3	-17.0	10.5	18.4

ZA-21-10-A-Perkna sp 2	ZA-21	*Perknaster sladeni*	10.0	A	1.2	0.2	-17.4	9.9	17.1
ZA-21-10-A-Perkna sp 3	ZA-21	*Perknaster sladeni*	10.0	A	0.8	0.2	-17.4	10.1	17.9
ZA-21-10-A-Perkna sp 4	ZA-21	*Perknaster sladeni*	10.0	A	0.9	0.2	-17.4	10.9	18.4
ZA-21-10-A-Perkna sp 5	ZA-21	*Perknaster sladeni*	10.0	A	1.0	0.2	-16.3	6.6	NA
ZA-21-10-A-Perkna sp 6	ZA-21	*Perknaster sladeni*	10.0	A	0.7	0.1	-18.8	8.3	14.9
ZA-21-10-A-Perkna sp 7	ZA-21	*Perknaster sladeni*	10.0	A	0.9	0.1	-17.2	10.8	17.6
ZA-21-10-A-Perkna sp 8	ZA-21	*Perknaster sladeni*	10.0	A	0.8	0.1	-18.7	9.5	17.5
ZA-21-10-A-Perkna sp 9	ZA-21	*Perknaster sladeni*	10.0	A	0.6	0.5	-20.0	8.4	15.6
ZA-21-10-B-Dipla sp 1	ZA-21	*Diplasterias brandti*	10.0	B	5.7	0.9	-21.1	8.7	17.2
ZA-21-10-B-Odo val 1	ZA-21	*Odontaster validus*	10.0	B	1.8	0.8	-16.3	8.6	12.4
ZA-21-10-B-Odo val 2	ZA-21	*Odontaster validus*	10.0	B	3.8	1.5	-17.1	10.4	17.0
ZA-21-10-B-Odo val 3	ZA-21	*Odontaster validus*	10.0	B	3.4	1.3	-16.7	9.7	18.3
ZA-21-10-B-Odo val 4	ZA-21	*Odontaster validus*	10.0	B	3.0	1.0	-15.9	10.1	18.4
ZA-21-20-A-Dipla sp 1	ZA-21	*Diplasterias brandti*	20.0	A	3.2	0.4	-16.0	10.0	17.9
ZA-21-20-A-Dipla sp 10	ZA-21	*Diplasterias brandti*	20.0	A	0.7	0.1	-16.7	8.4	16.0
ZA-21-20-A-Dipla sp 10-2	ZA-21	*Diplasterias brandti*	20.0	A	0.8	0.1	-16.8	8.7	15.2
ZA-21-20-A-Dipla sp 12	ZA-21	*Diplasterias brandti*	20.0	A	0.8	0.1	-17.9	8.7	17.8
ZA-21-20-A-Dipla sp 13	ZA-21	*Diplasterias brandti*	20.0	A	1.0	0.1	-16.5	9.4	16.9
ZA-21-20-A-Dipla sp 2	ZA-21	*Diplasterias brandti*	20.0	A	2.2	0.2	-16.8	9.3	17.1
ZA-21-20-A-Dipla sp 3	ZA-21	*Diplasterias brandti*	20.0	A	2.8	0.3	-18.4	9.2	16.7
ZA-21-20-A-Dipla sp 4	ZA-21	*Diplasterias brandti*	20.0	A	1.3	0.1	-16.5	8.1	16.0
ZA-21-20-A-Dipla sp 5	ZA-21	*Diplasterias brandti*	20.0	A	1.6	0.2	-16.8	9.7	17.6
ZA-21-20-A-Dipla sp 6	ZA-21	*Diplasterias brandti*	20.0	A	1.5	0.2	-16.3	9.8	16.3
ZA-21-20-A-Dipla sp 7	ZA-21	*Diplasterias brandti*	20.0	A	1.4	0.1	-17.7	8.7	16.5
ZA-21-20-A-Dipla sp 8	ZA-21	*Diplasterias brandti*	20.0	A	1.0	0.1	-17.3	8.0	16.7
ZA-21-20-A-Dipla sp 9	ZA-21	*Diplasterias brandti*	20.0	A	1.2	0.1	-16.0	8.7	15.9
ZA-21-20-A-Odo val 1	ZA-21	*Odontaster validus*	20.0	A	1.2	0.2	-17.1	10.6	18.7
ZA-21-20-A-Odo val 2	ZA-21	*Odontaster validus*	20.0	A	2.1	0.9	-20.8	8.7	16.8
ZA-21-20-A-Odo val 3	ZA-21	*Odontaster validus*	20.0	A	1.6	0.6	-19.6	9.1	17.1
ZA-21-20-A-Odo val 4	ZA-21	*Odontaster validus*	20.0	A	0.8	0.3	-15.3	9.4	17.7
ZA-21-20-A-Odo val 5	ZA-21	*Odontaster validus*	20.0	A	1.0	0.3	-21.0	7.9	18.2
ZA-21-20-B-Dipla sp 1	ZA-21	*Diplasterias brandti*	20.0	B	2.1	0.1	-19.5	8.2	17.8
ZA-21-20-B-Dipla sp 2	ZA-21	*Diplasterias brandti*	20.0	B	4.5	0.3	-16.8	9.4	17.5
ZA-21-20-B-Dipla sp 3	ZA-21	*Diplasterias brandti*	20.0	B	5.2	0.6	-19.4	9.5	19.0
ZA-21-20-B-Odo val 1	ZA-21	*Odontaster validus*	20.0	B	3.4	1.4	-16.6	8.9	17.9
ZA-21-20-B-Odo val 2	ZA-21	*Odontaster validus*	20.0	B	3.5	1.2	-15.1	9.0	17.7
ZA-21-20-B-Odo val 3	ZA-21	*Odontaster validus*	20.0	B	3.4	1.2	-18.3	9.2	17.6
ZA-21-20-B-Perkna sp 1	ZA-21	*Perknaster sladeni*	20.0	B	3.9	1.2	-21.8	8.8	17.8
ZA-21-20-B-Perkna sp 2	ZA-21	*Perknaster sladeni*	20.0	B	0.9	0.2	-19.7	9.2	18.5
ZA-21-20-B-Perkna sp 3	ZA-21	*Perknaster sladeni*	20.0	B	0.6	0.1	-19.5	7.3	13.8
ZA-21-20-B-Perkna sp 4	ZA-21	*Perknaster sladeni*	20.0	B	1.0	0.2	-17.9	10.5	17.6

Chapter 6: Environmental drivers of sea stars feeding ecology in the Southern Ocean



Examples of sea star taxa assigned to trophic groups. From left to right, first row: taxon with unknown trophic group (*Kampylaster incurvatus*; picture by Arntz WE), predator of active prey (*Labidiaster annulatus*; picture by Arntz WE). Second row: predator of large sessile prey (*Perknaster* sp.; credit: Yale Peabody Museum of Natural History; picture by Lazo-Wasem EA); predator of encrusting prey (*Pteraster* sp.; picture by Arntz WE), suspension feeder (*Odinella nutrix*; picture by Arntz WE). Third row: sediment feeder (*Psilaster charcoti*; picture by Jossart Q), omnivore (*Glabraster antarctica*; picture from Moore et al., 2018), pelagos-based omnivore (*Henricia* sp.; picture by Arntz WE).

6.1 Introduction

6.1.1 Impact of environmental features on food web functioning and on the trophic ecology of sea stars

Various covarying environmental parameters influence the distribution of organisms, the structure of communities, and the functioning of associated food webs. Examples of such environmental parameters are light, nutrient availability, seabed morphology, current speed, turbidity and, more specifically in polar environments, ice presence and its dynamic. Many of these parameters may influence primary production processes (Boyd et al., 2010) and, as a consequence, impact the primary consumers and, subsequently, higher trophic levels. This bottom-up process may notably be observed in pelagic environments of the Southern Ocean, where light and iron availability condition, step by step, summer phytoplankton blooms (Martin et al., 1990), krill presence (Loeb et al., 1997; Nicol et al., 2000), and finally higher trophic levels such as sea birds and baleen whales (Nicol et al., 2000).

Light and nutrients, two key factors in primary production, condition in the structure and development of photosynthetic communities at the baseline of the food webs (King and Schramm, 1976; Latasa et al., 2016; Bristow et al., 2017; Mousing et al., 2018). Covarying seabed morphology and bottom current speed are other important factors in the structure of benthic communities. Mobile deposit feeders are usually associated with soft bottoms and sessile suspension feeders with hard or coarse bottoms providing a substrate for attachment (Thiel and Ullrich, 2002; Barry et al., 2003; Gutt, 2007). Similarly, low current speed allows particle deposition in the bottom and is thus associated with deposit feeders while higher current speed influences particle sedimentation, suspension and lateral transport, as well as their capture by suspension feeders (Wildish and Peer, 1983; Leonard et al., 1988; Gutt et al., 1998; Barry et al., 2003). Particles quality and density in the water column also impact benthic communities. In particular, high inorganic matter content and concentration dilute organic matter and clog the feeding structures of suspension feeders (Thrush et al., 2004; Donohue and Garcia Molinos, 2009; Bell et al., 2015), resulting in reduced species and functional diversities in areas with high turbidity linked to sediment load (Wlodarska-Kowalczuk et al., 2005, 2019; Pasotti et al., 2015a; Sahade et al., 2015; Jordán-Garza et al., 2017).

Depth covaries with other environmental parameters and thus has strong impacts on benthic communities, because the absence of light in deep areas prevents the development of photosynthetic organisms. As a result, most of benthic communities from deep continental shelves or abyssal zones

are indirectly supported by the surface photosynthetic production through bentho-pelagic coupling, with low trophic levels organisms consuming phytodetritus sedimenting from the surface (Le Loc'h et al., 2008; Gontikaki et al., 2011; Valls et al., 2014). Therefore, the benthic biomass in abyssal environments is linked to the importance of organic matter inputs from surface primary production (Galéron et al., 2000; Johnson et al., 2007; Sweetman and Witte, 2008). Similarly, the trophic structure of the deep ocean is tightly linked to the importance of particle fluxes and to the subsequent sediment characteristics. High particle fluxes cause high organic carbon content in surface sediment, resulting in prevalence of deposit feeders, while limited sedimentation results in low organic carbon content in sediment and the preponderance of suspension feeders (Sokolova, 1959; 1972).

The previously cited environmental parameters impact most of benthic communities, including polar ones. Sea ice specifically impacts benthic communities from polar waters by influencing light transmission and, thus, pelagic and benthic primary productions (Clark et al., 2015), but also by providing substrate for an associated photosynthetic microbial community (i.e. sympagic community; Arrigo, 2017) that can provide food to benthic organisms (Norkko et al., 2007; Wing et al., 2012; 2018; Michel et al., 2019; Rossi et al., 2019). However, contrasting results were observed regarding the importance of ice-derived materials in the Antarctic benthic food web functioning. Gillies et al. (2012; 2013) considered the sympagic community being a secondary food source of coastal food webs, and other studies considered it as a seasonal food source for coastal benthic organisms (Norkko et al., 2007; Rossi et al., 2019). Finally, ice-derived materials appeared as one of the main carbon sources in coastal benthic food webs if sea ice persists over time (Wing et al., 2012; 2018; Michel et al., 2019). These results may indicate that sea ice presence and the ice season duration influences the relative importance of ice-derived materials in benthic communities of the Southern Ocean. However, these studies are mostly limited to coastal Antarctic. More limited results and assessments are available regarding the potential consumption of the sea ice microbial community in benthic food webs from the Antarctic continental shelf or the deep sea (Moens et al., 2007; Mincks et al., 2008).

Yet, the sea ice dynamic has an important bottom-up impact on the ecosystem functioning in the Southern Ocean. The melting of sea ice induces summer phytoplankton blooms (Garibotti et al., 2005; Rozema et al., 2017) while its absence during winter (Montes-Hugo et al., 2009; Rozema et al., 2017) or its persistence during summer prevents blooms (Hegseth and Von Quillfeldt, 2002; Mendes et al., 2013). Summer phytoplankton blooms are of critical importance for pelagic food

webs of the Southern Ocean and are associated with the presence of Antarctic krill and of its predators (Loeb et al., 1997; Nicol et al., 2000). Furthermore, the sea ice microbial community constitutes another food source for pelagic organisms such as krill (Brierley and Thomas, 2002; Leventer, 2003; Kohlbach et al., 2017; 2019).

As a result of the impact of sea ice on pelagic primary production, sea ice also has an effect on the functioning of benthic food webs on the continental shelves and deeper areas of the Southern Ocean as benthic communities from deeper waters are supported by surface primary production. Furthermore, the sea ice microbial community is known to be exported to the seabed in Arctic waters, where it is consumed by benthic organisms even below 4000 m (Brown and Belt, 2012; Boetius et al., 2013; Søreide et al., 2013). Consequently, export of the sea ice microbial community to the seabed of the continental shelf and in deeper environments and its consumption by the benthos may also be expected in Antarctic waters. Yet, the benthos of the continental shelf in the Western Antarctic Peninsula (WAP) did not appear to rely on ice-derived materials but instead on phytodetritus derived from the phytoplankton bloom (Mincks et al., 2008). However, this study was conducted in an area with a short, and currently decreasing (Stammerjohn et al., 2008a), ice season duration. Consequently, studies on areas covered by sea ice during a longer period are necessary to understand the importance of sea ice in the food web functioning of the Antarctic continental shelf.

The trophic ecology of sea stars has mostly been assessed in coastal areas, using stomach content analyses (e.g. Carey, 1972; Ganmanee et al., 2003; Baeta and Ramón, 2013; Fernandez et al., 2017). By contrast, studies on the trophic ecology of sea stars from deeper waters have been more limited but conducted with a higher diversity of methods, including stomach contents (e.g. Carey, 1972; Howell et al., 2003; Gale et al., 2013), stable isotopes (Gale et al., 2013), fatty acids (Howell et al., 2003) and pigment biomarkers (Howell et al., 2004). These studies highlighted the occurrence of diverse feeding strategies in deeper areas. However, depth may influence the trophic ecology of sea stars, as suggested by the increased occurrence of omnivores and reduced occurrence of predators as depth increases (Carey, 1972). Similarly, detailed investigations of the diet of Antarctic (Pearse, 1965; Dayton et al., 1974; Dearborn et al., 1991) and Subantarctic (Blankley, 1984; McClintock, 1985) sea stars are mostly limited to coastal or shallow waters and no studies were conducted on the variations of their trophic ecology with depth in the Southern Ocean. Yet, considering the impact of depth on the distribution of benthic organisms (Brandt et al., 2009; Barnes and Kuklinski, 2010; Neal et al., 2018), including sea stars (Moles et al., 2015), and on food web functioning, depth is expected to influence the feeding behaviour. Similarly, sea ice likely modulates the trophic ecology

of sea stars. For example, sea ice persistence was observed to impact directly their trophic ecology by inducing a herbivore behaviour in *Diplasterias brucei* and *Odontater validus* (Michel et al., 2019), despite both species being initially known as omnivores (Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; reviewed in McClintock, 1994). However, studies on the trophic ecology of sea stars of the Southern Ocean are usually restricted to some species and spatially limited and thus constitute snapshots of the global patterns of the feeding ecology of sea stars. Indeed, their trophic ecology may differ between studies, linked to the sampling in different locations or periods, and thus in different environmental conditions. Consequently, more global studies are necessary to determine what may be the environmental drivers of the trophic ecology of sea stars from the Southern Ocean.

6.1.2 Biogeographic classification of the Southern Ocean in relation to their environmental features

The combined knowledge on the distribution of environmental parameters, of organisms and of communities allows the classification of geographic regions into broad ecoregions characterised by a given pattern of environmental conditions and by specific communities (e.g. Sokolova, 1972; Rueda et al., 2010; Spalding et al., 2012). As a result, the presence of specific organisms in a given ecoregion would be the result of matching environmental conditions of this ecoregion. In particular, food availability would affect the distribution of organisms and then biogeographic patterns of food webs functioning may be expected. For example, the biogeographic distribution of the species richness of frugivore, nectarivore and scavenger birds can be linked to the distribution of the diversity of fleshy fruited plants, nectar-rich plants and large mammals, respectively (Kissling et al., 2012).

Biogeographic classifications of the regions of the Southern Ocean have been regularly attempted (De Broyer and Koubbi, 2014) by using abiotic (Raymond, 2014) or biotic factors such as taxa distributions (e.g. Pierrat et al., 2013; Moles et al., 2015; Moreau et al., 2017; Fabri-Ruiz et al., 2020). Raymond (2014) notably classified pelagic regions from the Southern Ocean into 20 clusters according to three main abiotic properties: the sea surface temperature (SST), the depth, and the sea ice season duration. The results of this study showed a latitudinal regionalisation of the open ocean areas, consistent with the oceanic fronts. This classification was further refined into a new classification for benthic environments by including biotic data (Douglass et al., 2014b; 2014c). This classification of benthic ecoregions is readily available for Geographic Information

System (GIS) analyses (Douglass et al., 2014a) and was supported by more recent results in echinoids (Fabri-Ruiz et al., 2020).

In this classification, the borders of previously defined ecoregions based on species distribution were also refined by a set of abiotic and biotic features. Abiotic factors include depth, geomorphology, seabed temperature, sea ice season duration, ocean currents, barriers to dispersal. Biotic factors include surface primary production, endemism and biogeographic distribution of species. Benthic environments of the Southern Ocean (excluding South America and New Zealand) were further classified into 562 unique types of environments according to their ecoregion, their geomorphic features and their bathome (Douglass et al., 2014b; 2014c). The geomorphic features are a classification of the seabed according to its surface morphology. Consequently, geomorphic features delineate distinct sedimentary and oceanographic environments that can be related to major habitat characteristics. Bathomes are broad depth classes whose boundaries were established on the basis of the depths at which rapid transitions in the species composition are expected to occur.

6.1.3 Study objectives

The objectives of this study are to assess how the depth, the sea ice and their interactions affect the trophic ecology of sea stars of the global Southern Ocean. Using an extensive dataset which encompassed 14 of the ecoregions defined by Douglass et al. (2014b; 2014c), we tried to assess if the trophic ecology and food sources of sea stars, and by extension, of benthic communities from the Southern Ocean, change between shallow and deeper environments and between ice-free and ice-covered areas. Furthermore, we tried to determine if depth and sea ice induce different degrees of trophic diversity between sea star taxa using an isotopic niche metrics approach. Implications on differences of trophic ecology between ecoregions were then assessed.

6.2 Material and methods

6.2.1 Sampling and environmental parameters in sampling stations

Sea stars (n = 2658) were sampled from January 1985 to January 2018 throughout multiple oceanographic campaigns and surveys during austral springs or summers (see section 2.2 in chapter 2). Environmental parameters were assigned to each sampling station using the method described below (Fig. 6.1).

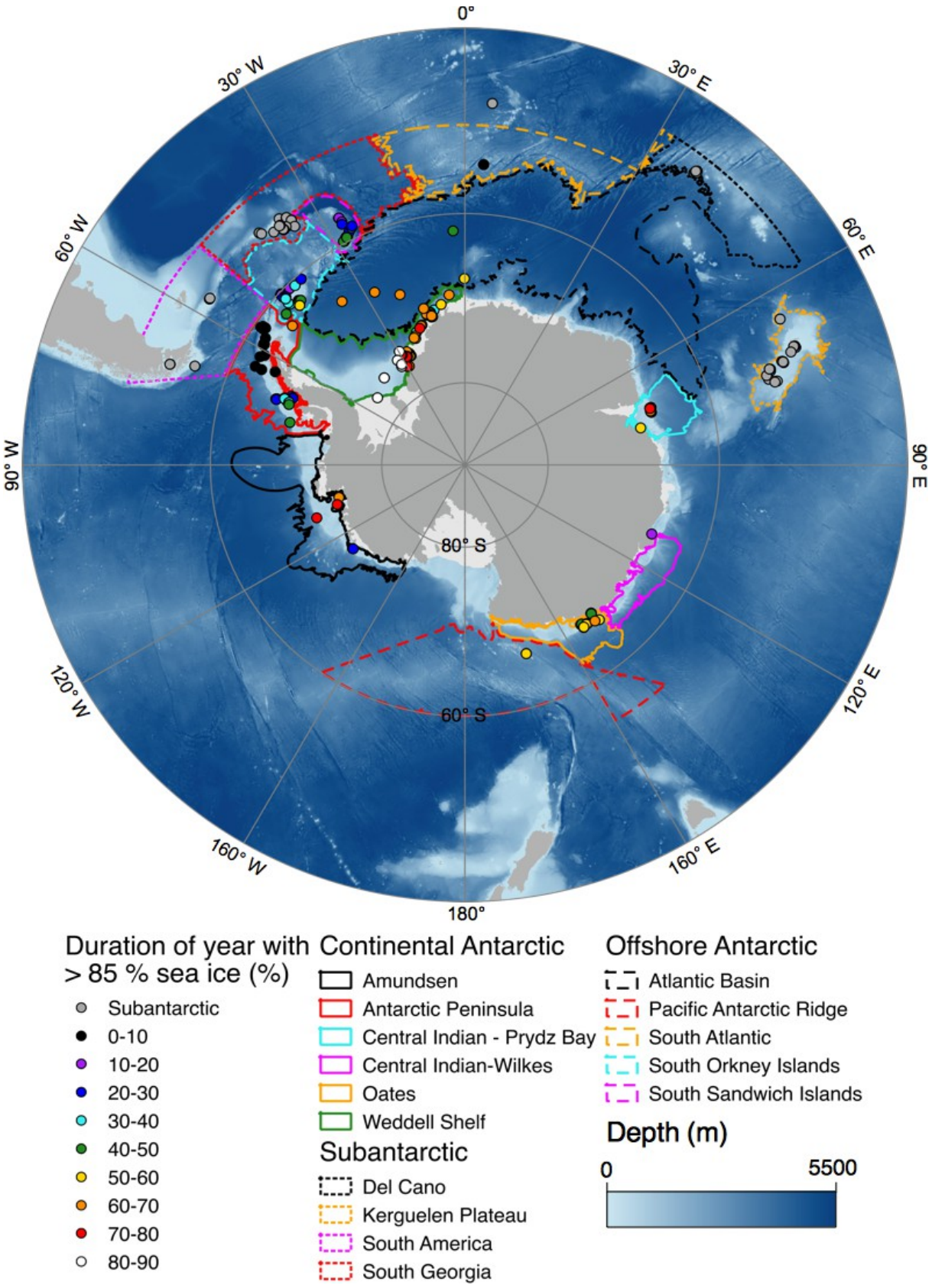


Fig. 6.1. Location of the sampling stations (coloured circles) and borders of the sampled ecoregions. Colours in circles correspond to the percentage of the year with a concentration of ice greater than 85%. The bathymetry of the Southern Ocean is also shown.

*6.2.1.1 Depth and bathome*s

Depth was recorded during the sampling campaigns (see section 2.2 in chapter 2). If the sampling occurred within a range of depths (e.g. 0-15 m for coastal station from South America and 0-30 m for data from Gillies and Stark, 2008) instead of a precise measurement, the mean depth (e.g. 7.5 m for coastal station from South America and 15 m for data from Gillies and Stark, 2008) was considered as the sampling depth. Sea stars sampled in Ezcurra Inlet (Admiralty Bay in King George Island; South Shetland Islands) in December 2010 (see chapter 5) were sampled in replicates at discrete depths within a same station (e.g. one station with replicates at 10 m and replicates at 20 m). Consequently, each sampling depth for each station was considered as an individual sampling station for this sampling campaign.

In order to investigate the effect of depth on trophic diversity of sea stars with isotopic metrics, depth has to be transformed into a categorical variable. Consequently, sampling stations were assigned to depth classes, i.e. bathomes, according to their sampling depth. The separation of depth into bathomes was done according to Douglass et al. (2014b; 2014c), with depth classes whose boundaries correspond to rapid transitions in the species composition in the Southern Ocean. The bathomes were 0-100 m, i.e. shallow water and coastal depths, 100-200 m, 200-500 m, 500-1000 m, 1000-1500 m, 1500-2000 m, 2000-3000 m, 3000-4500 m and 4500+ m.

6.2.1.2 Sea ice concentration data

Sea ice concentration of an area is the fraction of its surface (0-100 %) covered by sea ice. Sea ice concentration data were obtained from the GES-DISC (Goddard Earth Sciences Data and Information Services Center) Interactive Online Visualization ANd aNalysis Infrastructure (Giovanni, https://giovanni.gsfc.nasa.gov/giovanni/) application (Global Modeling and Assimilation Office, 2015). This tool provides a gridded representation of sea ice concentration over a selected monthly period with a 0.5×0.625° resolution and calculated with the model Modern-Era Retrospective Analysis for Research and Applications, version 2 (MERRA-2; Gelaro et al., 2017).

Rossi et al. (2019) reported that, in the Ross Sea, stable isotope ratios of benthic organisms showed a shift resulting of the integration of the sea ice microbial community in their diet 63 days after the sea ice breakup. Consequently, 2 months was considered a relevant timeframe for sea star tissues to integrate the isotopic signal of their food and/or the source at the baseline of the food web. The MERRA-2 model was thus used to retrieve the mean sea ice concentration data in the Southern Ocean over a 2 months period including the month of the sampling date and the previous one. The

sea ice concentration value in a given sampling station is the one calculated in the cell of the grid in which this station is present. As the Giovanni application provides gridded representations of data, sea ice concentrations calculated in a cell of the grid where landmass is present may be underestimated, as the landmass should be considered as not covered by sea ice. Consequently, stations sampled close to a coastline were given the sea ice concentration from the closest cell in the grid where no landmass was present.

6.2.1.3 Sea ice season duration data

Data on ice season duration were retrieved from the seaice_gt85 layer from the Polar Environmental Data Layers (https://data.aad.gov.au/metadata/records/Polar_Environmental_Data; Raymond, 2012). This file is readily available for GIS analyses and is provided in netCDF and ArcInfo ASCII grid formats. It provides a gridded representation of the proportion of time for which at least 85 % of the ocean is covered by sea ice over a 9 years period. These data were calculated from AMSR-E satellite estimates of daily sea ice concentration at 6.25 km resolution (Spreen et al., 2008) by using daily sea ice concentration data from 1 July 2002 to 30 June 2011. As the fraction of time each cell of the grid was covered at least by 85 % of sea ice was calculated over 9 years, the resulting values may be considered as a yearly mean of the sea ice season duration.

The ice season duration in a given sampling station (Fig. 6.1) is thus the one calculated in the cell of the grid in which this station is present. As the seaice_gt85 layer is a gridded representation of data, values of ice season duration were not calculated for cells where landmass was present. Consequently, stations sampled close to a coastline were not included in a cell from the grid. Therefore, stations sampled in an area where no sea ice season duration value was available were given the sea ice season duration value from the closest cell in the grid.

6.2.1.4 Ecoregions of the Southern Ocean

Stations were assigned to benthic ecoregions (Fig. 6.1) according to the Southern Ocean Benthic Classification (SOBC; Douglass et al., 2014a; 2014b; 2014c) except for stations in Patagonia and Falklands Islands as these regions were not included in the SOBC. Patagonia and Falkland Islands were considered as a single ecoregion, i.e. South America, because of the similarity (Moreau et al., 2017) and the connectivity (Moore et al., 2018) of sea star assemblages between the two areas. Another station was sampled in the deep South Atlantic, outside of the SOBC spatial coverage. However, as only one individual was sampled in this station, no ecoregion was assigned to this

sampling station.

Ecoregions were separated into three groups. The continental Antarctic ecoregions are those covering the continental shelf and coastal areas of the Antarctic continent. The offshore Antarctic includes ecoregions whose borders do not contact the Antarctic continent and where seasonal sea ice is present. Subantarctic ecoregions are those within or at the north of the Antarctic Circumpolar Current (ACC) characterised by warmer sea surface temperature and no sea ice season (Douglass et al., 2014c; Raymond, 2014). The northern part of the South Atlantic ecoregion is not covered by sea ice, and may thus be considered as a Subantarctic ecoregion, but its southern part is characterised by a short sea ice season (Raymond, 2012; Douglass et al., 2014c), and could thus be considered as an Antarctic ecoregion. The sampling in the South Atlantic ecoregion occurred near Bouvet Island, which is at the Southern part of the ecoregion and at the south of the ACC. Furthermore, Bouvet Island has more faunal similarity with Antarctic than Subantarctic ecoregions (Koubbi et al., 2014). Consequently, the South Atlantic was considered as an offshore Antarctic ecoregion.

The ecoregions and the range of their sampled environmental conditions (depth, sea ice concentration, ice season duration) are detailed in the table 6.1.

6.2.2 Species identification and trophic group assignation

6.2.2.1 Species identification

In the laboratory, sea stars were identified to the lowest taxonomic level possible either visually or by genetic analysis. Moreover, in several genera where clades showed a clear pattern of geographic or bathymetric distribution, results of genetic analyses were used as proxies to assign specimens to a probable species (Moreau, 2019; Moreau et al., 2019).

Table 6.1. List of sampled ecoregions as defined by Douglass et al. (2014b; 2014c), range of environmental parameters (depth, sea ice concentration and ice season duration) values, number of sea star species and of individuals in the corresponding sampling stations, and reason for exclusion from the principal component analyses (PCA) within ecoregion.

Ecoregion	Depth range (m)	Sea ice concentration range (%)	Range of duration of year with > 85 % sea ice (%)	n taxa	n	Exclusion from the PCAs
Continental Antarctic						
Amundsen	270-1203	0-31	20-76	10	14	Four values of sea ice concentration
Antarctic Peninsula	6-3799	0-36	2-61	50	600	
Central Indian-Prydz Bay	15-530	9-12	54-71	21	74	Four values of sea ice concentration
Central Indian-Wilkes	15	25-36	11	6	25	Single sampling station.
Oates	15-1194	5-84	42-62	32	298	
Weddell Sea	186-2147	0-90	31-89	59	772	
Offshore Antarctic						
Atlantic Basin	4392-5338	0-84	45-68	12	40	Three values of sea ice concentration
Pacific Antarctic Ridge	357-600	0	52	3	10	Two sampling stations
South Atlantic	240-399	0	0	10	34	Three sampling stations.
South Orkney Islands	199-3404	0-7	9-52	33	184	Four values of sea ice concentration
South Sandwich Islands	130-1677	0	15-41	21	79	One value of sea ice concentration
Subantarctic						
Deep South Atlantic	4579	0	0	1	1	Single sampling station and single individual
Del Cano	63-280	0	0	4	17	Only one trophic group with more than 5 individuals
Kerguelen plateau	9-640	0	0	32	326	
South America	8-510	0	0	16	84	Four depth values
South Georgia	125-325	0	0	19	100	

Bathybiaster sp. individuals sampled between 0 and 1000 m on the Antarctic continental shelf were considered as *Bathybiaster loripes*, those sampled deeper than 2000 m, as well as on the Kerguelen Plateau and Del Cano ecoregions were considered as *Bathybiaster vexillifer* (Moreau, 2019) while no species was assigned to one individual sampled in the South Sandwich Islands between 1000 and 1500 m. *Chitonaster* sp. individuals sampled in Western Antarctic Peninsula and South Orkney Island were considered as *Chitonaster* sp. 2. *Diplasterias* sp. individuals sampled in Western Antarctic Peninsula and South Orkney Island were considered as *Diplasterias* sp. 1, those sampled in South Sandwich Islands and Oates as *Diplasterias* sp. 2 while no species was assigned to individuals sampled in the Weddell Shelf. *Lysasterias* sp. individuals sampled in Oates were considered as *Lysasterias* sp. 1. *Notasterias* sp. individuals sampled in South Orkney Islands were considered as *Notasterias* sp. 1. *Odontaster* sp. individuals sampled on the Kerguelen Plateau were considered as *Odontaster penicillatus*. *Psilaster charcoti* individuals sampled near Bouvet Island, in the South Atlantic ecoregion, were considered as *Psilaster charcoti* – clade 2.

By contrast, this method could not be used for genera for which no clear geographic or bathymetric patterns of distribution were recorded (e.g. *Acodontaster*). Consequently, these individuals remained identified down to the genus. Similarly, individuals that could not be identified further than the family were referred by their family name (Echinasteridae and Pterasteridae).

At the end of this work, sea stars were assigned in 142 taxa (table 6.2). Among them, 113 taxa were identified down to the species, 20 down to the genus and 2 down to the family. The last 7 groups contained undetermined species (even at family level) and 6 sea stars groups that were given the name indicated by Gillies and Stark (2008). All groups will be called “taxa” in the following text.

6.2.2.2 Trophic group of each taxon

Each sea star taxon was assigned to a trophic group according to its known diet (Table 6.2). However, as the trophic ecology of sea stars from the Southern Ocean has been investigated in detail in a limited number of taxa, species and genera for which no results on their trophic ecology are available were assigned to a trophic group according to the known diet of their congeners. If no information on the trophic ecology was available for a species or its congeners, the species was assigned to the “Unknown” trophic group.

Seven trophic groups were identified. Predators of active prey are feeding on mobile megafauna

such as gastropods, crustaceans, urchins, ophiuroids and/or other sea stars. Predators of large sessile prey feed on large attached prey such as large sponges or crinoids, or on bivalves. Predators of encrusting prey feed on small epifaunal, colonial and encrusting sponges or bryozoans. Suspension feeders feed on suspended organic matter and/or plankton. Sediment feeders ingest sediment to consume their organic matter or their infauna. Omnivores may display different feeding strategies, such as being both a predator of large prey and of microbial organisms. Similarly, pelagos-based omnivores may also display omnivory by consuming organic matter directly or by being a predator of large prey. However, their predatory behaviour is restricted to sessile prey exploiting the pelagic environment, such as suspension feeding sponges and bivalves.

Table 6.2. List of sampled sea star taxa (species, genus or family) and trophic group, and number of sampled individuals.

Taxon	Trophic group	n	Reference(s)	Note
PAXILLOSIDA				
ASTROPECTINIDAE				
Bathybiaster loripes	Sediment feeders	69	Dearborn, 1977	
Bathybiaster vexillifer	Predator of active prey	55	Tyler et al., 1993	
Bathybiaster sp.	Unknown	1		Different trophic groups for *Bathybiaster loripes* and *Bathybiaster vexillifer*
Dytaster felix	Omnivores	8	Jangoux, 1982; Howell et al., 2003	Inferred from *Dytaster rigidus* and *Dytaster grandi*
Leptychaster flexuosus	Sediment feeders	8	Gale et al., 2013	Inferred from *Leptychaster arcticus*
Leptychaster kerguelensis	Predators of active prey	30	chapter 4	
Macroptychaster accrescens	Predators of active prey	15	Dayton et al., 1974; Dearborn, 1977	
Psilaster charcoti	Sediment feeders	96	Dearborn, 1977	
Psilaster charcoti clade 1	Sediment feeders	15	Dearborn, 1977	
Psilaster charcoti clade 2	Sediment feeders	10	Dearborn, 1977	
Psilaster charcoti clade 3	Sediment feeders	25	Dearborn, 1977	
PORCELLANASTERIDAE				
Eremicaster pacificus	Sediment feeders	20	Jangoux, 1982	
Eremicaster sp. 2	Sediment feeders	1	Jangoux, 1982	Inferred from *Eremicaster pacificus*
Hyphalaster sp. 3	Sediment feeders	1	Jangoux, 1982; Howell et al., 2003; 2004	Inferred from *Hyphalaster inermis*
Hyphalaster sp. 4266	Sediment feeders	7	Jangoux, 1982; Howell et al., 2003; 2004	Inferred from *Hyphalaster inermis*
Hyphalaster sp. 4332	Sediment feeders	13	Jangoux, 1982; Howell et al., 2003; 2004	Inferred from *Hyphalaster inermis*
Porcellanaster ceruleus	Sediment feeders	15	Sumida et al., 2001	

Styracaster chuni	Sediment feeders	1	Jangoux, 1982; Howell et al., 2003; 2004	
PSEUDARCHASTERIDAE				
Pseudarchaster discus	Omnivores	1	Carey, 1972; Jangoux, 1982	Inferred from *Pseudarchaster dissonus* and *Pseudarchaster parelli*
NOTOMYOTIDA				
BENTHOPECTINIDAE				
Cheiraster (Luidiaster) gerlachei	Predators of active prey	30	Dearborn, 1977	
Cheiraster (Luidiaster) planeta	Predators of active prey	5	Dearborn, 1977	Inferred from *Cheiraster (Luidiaster) gerlachei*
Cheiraster complex	Predators of active prey	2	Dearborn, 1977	Inferred from *Cheiraster (Luidiaster) gerlachei*
Cheiraster hirsutus	Predators of active prey	1	Dearborn, 1977	Inferred from *Cheiraster (Luidiaster) gerlachei*
Cheiraster sp.	Predators of active prey	22	Dearborn, 1977	Inferred from *Cheiraster (Luidiaster) gerlachei*
VALVATIDA				
ASTERINIDAE				
Asterina fimbriata	Omnivores	4	Jangoux, 1982	Inferred from 5 *Asterina* species
cf. *Anseropoda*	Unknown	2		
Kampylaster incurvatus	Unknown	27		
Tremaster mirabilis	Predators of sessile prey	2	Gale et al., 2013	
GANERIIDAE				
Cuenotaster involutus	Predators of active prey	42	Dearborn, 1977	
Cycethra verrucosa	Unknown	7		
Perknaster aurorae	Predators of sessile prey	2	Dayton et al., 1974	Inferred from *Perknaster fuscus*
Perknaster densus	Predators of sessile prey	45	Dayton et al., 1974	Inferred from *Perknaster fuscus*
Perknaster fuscus	Predators of sessile prey	1	Dayton et al., 1974	
Perknaster sladeni	Predators of sessile prey	17	Dayton et al., 1974	Inferred from *Perknaster fuscus*
Perknaster sp.	Predators of sessile prey	49	Dayton et al., 1974	Inferred from *Perknaster fuscus*
Perknaster sp. 2	Predators of sessile prey	1	Dayton et al., 1974	Inferred from *Perknaster fuscus*
GONIASTERIDAE				
Chitonaster sp.	Unknown	5		
Chitonaster sp. 1	Unknown	4		
Chitonaster sp. 2	Unknown	16		
Hippasteria phrygiana	Predators of sessile prey	2	Gale et al., 2013	
Notioceramus anomalus	Unknown	60		
ODONTASTERIDAE				
Acodontaster capitatus	Predators of sessile prey	1	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster cf. *capitatus*	Predators of sessile prey	3	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster cf. *hodgsoni*	Predators of sessile prey	3	Dayton et al., 1974	
Acodontaster conspicuus	Predators of sessile prey	19	Dayton et al., 1974	

Acodontaster elongatus	Predators of sessile prey	3	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster hodgsoni	Predators of sessile prey	6	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster marginatus	Predators of sessile prey	12	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster elongatus	Predators of sessile prey	3	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster hodgsoni	Predators of sessile prey	6	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster marginatus	Predators of sessile prey	12	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster sp.	Predators of sessile prey	20	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster sp. 1	Predators of sessile prey	6	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster sp. 5	Predators of sessile prey	1	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster sp. 6	Predators of sessile prey	11	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster sp. 7	Predators of sessile prey	1	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Acodontaster sp. 8	Predators of sessile prey	2	Dayton et al., 1974	Inferred from *Acodontaster* cf. *hodgsoni* and *Acodontaster conspicuus*
Diplodontias singularis	Unknown	3		
Odontaster meridionalis	Predators of sessile prey	16	Dayton et al., 1974	
Odontaster pearsei	Omnivores	4	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	Inferred from *Odontaster validus*
Odontaster penicillatus	Omnivores	27	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	Inferred from *Odontaster validus*
Odontaster roseus	Omnivores	1	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	Inferred from *Odontaster validus*

Odontaster sp.	Omnivores	22	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	Inferred from *Odontaster validus*
Odontaster sp. 2	Omnivores	1	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	Inferred from *Odontaster validus*
Odontaster sp. 3	Omnivores	2	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	Inferred from *Odontaster validus*
Odontaster validus	Omnivores	261	Pearse, 1965; Dayton et al., 1974; Dearborn, 1977; Michel et al., 2019	
PORANIIDAE				
Glabraster antarctica	Omnivores	234	Dearborn, 1977; Bowden et al., 2011	
SOLASTERIDAE				
Lophaster furcilliger	Omnivores	1	Carey, 1972	
Lophaster gaini	Omnivores	6	Carey, 1972	Inferred from *Lophaster furcilliger*
Lophaster sp.	Omnivores	13	Carey, 1972	Inferred from *Lophaster furcilliger*
Lophaster stellans	Omnivores	12	Carey, 1972	Inferred from *Lophaster furcilliger*
Paralophaster antarcticus	Unknown	12		
Paralophaster lorioli	Unknown	2		
Paralophaster sp.	Unknown	5		
Paralophaster sp. 3	Unknown	1		
Paralophaster sp. 4321	Unknown	10		
Solaster longoi	Predators of active prey	2	Mauzey et al., 1968	Inferred from *Solaster dawsoni*, *Solaster simpsoni* and *Solaster endeca*
Solaster regularis	Predators of active prey	4	Mauzey et al., 1968	Inferred from *Solaster dawsoni*, *Solaster simpsoni* and *Solaster endeca*
Solaster sp.	Predators of active prey	12	Mauzey et al., 1968	Inferred from *Solaster dawsoni*, *Solaster simpsoni* and *Solaster endeca*
VELATIDA				
KORETHRASTERIDAE				
Peribolaster folliculatus	Unknown	13		
Peribolaster macleani	Unknown	40		
Peribolaster sp.	Unknown	5		
Remaster gourdoni	Unknown	7		
MYXASTERIDAE				
Mixaster sp.	Unknown	1		
PTERASTERIDAE				
Hymenaster sacculatus	Omnivores	1	Carey, 1972; Jangoux, 1982; Howell et al., 2003	Inferred from *Hymenaster blegvadi*, *Hymenaster membranaceus*, *Hymenaster pellucidus* and *Hymenaster quadrispinosus*

Hymenaster sp. 1	Omnivores	1	Carey, 1972; Jangoux, 1982; Howell et al., 2003	Inferred from *Hymenaster blegvadi*, *Hymenaster membranaceus*, *Hymenaster pellucidus* and *Hymenaster quadrispinosus*
Hymenaster coccinatus/praecoquis/densus	Omnivores	1	Carey, 1972; Jangoux, 1982; Howell et al., 2003	Inferred from *Hymenaster blegvadi*, *Hymenaster membranaceus*, *Hymenaster pellucidus* and *Hymenaster quadrispinosus*
Pteraster affinis	Predators of encrusting prey	36	Mauzey et al., 1968	Inferred from *Pteraster tesselatus*
Pteraster militaris/affinis	Predators of encrusting prey	2	Mauzey et al., 1968	Inferred from *Pteraster tesselatus*
Pteraster sp.	Predators of encrusting prey	5	Mauzey et al., 1968	Inferred from *Pteraster tesselatus*
Pteraster stellifer	Predators of encrusting prey	27	Mauzey et al., 1968	Inferred from *Pteraster tesselatus*
Pteraster stellifer sp. 5	Predators of encrusting prey	1	Mauzey et al., 1968	Inferred from *Pteraster tesselatus*
Pterasteridae	Unknown	63		
SPINULOSIDA				
ECHINASTERIDAE				
Echinasteridae	Omnivores	5	chapter 4	
Henricia smilax	Pelagos-based omnivores	4	Mauzey et al., 1968; Jangoux, 1982; Sheild and Witman, 1993	Inferred from *Henricia leviuscula*, *Henricia oculata* and *Henricia sanguinolenta*
Henricia sp.	Pelagos-based omnivores	4	Mauzey et al., 1968; Jangoux, 1982; Sheild and Witman, 1993	Inferred from *Henricia leviuscula*, *Henricia oculata* and *Henricia sanguinolenta*
Rhopiella hirsuta	Unknown	33		
FORCIPULATIDA				
ASTERIIDAE				
Adelasterias papillosa	Unknown	5		
Anasterias antarctica	Predators of active prey	19	Laptikhovsky et al., 2014	
Anasterias perrieri	Predators of active prey	23	McClintock, 1985; chapter 4	
Anasterias sp.	Predators of active prey	6	chapter 4	
Diplasterias brandti	Omnivores	108	Dayton et al., 1974; Rauschert, 1986ab; Michel et al., 2019; chapter 5	Inferred from *Diplasterias brucei*
Diplasterias brucei	Omnivores	51	Dayton et al., 1974; Rauschert, 1986ab; Michel et al., 2019	
Diplasterias meridionalis	Predators of active prey	52	chapter 4	
Diplasterias sp.	Omnivores	15	Dayton et al., 1974; Rauschert, 1986ab; Michel et al., 2019	Inferred from *Diplasterias brucei*

Diplasterias sp. 1	Omnivores	50	Dayton et al., 1974; Rauschert, 1986ab; Michel et al., 2019	Inferred from *Diplasterias brucei*
Diplasterias sp. 2	Omnivores	29	Dayton et al., 1974; Rauschert, 1986ab; Michel et al., 2019	Inferred from *Diplasterias brucei*
Kenrickaster pedicellaris	Unknown	3		
Lysasterias adeliae	Omnivores	2	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias cf. *lactea*	Omnivores	1	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias digitata	Omnivores	6	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias joffrei	Omnivores	1	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias sp.	Omnivores	4	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias sp. 1	Omnivores	13	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias sp. 2	Omnivores	8	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias sp. 3	Omnivores	10	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Lysasterias sp. 4	Omnivores	1	Dearborn, 1977	Inferred from *Lysasterias perrieri*
Notasterias armata	Pelagos-based omnivores	1	Dearborn, 1977; Brueggeman, 1998	
Notasterias bongraini	Pelagos-based omnivores	23	chapter 5	
Notasterias candicans	Pelagos-based omnivores	7	Dearborn, 1977; Brueggeman, 1998; chapter 5	Inferred from *Notasterias armata* and *Notasterias bongraini*
Notasterias sp.	Pelagos-based omnivores	9	Dearborn, 1977; Brueggeman, 1998; chapter 5	Inferred from *Notasterias armata* and *Notasterias bongraini*
Notasterias sp. 1	Pelagos-based omnivores	72	Dearborn, 1977; Brueggeman, 1998; chapter 5	Inferred from *Notasterias armata* and *Notasterias bongraini*
Notasterias sp. 2	Pelagos-based omnivores	11	Dearborn, 1977; Brueggeman, 1998; chapter 5	Inferred from *Notasterias armata* and *Notasterias bongraini*
Notasterias sp. 3	Pelagos-based omnivores	1	Dearborn, 1977; Brueggeman, 1998; chapter 5	Inferred from *Notasterias armata* and *Notasterias bongraini*
Notasterias stolophora	Pelagos-based omnivores	3	Dearborn, 1977; Brueggeman, 1998; chapter 5	Inferred from *Notasterias armata* and *Notasterias bongraini*
Psalidaster mordax	Unknown	2		
Saliasterias brachiata	Predators of active prey	30	McClintock, 1994; Lawrence, 2012; Michel et al., 2019	Inferred from necrophagy, trophic level calculation and multiarmed morphology
HELIASTERIDAE				
Labidiaster annulatus	Predators of active prey	92	Dearborn et al., 1991	
Labidiaster radiosus	Predators of active prey	6	Dearborn et al., 1991	Inferred from *Labdiaster annulatus*
PEDICELLASTERIDAE				
Anteliaster scaber	Unknown	1		
Pedicellaster sp.	Predators of active prey	1	Jangoux, 1982	Inferred from *Pedicellaster magister*
STICHASTERIDAE				

Cosmasterias lurida	Predators of active prey	6	Castilla, 1985; Adami and Gordillo, 1999	
Smilasterias scalprifera	Predators of active prey	5	Jangoux, 1982	Inferred from *Smilasterias irregularis*
Smilasterias sp.	Predators of active prey	3	Jangoux, 1982	Inferred from *Smilasterias irregularis*
Smilasterias triremis	Predators of active prey	113	Jangoux, 1982	Inferred from *Smilasterias irregularis*
BRISINGIDA				
BRISINGIDAE				
Odinella nutrix	Suspension feeders	15	Jangoux, 1982; Emson and Young, 1994	Inferred from Brisingida feeding mechanisms
FREYELLIDAE				
Freyastera tuberculata	Suspension feeders	1	Emson and Young, 1994	Inferred from Brisingida feeding mechanisms
Freyella attenuata	Suspension feeders	2	Jangoux, 1982; Howell et al., 2003	Inferred from *Freyella elegans*
UNDETERMINED				
Asteroidea	Unknown	8		Data from Gillies and Stark, 2008
Asteroidea sp. 1	Unknown	7		Data from Gillies and Stark, 2008
Asteroidea sp. 2	Unknown	2		Data from Gillies and Stark, 2008
Asteroidea sp. 3	Unknown	2		Data from Gillies and Stark, 2008
Asteroidea sp. 4	Unknown	2		Data from Gillies and Stark, 2008
Asteroidea sp. 5	Unknown	2		Data from Gillies and Stark, 2008
Undetermined species	Unknown	99		
Total		**2658**		

6.2.3 Data analyses

The data analyses were carried out in three steps. In a first step, the influence of trophic group, depth, sea ice concentration and ice season duration on stable isotope values was assessed with a statistical analysis to know how trophic ecology differs between trophic groups and if environmental parameters induce changes in the feeding behaviour of sea stars. Secondly, the impact of trophic group, depth, sea ice concentration and ice season duration on the variability of stable isotope values was assessed with isotopic niche metrics to know if trophic groups are characterised by different levels of trophic diversity and if environmental parameters induce the diversification of feeding behaviours between sea star taxa. Finally, the relationships of depth, sea ice concentration, ice season duration with $\delta^{13}C$ and $\delta^{15}N$ values were summarised between and within the ecoregions by using principal component analyses (PCA). The assessment of the relationships between environmental parameters and stable isotope values within ecoregions with different ranges of environmental parameter values allowed to determine if the relationships observed in the global statistical analysis also occur within ecoregions.

6.2.3.1 Influence of trophic groups and environmental parameters on stable isotope values

Because the sampling depth is skewed toward depths lower than 1000 m, depths values were log-transformed prior to subsequent analyses.

The influences of trophic group, log-transformed depth, sea ice concentration and sea ice season duration on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were assessed with linear models and subsequent type III analyses of covariance (ANCOVAs). First order interactions between covariates and between covariates and the trophic group factor were included in the model.

However, the differences of environmental conditions between Antarctic and Subantarctic environments may induce a north-south gradient of decreasing $\delta^{13}C$ values in particulate organic matter (Espinasse et al., 2019). By contrast, the sea ice microbial community has high $\delta^{13}C$ values compared to pelagic phytoplankton in Antarctic (Rau et al., 1991a; Leventer, 2003; Mincks et al., 2008; Wing et al., 2018). As a result, non-linear variations of $\delta^{13}C$ values with sea ice concentration or ice season duration may occur if data from Subantarctic ecoregions are included in the ANCOVAs as no sea ice is present in Subantarctic areas. Consequently, the type III ANCOVAs were performed twice: firstly, by including Subantarctic sea stars and by assessing only the effects of trophic group, log-transformed depth and their interaction on $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values and, secondly, by focusing on Antarctic sea stars only and by adding sea ice concentration and sea ice season duration in the model.

Post-hoc Scheffé analyses were performed to test the effect of the trophic group on stable isotope values. The effects of the log-transformed depth on stable isotope values were further assessed with correlation coefficients computed using both Antarctic and Subantarctic sea stars (r_{All}). By contrast, the effects of the sea ice concentration and sea ice season duration on stable isotope values was further investigated with correlation coefficients computed only with the Antarctic sea stars, i.e. without the Subantarctic individuals (r_{Ant}). The effects of sea ice concentration and ice season duration on stable isotope values were also further assessed by computing the correlations between $\delta^{13}C$ and $\delta^{15}N$ and/or $\delta^{34}S$ with the covariates in 3 ecoregions with high variability of both sea ice concentration and ice season duration values. These ecoregions were the Antarctic Peninsula (longitude from *ca* 50 to 80° W), Oates (longitude from *ca* 140 to 170° E) and Weddell Sea (longitude from *ca* 0 to 60° W). These ecoregions were chosen because of their the high number of sampled individuals and stations, providing then high numbers and/or ranges of values of sea ice concentration and sea ice season duration (Table 6.1). Furthermore, the sea ice conditions differ between these ecoregions, with low sea ice concentrations and sea ice season durations in Antarctic

Peninsula, more seasonal sea ice in Oates and perennial sea ice being present in Weddell Sea.

It should be noted that when working with very high sample numbers, as in the present case, very weak correlation coefficient can be significant while explaining only a tiny part of the variance. A correlation coefficient r = 0.10, for example, only explains 1 % of the variance (r^2 = 0.01).

The potential effects of the interactions between the log-transformed depth and the sea ice concentration and between the log-transformed depth and the sea ice season duration were further assessed by computing the correlations between $\delta^{13}C$, $\delta^{15}N$ and/or $\delta^{34}S$ with the sea ice concentration within the 0-100, 200-500 and 500-1000 m bathomes. These bathomes were chosen because they cover a wide range of sea ice concentrations without major gaps. Furthermore, the 0-100 m bathome corresponds to coastal and shallow water sea stars while the 200-500 and 500-1000 m bathomes correspond to sea stars from the continental shelf. Investigating the relationship between sea ice concentration and stable isotope values would highlight if sea ice concentration impacts differently the trophic ecology of sea stars in these two types of environments. The same procedure was used to assess the influence of the interaction between the log-transformed depth and the sea ice season duration on stable isotope values.

6.2.3.2 Influence of trophic groups and environmental parameters on the variability of stable isotope values

The influence of the trophic group, depth, sea ice concentration and sea ice season duration on the trophic diversity between sea star species was also assessed. To do so, the general methodology was to generate standard ellipses with the means of each taxon in each level of trophic group factor, in each bathome, sea ice concentration and sea ice season duration category. For each investigated factor, Bayesian estimations of the niche metrics (Jackson et al., 2011; see section 2.3.3 from chapter 2) were then computed for each level and subsequent pairwise comparisons were performed.

Depth, sea ice concentration and sea ice season duration are continuous variables. Consequently, isotopic niche metrics were calculated within bathomes to investigate the effect of depth on the trophic diversity of sea stars. Similarly, isotopic niche metrics were calculated within intervals of sea ice concentration and sea ice season duration. Consequently, sea ice concentration and sea ice season duration values were grouped into 10 % intervals, except for data from Subantarctic ecoregions that were grouped into a “Subantarctic” group.

As the ellipses were generated at the scale of the whole Southern Ocean, they may contain a variety of stations that may be very distant from each other or sampled at different depths. Consequently, stable isotope values in sea stars may differ between sampling stations because of spatial variations of stable isotope values of the primary food sources at the baseline of the food webs, or of the potential influence of the environmental parameters on stable isotope values. To avoid this issue, stable isotope values were mean-corrected for each station according to the procedure described in the section 2.4 of the chapter 2. Following the mean-correction, the means of stable isotope values for each taxon in each trophic group, bathome, sea ice concentration interval or sea ice season duration interval, were computed.

For each level of each investigated factor, sample-size corrected (SEA_C) and Bayesian (based on 10^5 successive iterations; SEA_B) estimates of standard ellipse area (SEA) were computed with the SIBER package (Jackson et al., 2011) by using the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of taxa. Sample-size corrected and Bayesian estimates of the pseudo-standard deviation (PSD, see section 2.3.3 from chapter 2) for $\delta^{13}C$ (PSD_{CC} and PSD_{CB}, respectively) and $\delta^{15}N$ (PSD_{NC} and PSD_{NB}, respectively) values were also computed to assess specifically the variability of $\delta^{13}C$ and $\delta^{15}N$ values between sea star taxa. $\delta^{34}S$ values were not available for *ca* 13 % of sea star individuals, notably those in data from the literature (Gillies and Stark, 2008; Zenteno et al., 2019) or provided by colleagues. Consequently, SEA was not estimated using station-corrected $\delta^{13}C$ and $\delta^{34}S$ values. Nevertheless, standard ellipses were still generated with station-corrected $\delta^{13}C$ and $\delta^{34}S$ values, and sample-size corrected and Bayesian estimates of the pseudo-standard deviation for $\delta^{34}S$ (PSD_{SC} and PSD_{SB}, respectively) were calculated for each trophic group, each bathome and each interval of the sea ice concentration and of the sea ice season duration

Pairwise comparisons of SEA_B, PSD_{CB} and PSD_{NB} between trophic groups, between bathomes, between sea ice concentration intervals and between sea ice season durations intervals were performed by calculating the percentage of the estimated SEA, PSD_C or PSD_N that differed between each pair of standard ellipse. This percentage is the posterior probability (p) that a given standard ellipse has larger or smaller SEA, PSD_C or PSD_N than the other one. If this percentage exceeded 95 % or is lower than 5 %, the probability that two ellipses have different SEA, PSD_C or PSD_N is higher than 95 % and then, the differences between compared SEA, PSD_C or PSD_N were considered as meaningful. For each analysed factor and computed isotopic metric, p values higher than 50 % were transformed into (1 – p) values. Then, the orderPvalue function in the agricolae package in R (de Mendiburu, 2020) was used to order the p and (1 – p) values according to the group modes. Groups

for which probability of difference was less than 95 % were attributed an identical symbol. For instance, groups 1, 2, 3 got the symbol a, b, c when the probability that each differed from the others exceeded 95 %. Conversely, symbols a, ab, b suggested that probability of difference between groups 1 and 3 was higher than 95 %, while group 2 had less than 95 % chances to be different from both other groups.

6.2.3.3 Links between stable isotope values and environmental parameters at the scale of ecoregions

A PCA was performed on the whole dataset with the $\delta^{13}C$ and $\delta^{15}N$ values, the log-transformed depth, the sea ice concentration and the sea ice season duration to investigate the differences of stable isotope values between the different ecoregions and the link with their environmental conditions.

The relationship between environmental parameters and stable isotope values was further assessed within selected ecoregions. Selected Antarctic ecoregions were those for which at least 5 different values of depth, sea ice concentration and sea ice season duration and at least 5 individual sea stars in at least 2 trophic groups were available. Selected Antarctic ecoregions were Antarctic Peninsula, Oates and Weddell Sea. PCAs were then performed within the selected Antarctic ecoregions. The same procedure was applied to Subantarctic ecoregions, except that the ecoregion selection and the subsequent PCAs were performed without using sea ice concentration and sea ice season duration as sea ice is usually absent in these ecoregions. Selected Subantarctic ecoregions were the Kerguelen Plateau and South Georgia.

6.3 Results

$\delta^{13}C$ value ranged from –26.0 to –8.5 ‰. The lowest $\delta^{13}C$ value was recorded in the Antarctic Peninsula ecoregion in a *Perknaster* sp. individual, i.e. a predator of sessile prey, sampled at 130 m. The highest $\delta^{13}C$ value was recorded in the Prydz Bay in an omnivore *Odontaster validus* individual, sampled at 15 m. $\delta^{15}N$ value ranged from 4.4 to 19.8 ‰, the lowest value being recorded in the Antarctic Peninsula ecoregion in an omnivore *Diplasterias* sp. 1 individual sampled at 199 m, and the highest value in the Antarctic Peninsula in an omnivore *Odontaster pearsei* individual, sampled at 255 m. $\delta^{34}S$ values ranged from 2.1 to 23.8 ‰, the lowest value being recorded in the Oates ecoregion in a sediment feeding *Bathybiaster loripes* sampled at 465 m, and the highest in a *Notasterias* sp. 1, i.e. a pelagos-based omnivore, from the South Orkney Islands and sampled at 459

m.

6.3.1 Effect of trophic groups and environmental parameters on sea star stable isotope values

The results of the ANCOVAs show that several variables influence stable isotope values (Table 6.3). In this section, the results for each variable are presented in specific subsections.

Table 6.3. Results of the ANCOVAs assessing the effects of trophic groups and environmental parameters on stable isotope values. a) ANCOVAs on all sea stars and excluding sea ice concentration and sea ice season duration from the model. b) ANCOVAs on Antarctic sea stars only and including sea ice concentration and sea ice season duration in the model. Bold results are significant.

a)

	$\delta^{13}C$			$\delta^{15}N$			$\delta^{34}S$		
	df	F	P	df	F	P	df	F	P
Trophic groups	7	**66.931**	**< 0.001**	7	**67.957**	**< 0.001**	7	**2.371**	**0.021**
$\log_{10}$(Depth)	1	**78.462**	**< 0.001**	1	**22.140**	**< 0.001**	1	0.004	0.952
Trophic group:$\log_{10}$(Depth)	7	**57.188**	**< 0.001**	7	**61.495**	**< 0.001**	7	**2.444**	**0.017**
Residuals	2642			2642			2297		

b)

	$\delta^{13}C$			$\delta^{15}N$			$\delta^{34}S$		
	df	F	P	df	F	P	df	F	P
Trophic groups	7	**39.933**	**< 0.001**	7	**30.604**	**< 0.001**	7	**4.047**	**< 0.001**
$\log_{10}$(Depth)	1	**16.475**	**< 0.001**	1	0.822	0.365	1	0.205	0.651
Sea ice concentration	1	**5.938**	**0.015**	1	0.194	0.660	1	**8.392**	**0.004**
Ice season duration	1	0.854	0.356	1	3.704	0.054	1	0.004	0.948
Trophic group:$\log_{10}$(Depth)	7	**34.838**	**< 0.001**	7	**25.515**	**< 0.001**	7	**2.195**	**0.032**
Trophic group:Sea ice concentration	7	**4.561**	**< 0.001**	7	**6.577**	**< 0.001**	7	**4.143**	**< 0.001**
Trophic group:Ice season duration	7	**6.006**	**< 0.001**	7	**9.100**	**< 0.001**	7	1.476	0.171
$\log_{10}$(Depth):Sea ice concentration	1	**4.136**	**0.042**	1	**21.288**	**< 0.001**	1	3.592	0.058
$\log_{10}$(Depth):Ice season duration	1	1.290	0.256	1	1.185	0.276	1	3.467	0.063
Sea ice concentration:Ice season duration	1	**11.121**	**< 0.001**	1	**47.149**	**< 0.001**	1	1.183	0.277
Residuals	2095			2095			1770		

6.3.1.1 Impact of trophic groups on stable isotope values

The trophic group had a consistently significant impact on $\delta^{13}C$ and $\delta^{15}N$ values of sea stars, whether Subantarctic sea stars were included in the ANCOVAs or not (Table 6.3).

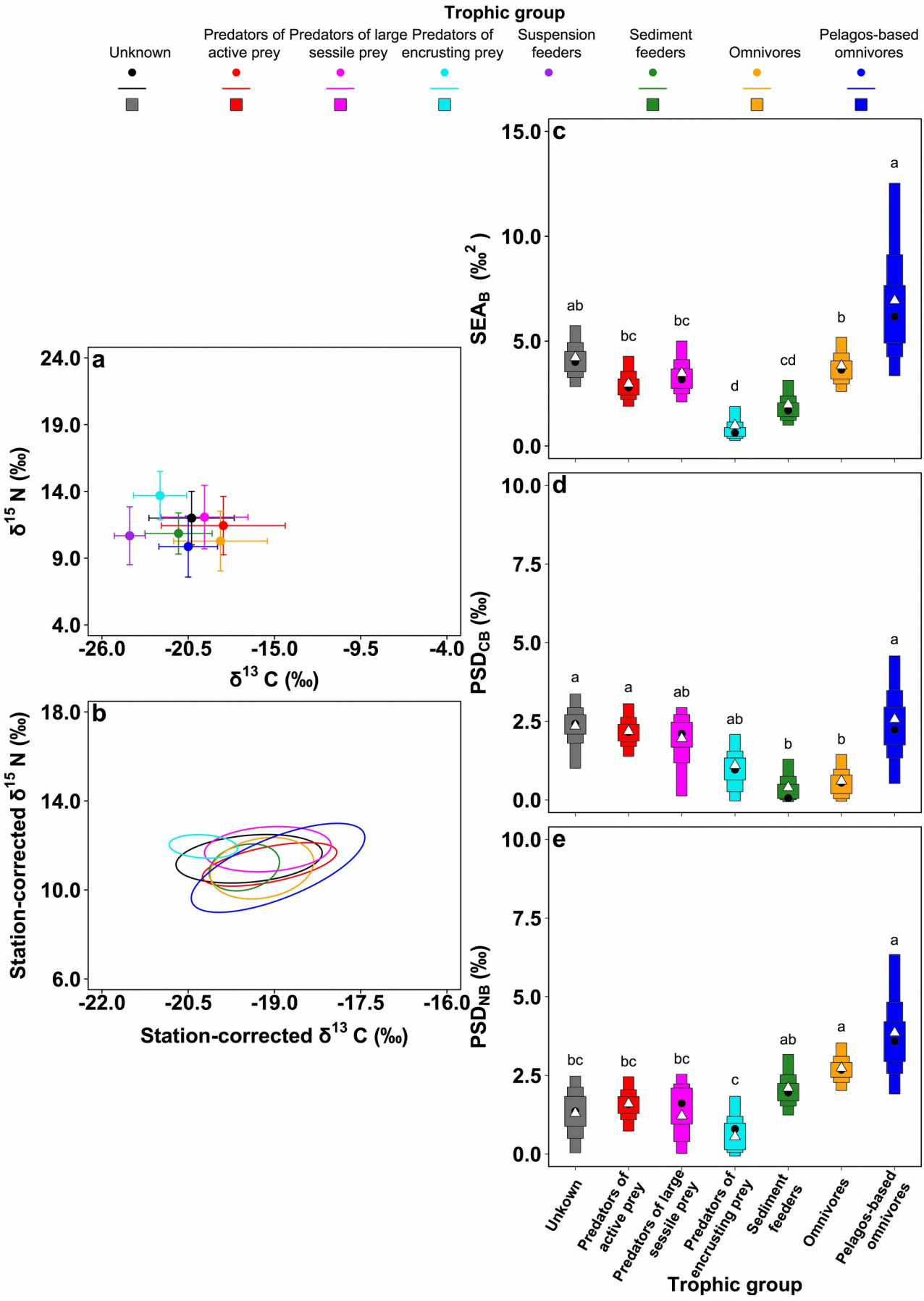
For $\delta^{13}C$ values, the post-hoc analysis showed that the suspension feeders (–24.2 ± 1.0 ‰; mean ± SD) and predators of encrusting prey (–22.3 ± 1.7 ‰) had the lowest $\delta^{13}C$, followed by the sediment feeders (–21.1 ± 2.1 ‰), the pelagos-based omnivores (–20.5 ± 1.9 ‰), followed by sea stars with an unknown trophic group (–20.3 ± 2.7 ‰). Higher $\delta^{13}C$ values were recorded in the

predators of sessile prey (–19.5 ± 2.8 ‰). The omnivores (–18.4 ± 3.0 ‰) and the predators of active prey (–18.3 ± 3.9 ‰) had the highest values (Fig. 6.2.a). To summarise, sea stars feeding on sediment or sessile prey had lower $\delta^{13}C$ values than omnivore or predatory sea stars.

For $\delta^{15}N$ values, the post-hoc analysis showed that the pelagos-based omnivores (9.9 ± 2.3 ‰) and the omnivores (10.3 ± 2.2 ‰) and the suspension feeders (10.7 ± 2.2 ‰) had the lowest values. They were followed by the sediment feeders (10.9 ± 1.5 ‰) and then the predators of active prey (11.4 ± 2.2 ‰), and then by the sea stars with an unknown trophic group (12.0 ± 2.0 ‰) and the predators of sessile prey (12.1 ± 2.4 ‰). The predators of encrusting prey had the highest values (13.7 ± 1.8 ‰; Fig. 6.2.a). To sum up, suspension feeders and sea stars with an omnivore diet had lower $\delta^{15}N$ values than sediment feeders and predators of other organisms.

The generation of standard ellipses for each trophic group with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa (Fig. 6.2.b) and the subsequent computation of SEA_B showed that predators of encrusting prey had the smallest SEA_B (mode = 0.6 ‰^{2}, 95 % credibility interval CI_{95} = 0.3-1.9 ‰^{2}) followed by the sediment feeders (mode = 1.7 ‰^{2}, CI_{95} = 1.0-3.1 ‰^{2}). The pelagos-based omnivores had the highest SEA_B (mode = 6.3 ‰^{2}, CI_{95} = 3.2-12.3 ‰^{2}). That means that more important differences in mean stable isotope values and isotopic space positions occur between taxa among the pelagos-based omnivores. Finally, SEA_B was similar for the predators of active and sessile prey and the omnivores (mode range: 2.7-3.6 ‰^{2}; Fig. 6.2.c). Higher PSD_{CB}, i.e. higher differences of $\delta^{13}C$ values between taxa within trophic groups, were observed in predators of active prey, of sessile prey and pelagos-based omnivores (mode range: 2.1-2.2 ‰) while lower PSD_{CB} were observed in predators of encrusting prey, sediment feeders and omnivores (mode range: 0.1-1.0 ‰; Fig. 6.2.d). Higher PSD_{NB}, i.e. higher differences of $\delta^{15}N$ values between taxa within trophic groups, were observed in sediment feeders, omnivores and pelagos-based omnivores (mode range: 2.0-3.5 ‰), while lower PSD_{NB} were observed in predators of active prey, of sessile prey and of encrusting prey (mode range: 0.8-1.7 ‰; Fig. 6.2.e).

Fig. 6.2. Effect of trophic groups on sea star $\delta^{13}C$ and $\delta^{15}N$ values: a) mean $\delta^{13}C$ and $\delta^{15}N$ values for each trophic group. b) Standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star species and subsequent sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of c) standard ellipse area (SEA), d) pseudo-standard deviation for $\delta^{13}C$ values (PSD_C) and e) for $\delta^{15}N$ values (PSD_N) for each trophic group. Standard ellipses were not computed for suspension feeders as only 3 taxa were available for this trophic group.


Trophic group
Unknown
Predators of active prey
Predators of large sessile prey
Predators of encrusting prey
Suspension feeders
Sediment feeders
Omnivores
Pelagos-based omnivores
a
b
c
d
e
δ15 N (‰)
δ13 C (‰)
Station-corrected δ15 N (‰)
Station-corrected δ13 C (‰)
SEAB (‰2)
PSDCB (‰)
PSDNB (‰)
Trophic group

The trophic group had a weak but significant effect on $\delta^{34}S$ values (Table 6.3). The post-hoc test for the ANCOVAs showed that suspension feeders (14.9 ± 2.2 ‰), sea stars with no known trophic group (15.5 ± 2.9 ‰), predators of active prey (15.6 ± 2.1 ‰) and sediment feeders (15.6 ± 2.4 ‰) had the lowest $\delta^{34}S$ values, followed by omnivores (16.4 ± 2.0 ‰), pelagos-based omnivores (16.7 ± 2.1 ‰) and predators of sessile prey (16.9 ± 1.9 ‰). Predators of encrusting prey had the highest values (18.0 ± 0.8 ‰; Fig. 6.3.a). PSD_{SB} did not differ between trophic groups and the mode was always lower than 2.5 (Fig. 6.3.b), suggesting limited differences of $\delta^{34}S$ values between species within trophic groups.

6.3.1.2 Depth and its interaction with trophic groups

$\delta^{13}C$ values decreased with depth (Table 6.3; Fig. 6.4.a). $\delta^{15}N$ values increased with depth according to the first ANCOVA results (Table 6.3; Fig. 6.4.b). However, depth did not influence $\delta^{15}N$ values in the second ANCOVA including sea ice concentration and sea ice season duration covariates, suggesting that the correlation between $\delta^{15}N$ values and depth is the result of the influence of other variables and interactions on $\delta^{15}N$ values. The generation of standard ellipses with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa (Fig. 6.4.c) and the subsequent computation of SEA_B did not result in a consistent pattern of SEA_B values between bathomes (Fig. 6.4.d). However, PSD values consistently changed between bathomes. The PSD_{CB} was higher between 0 and 100 m (mode = 2.8 ‰, CI_{95} = 2.2-3.6 ‰) than in other bathomes (mode lower or equal to 1.7), meaning that there were larger differences of $\delta^{13}C$ values between taxa in this bathome than in others. However, sea stars sampled between 500 and 1000 m (mode = 2.5 ‰, CI_{95} = 1.3-3.4 ‰) and between 1500 and 2000 m (mode = 2.6 ‰, CI_{95} = 0.8-5.3 ‰) may potentially have a PSD_{CB} value similar to those sampled between 0 and 100 m (Fig. 6.4.e). PSD_{NB} appeared to increase with depth (mode from 1.0 ‰ at 0-100 m to 4.9 ‰ at more than 4500 m), indicating higher differences of $\delta^{15}N$ values between taxa as depth increased (Fig. 6.4.e).

Depth had no impact on $\delta^{34}S$ values (Table 6.3) despite their significant correlation (Fig. 6.5.a). This very weak correlation is significant because of the very high number of individuals, limiting its ecological relevance. PSD_{SB} did not change consistently between bathomes either (Fig. 6.5.b).

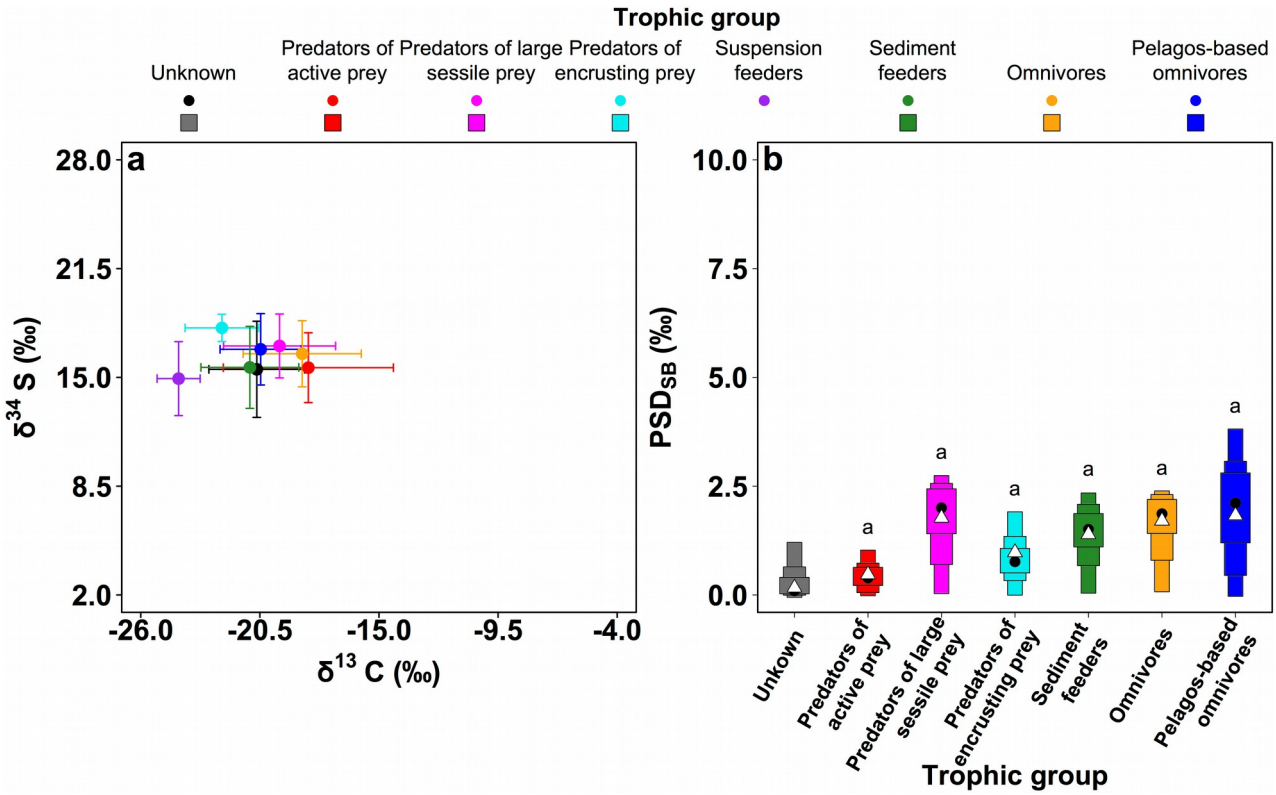


Fig. 6.3. Effect of trophic groups on sea star $\delta^{34}S$ values: a) mean $\delta^{13}C$ and $\delta^{34}S$ values for each trophic group. b) Sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of pseudo-standard deviation for $\delta^{34}S$ values (PSD_S) for standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{34}S$ values of sea star species for each trophic group. PSD_{SB} were not computed for suspension feeders as only 3 taxa were available for this trophic group.

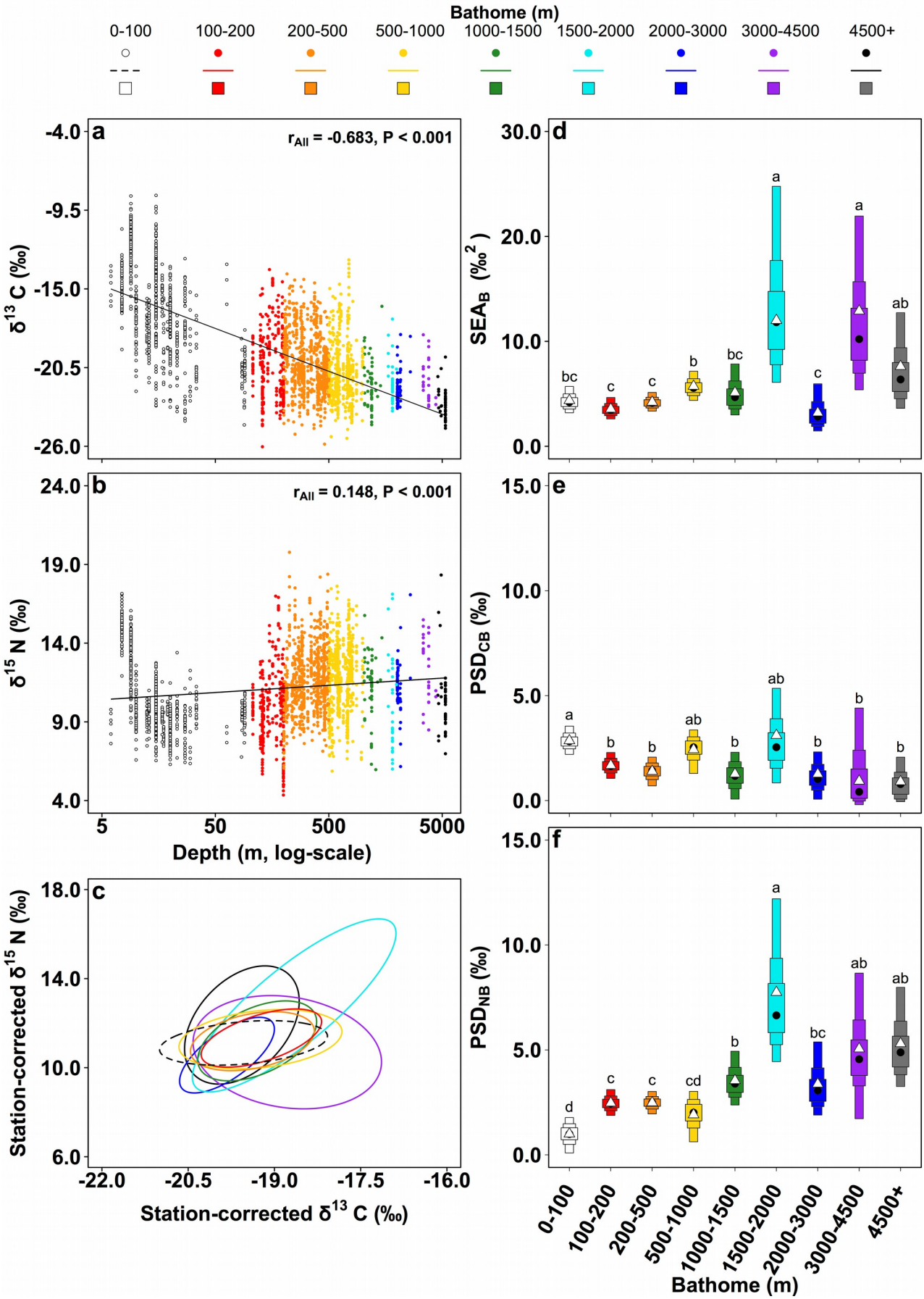

Bathome (m)
0-100
100-200
200-500
500-1000
1000-1500
1500-2000
2000-3000
3000-4500
4500+
a
r_{All} = -0.683, P < 0.001
δ^{13} C (‰)
b
r_{All} = 0.148, P < 0.001
δ^{15} N (‰)
Depth (m, log-scale)
c
Station-corrected δ^{15} N (‰)
Station-corrected δ^{13} C (‰)
d
SEA_B ($‰^2$)
e
PSD_{CB} (‰)
f
PSD_{NB} (‰)
Bathome (m)

Fig. 6.4. Effect of depth on sea star $\delta^{13}C$ and $\delta^{15}N$ values: relationships between depth and a) $\delta^{13}C$ and b) $\delta^{15}N$ values. c) Standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa and subsequent sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of d) standard ellipse area (SEA), e) pseudo-standard deviation for $\delta^{13}C$ values (PSD_C) and f) for $\delta^{15}N$ values (PSD_N) for each bathome.

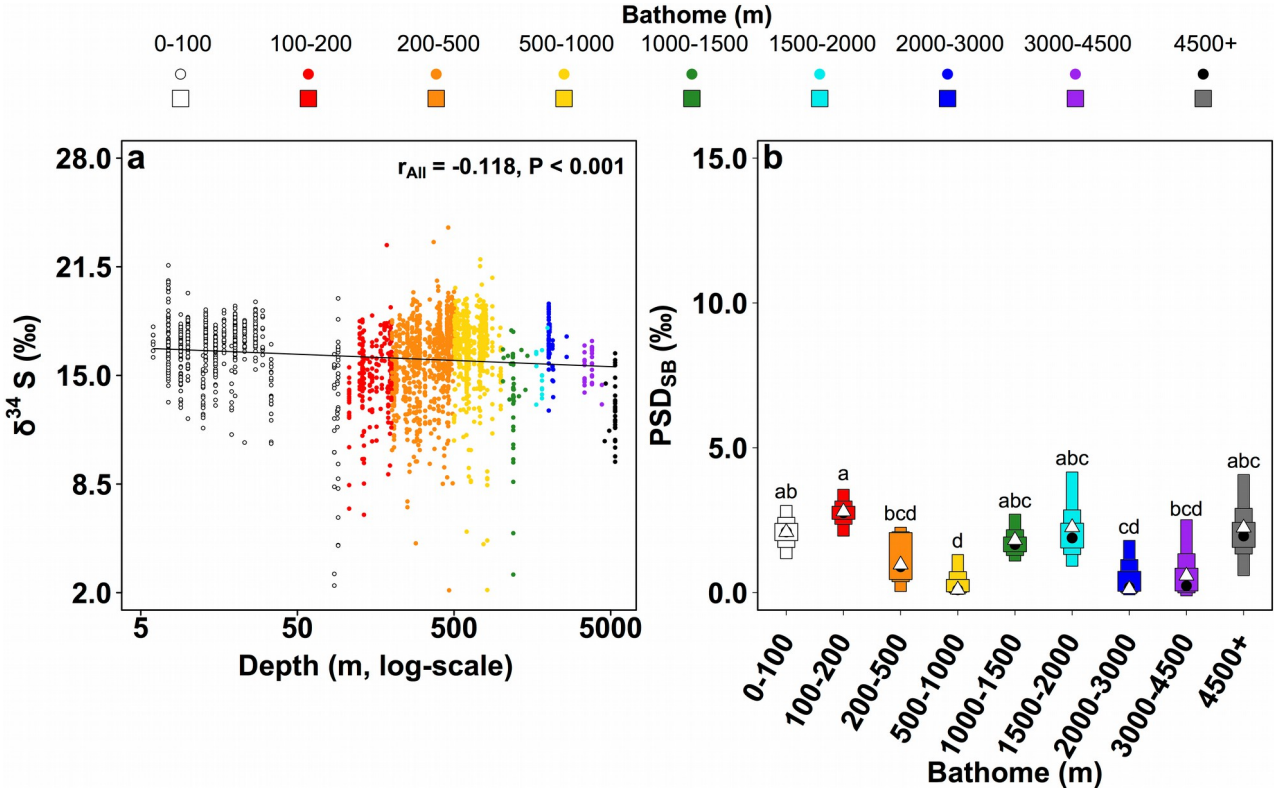


Fig. 6.5. Effect of depth on sea star $\delta^{34}S$ values: a) relationships between depth and $\delta^{34}S$ values. b) Sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of pseudo-standard deviation for $\delta^{34}S$ values (PSD_S) for standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{34}S$ values of sea star taxa for each bathome.

The interaction between depth and the trophic group consistently impacted stable isotope values (Table 6.3). $\delta^{13}C$ decreased with depth for most of the trophic groups, but remained stable for the suspension feeders and increased for the pelagos-based omnivores (Fig. 6.6.a). $\delta^{15}N$ values decreased with depth for the predators of active prey and of encrusting prey, and for the sediment feeders. By contrast, they increased for the predators of large sessile prey, suspension feeders, omnivores and pelagos-based omnivores (Fig. 6.6.b). $\delta^{34}S$ values slightly decreased with depth for the predators of active prey, the sediment feeders and the omnivores but remained stable for the other groups (Fig. 6.6.c). However, like for depth when considered alone, this interaction is significant only because of the high number of individuals, and its ecological relevance seems limited.

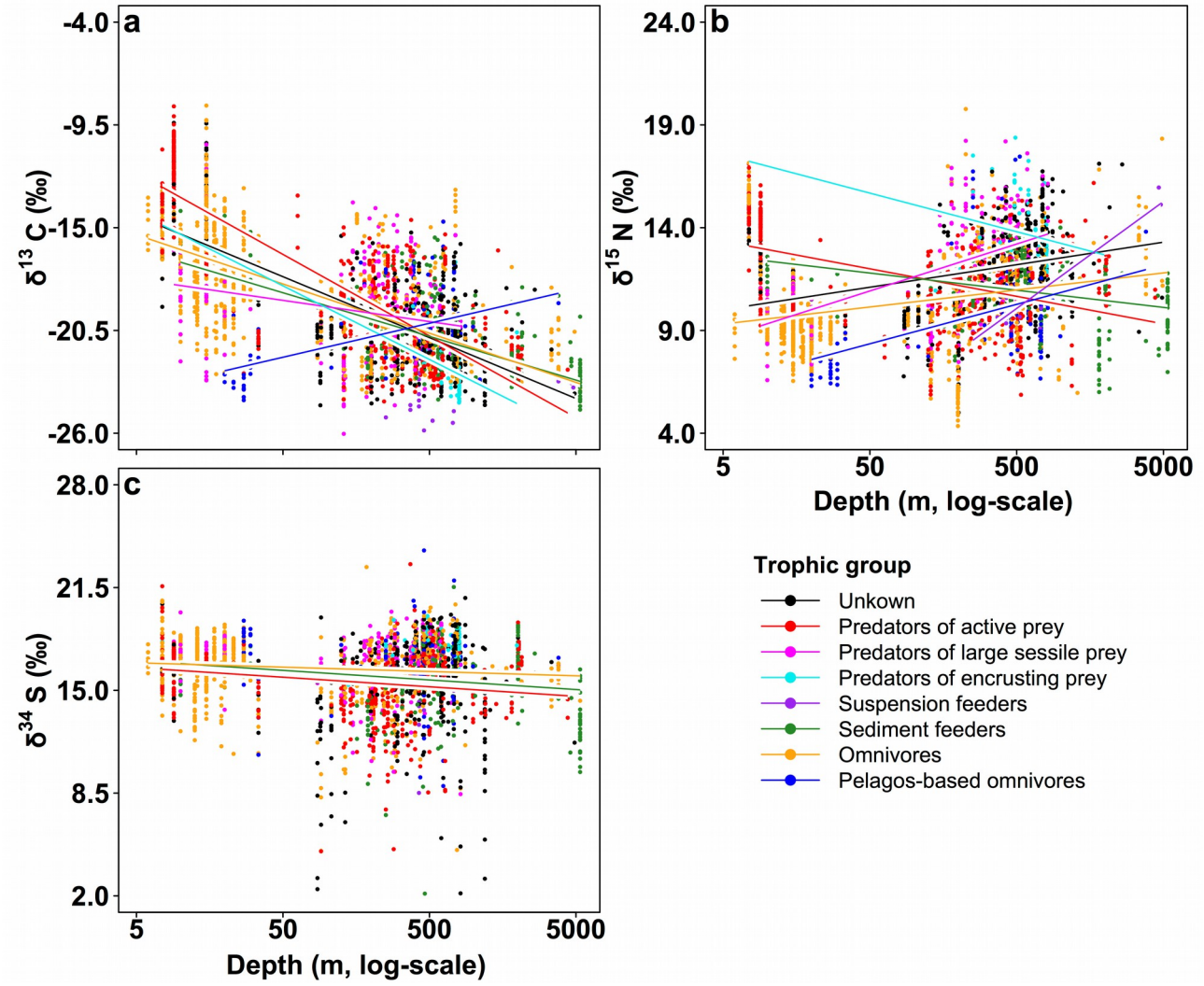


Fig. 6.6. Relationship between depth and a) $\delta^{13}C$, b) $\delta^{15}N$ and c) $\delta^{34}S$ values for each trophic group. Only significant regressions in each trophic group are shown.

6.3.1.3 Sea ice concentration and its interaction with trophic groups and depth

$\delta^{13}C$ increased with sea ice concentration (Table 6.3.b; Fig. 6.7.a). When investigating the relationship between sea ice concentration and $\delta^{13}C$ values within the 3 ecoregions with the highest variability of sampled sea ice concentrations, this relationship did appear in Oates ($r = 0.654$, $P < 0.001$) and Weddell Sea ($r = 0.530$, $P < 0.001$), where large ranges of sea ice concentration values (5-84 % for Oates and 0-90 % for Weddell Sea) were sampled, but not in Antarctic Peninsula ($r = –0.052$, $P = 0.208$), where a low range of sea ice concentration values was sampled (0-36 %; Table 6.1). $\delta^{15}N$ values were not affected by sea ice concentration despite their significant, but weak, correlation (Table 6.3.b; Fig. 6.7.b). The lack of pattern of the relationships between sea ice concentration and $\delta^{15}N$ values within the 3 most sampled ecoregions ($r = 0.599$, $P < 0.001$ for Antarctic Peninsula; $r = –0.408$, $P < 0.001$ for Oates; $r = 0.033$, $P = 0.366$ for Weddell Sea) further confirms this result.

The generation of standard ellipses with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa (Fig. 6.7.c) and the subsequent computation of SEA_B indicated that Antarctic sea stars had a higher SEA_B (mode range: 4.1-5.9 ‰^{2}) than Subantarctic ones (mode = 3.1 ‰^{2}, CI_{95} = 2.4-4.1 ‰^{2}), i.e. that Antarctic taxa had more different $\delta^{13}C$ and $\delta^{15}N$ values than Subantarctic ones (Fig. 6.7.d). PSD_{CB} appeared to be similar in all sea ice concentration intervals (mode range: 1.5-2.5 ‰). Except for sea stars sampled in zones with 20-30 % sea ice concentration (mode = 1.8 ‰, CI_{95} = 0.8-2.9 ‰), PSD_{NB} may also be generally higher in Antarctic sea stars (mode range: 2.3-3.2 ‰) than in Subantarctic ones (mode = 1.6 ‰, CI_{95} = 1.0-2.3 ‰), but large credible intervals in the 40-50 and 60-70 % sea ice concentration intervals prevent to confirm it (Fig. 6.7.e). Similarly, in Antarctic sea stars, PSD_{NB} may be smaller for sea stars sampled in zones with 20-30 % sea ice concentration but did not appear to differ between most of the sea ice concentration intervals.

$\delta^{34}S$ decreased slightly with sea ice concentration (Table 6.3.b; Fig. 6.8.a). However, the lack of patterns of the relationships between sea ice concentration and $\delta^{34}S$ values ($r = 0.091$, $P = 0.042$ for Antarctic Peninsula; $r = 0.182$, $P = 0.003$ for Oates; $r = –0.318$, $P < 0.001$ for Weddell Sea) may indicate a more limited influence of sea ice concentration on $\delta^{34}S$ values. In particular, $\delta^{34}S$ increased slightly with sea ice concentration in Oates and decreased in Weddell Sea, two ecoregions with large and similar ranges of sea ice concentration values (Table 6.1). PSD_{SB} inconsistently changed between the sea ice concentration intervals (Fig. 6.8.b).

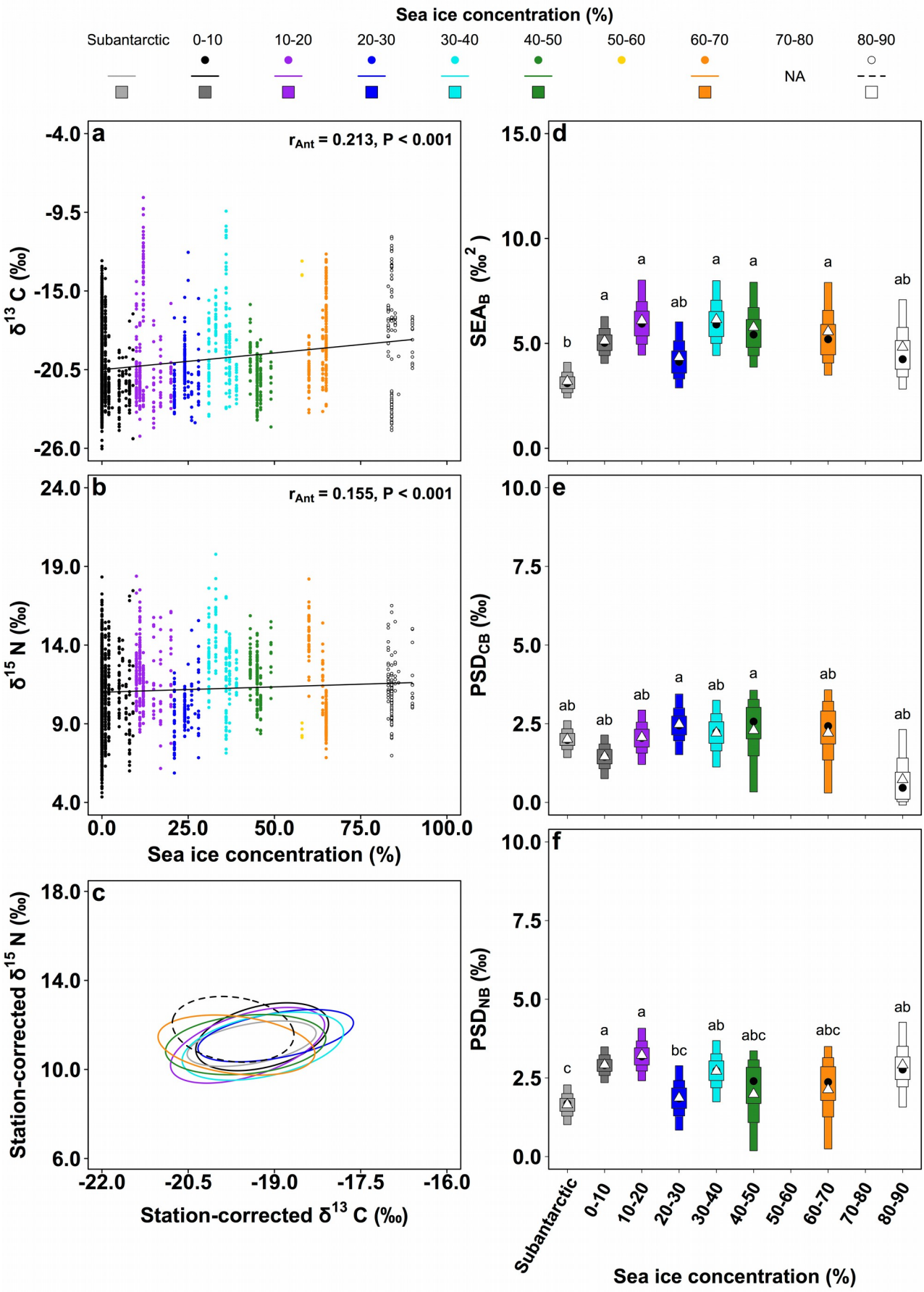

Sea ice concentration (%)
Subantarctic
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
NA
a
r_{Ant} = 0.213, P < 0.001
δ^{13} C (‰)
b
r_{Ant} = 0.155, P < 0.001
δ^{15} N (‰)
Sea ice concentration (%)
c
Station-corrected δ^{15} N (‰)
Station-corrected δ^{13} C (‰)
d
SEA_B ($‰^2$)
e
PSD_{CB} (‰)
f
PSD_{NB} (‰)
Subantarctic
Sea ice concentration (%)

Fig. 6.7. Effect of sea ice concentration on sea star $\delta^{13}C$ and $\delta^{15}N$ values: relationship of sea ice concentration with a) $\delta^{13}C$ values and b) $\delta^{15}N$ values in Antarctic sea stars only. c) Standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa and subsequent sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of d) standard ellipse area (SEA), e) pseudo-standard deviation for $\delta^{13}C$ values (PSD_C) and f) for $\delta^{15}N$ values (PSD_N) for each sea ice concentration interval. Standard ellipses were not computed for the 50-60 and 70-80 % intervals because of insufficient data being available for them.

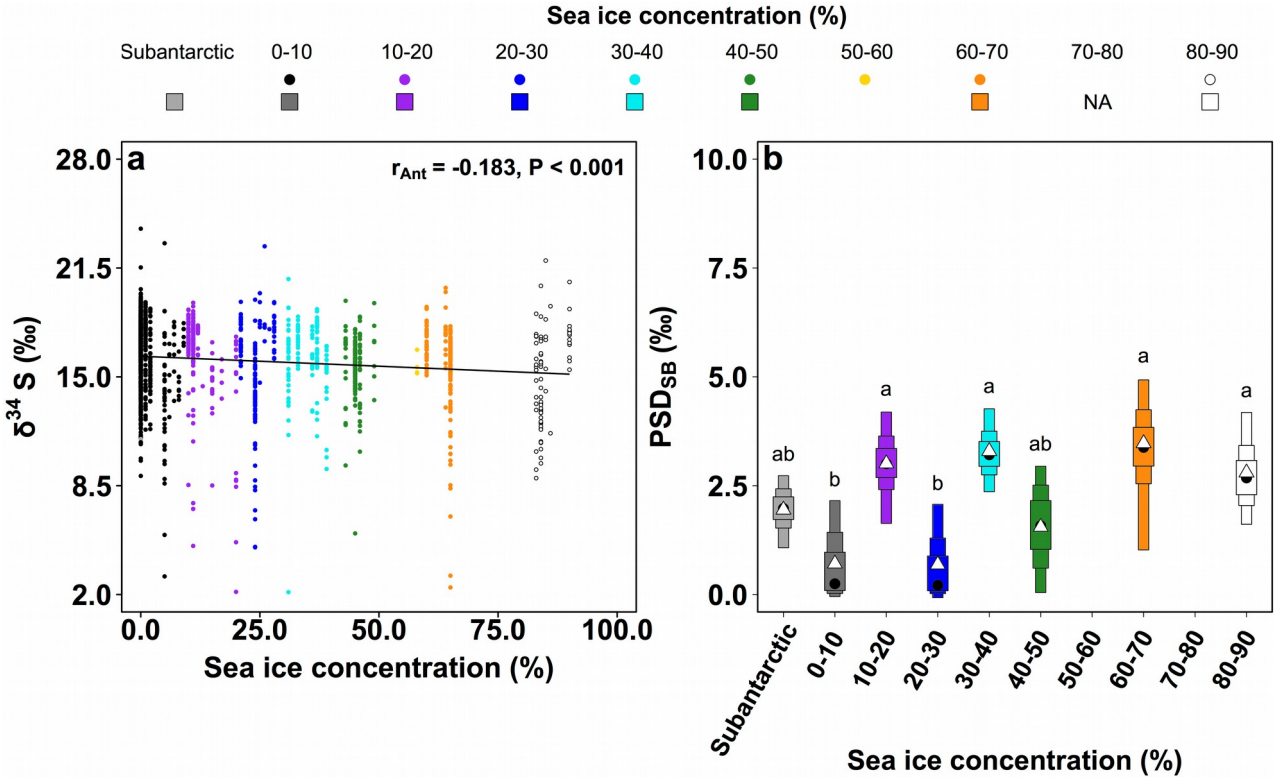


Fig. 6.8. Effect of sea ice concentration on sea star $\delta^{34}S$ values: a) relationships between sea ice concentration and $\delta^{34}S$ values in Antarctic sea stars only. b) Sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of pseudo-standard deviation for $\delta^{34}S$ values (PSD_S) for standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{34}S$ values of sea star taxa for each sea ice concentration interval. Standard ellipses were not computed for the 50-60 and 70-80 % intervals because of insufficient data being available for them.

The interaction between sea ice concentration and the trophic group impacted stable isotope values of Antarctic sea stars (Table 6.3). $\delta^{13}C$ increased with sea ice concentration for the unknown trophic group, predators of active prey and of encrusting prey, omnivores and pelagos-based omnivores and remained stable for predators of sessile prey and suspension feeders (Fig. 6.9.a). High variability of $\delta^{13}C$ values for individuals sampled at sea ice concentration higher than 80 % (–20.6 ± 3.2 ‰), with values ranging from –23.2 to –22.0 ‰ in a coastal station from Oates and from –20.4 to –15.4 ‰ in two stations from the continental shelf of Weddell Sea, may explain the lack of relationship between sea ice concentration and $\delta^{13}C$ values in predators of sessile prey. $\delta^{13}C$ values decreased with sea ice concentration only for sediment feeders, reaching –23.2 ± 1.0 at 84 % of sea ice concentration (Fig. 6.9.a). Similarly, $\delta^{15}N$ values increased with sea ice concentration for the unknown trophic group, predators of large sessile prey, omnivores and pelagos-based omnivores and remained stable for predators of active prey and of encrusting prey and suspension feeders. $\delta^{15}N$ values decreased with sea ice concentration only for sediment feeders (Fig. 6.9.b). $\delta^{34}S$ values decreased with sea ice concentration for the sediment feeders and the omnivores and increased for the predators of active prey (Fig. 6.9.c). The results on the relationships between stable isotope values and sea ice concentration should be interpreted with caution for suspension feeders and predators of encrusting prey as the former were sampled at concentrations lower than 15 ‰ while a single predator of encrusting prey was sampled above the 11 % concentration.

The interaction between sea ice concentration and depth impacted $\delta^{13}C$ values (Table 6.3.b). However, sea ice concentration and $\delta^{13}C$ values were positively correlated in the three observed bathomes (Fig. 6.10.a, b and c). However, the slopes are slightly more positive in the 200-500 and 500-1000 m bathomes than in the 0-100 m one, with $\delta^{13}C$ values on the regression line being *ca* –21.5 ‰ when there is no sea ice and *ca* –18.5 ‰ when sea ice concentration is 90 % (Fig. 6.10.b and c). It is worthy of note that ca 90 % of the individual $\delta^{13}C$ values at sea ice concentrations close to 90 % in the 500-1000 m bathome (all being observed in Weddell Sea) are notably higher than the ones predicted by the regression line, i.e. ranging from –18.2 to –13.0 ‰ (Fig. 6.10.c). $\delta^{15}N$ values were impacted by the interaction between sea ice concentration and depth. However, $\delta^{15}N$ values increased with sea ice concentration in the 3 investigated bathomes but the correlation coefficients were rather weak (Fig. 6.10.d, e and f). The influence of the interaction between sea ice concentration and depth on $\delta^{34}S$ values was not significant (Table 6.3) despite the significant, but rather weak, relationships between $\delta^{34}S$ values and sea ice concentration between 0 and 100 m and 500 and 1000 m, but not between 200 and 500 m (Fig. 6.10.g, h and i).

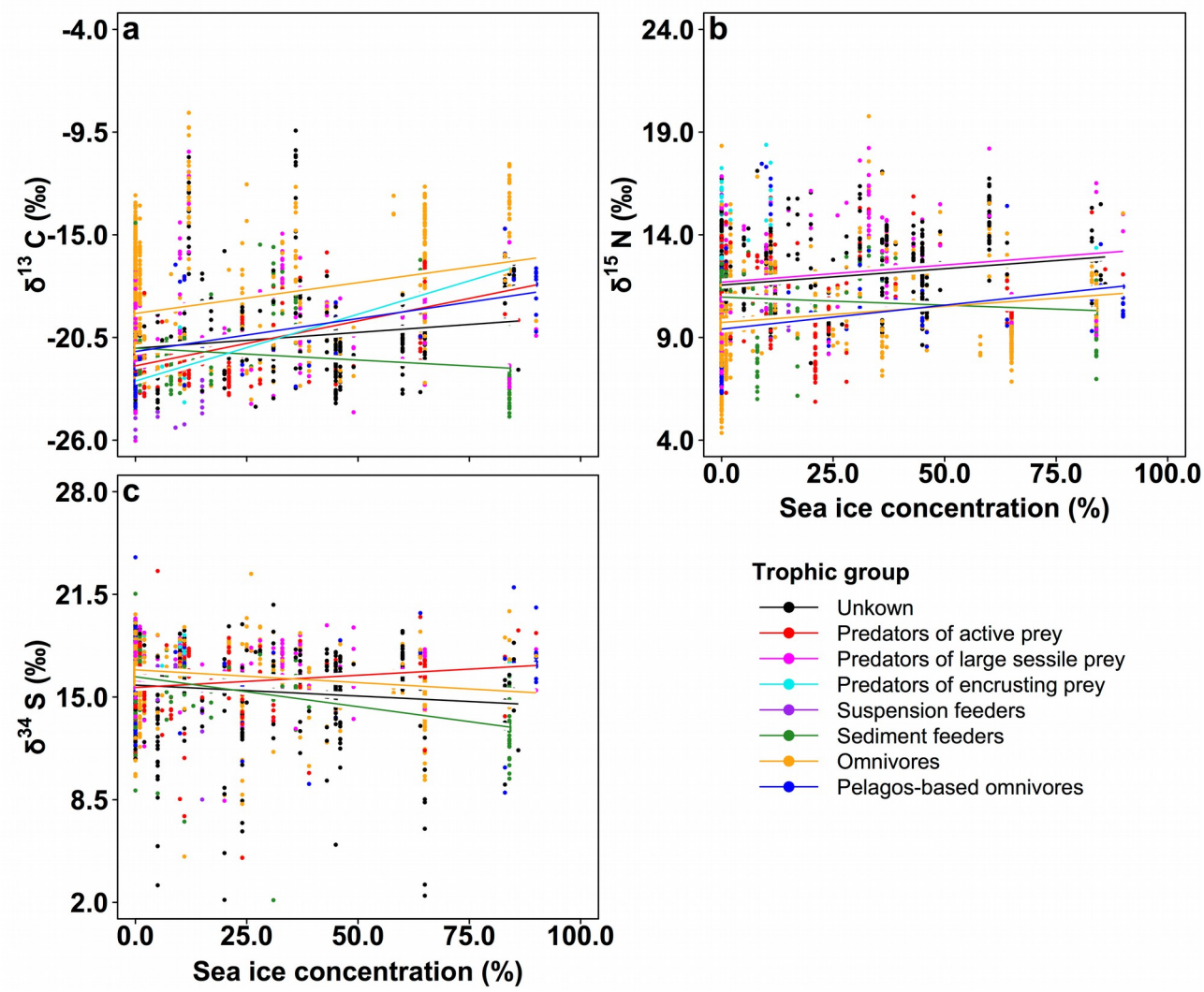


Fig. 6.9. Relationship between sea ice concentration and a) $\delta^{13}C$, b) $\delta^{15}N$ and c) $\delta^{34}S$ values for each trophic group in Antarctic sea stars only. Only significant regressions in each trophic group are shown.

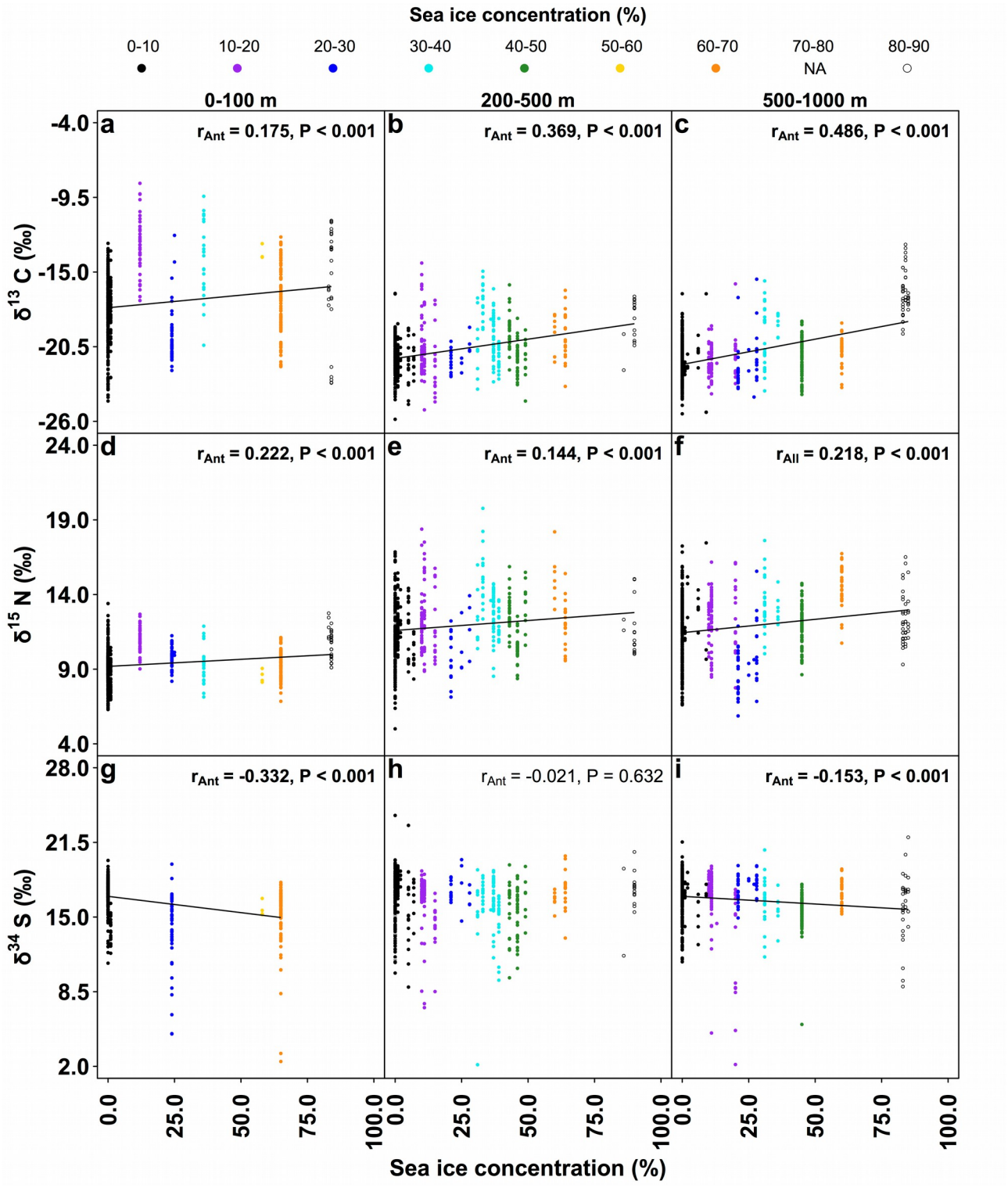


Fig. 6.10. Relationships between sea ice concentration and a, b, c) $\delta^{13}C$, d, e, f) $\delta^{15}N$ and g, h, i) $\delta^{34}S$ values for the a, d, g) 0-100 m, b, e, h) 200-500 m and c, f, i) 500-1000 m bathomes in Antarctic sea stars.

6.3.1.4 Sea ice season duration and its interaction with trophic groups and depth

Sea ice season duration had no significant effect on $\delta^{13}C$ and a marginally significant one on $\delta^{15}N$ values of Antarctic sea stars (Table 6.3.b) despite the negative and positive relationships of sea ice season duration with $\delta^{13}C$ (Fig. 6.11.a) and $\delta^{15}N$ values (Fig. 6.11.b), respectively. In particular, high $\delta^{13}C$ values were recorded for several low or intermediate values of sea ice season duration. In a type III ANCOVA, or any linear model, the effect of each factor, covariate, and interaction is estimated independently from all other factors, covariates, or interactions. When, a factor is linked to a covariate to some extent, adding their interaction in the model can modify the size of the principal effect of the factor, because the effect of this link is removed. For instance, regarding $\delta^{15}N$, the interaction between the trophic group and the ice season duration is large, showing that this duration has not the same effect in all trophic groups, which may lower the principal effect of sea ice duration: removing all interactions from the model makes that the F ratio for sea ice duration is now $F_{1,2119} = 175.556$ rather than $F_{1,2095} = 3.700$. Consequently, the significant correlations of $\delta^{13}C$ and $\delta^{15}N$ values with sea ice season duration were the result of the influence of other variables. The negative correlation of $\delta^{13}C$ values with sea ice season duration still occurred in Antarctic Peninsula ($r = –0.251$, $P < 0.001$), where a large range of sea ice season duration values was sampled (2-61 %, table 6.1). It also appeared in Oates ($r = –0.428$, $P < 0.001$) where a low range of sea ice season duration values was sampled (42-62 %, table 6.1). However, a positive relationship was observed in Weddell Sea ($r = 0.235$, $P < 0.001$), where the range of sea ice season duration values was similar to that of Antarctic Peninsula (31-89 %, table 6.1), but also where the longest sea ice season duration values (> 85 %) were sampled (Table 6.1). Indeed, $\delta^{13}C$ values from zones where sea ice lasts more than 85 % of the year appeared to be particularly high in comparison of $\delta^{13}C$ values from zones with lower sea ice season duration. $\delta^{15}N$ values and sea ice season duration were positively correlated (Fig. 6.11.b). However, the ANCOVA results showed that the effect of sea ice season duration on $\delta^{15}N$ values was only marginally significant (Table 6.3). The positive correlation of $\delta^{15}N$ values with sea ice season duration occurred in the 3 ecoregions ($r = 0.248$, $P < 0.001$ for Antarctic Peninsula; $r = 0.332$, $P < 0.001$ for Oates; $r = 0.185$, $P < 0.001$ for Weddell Sea).

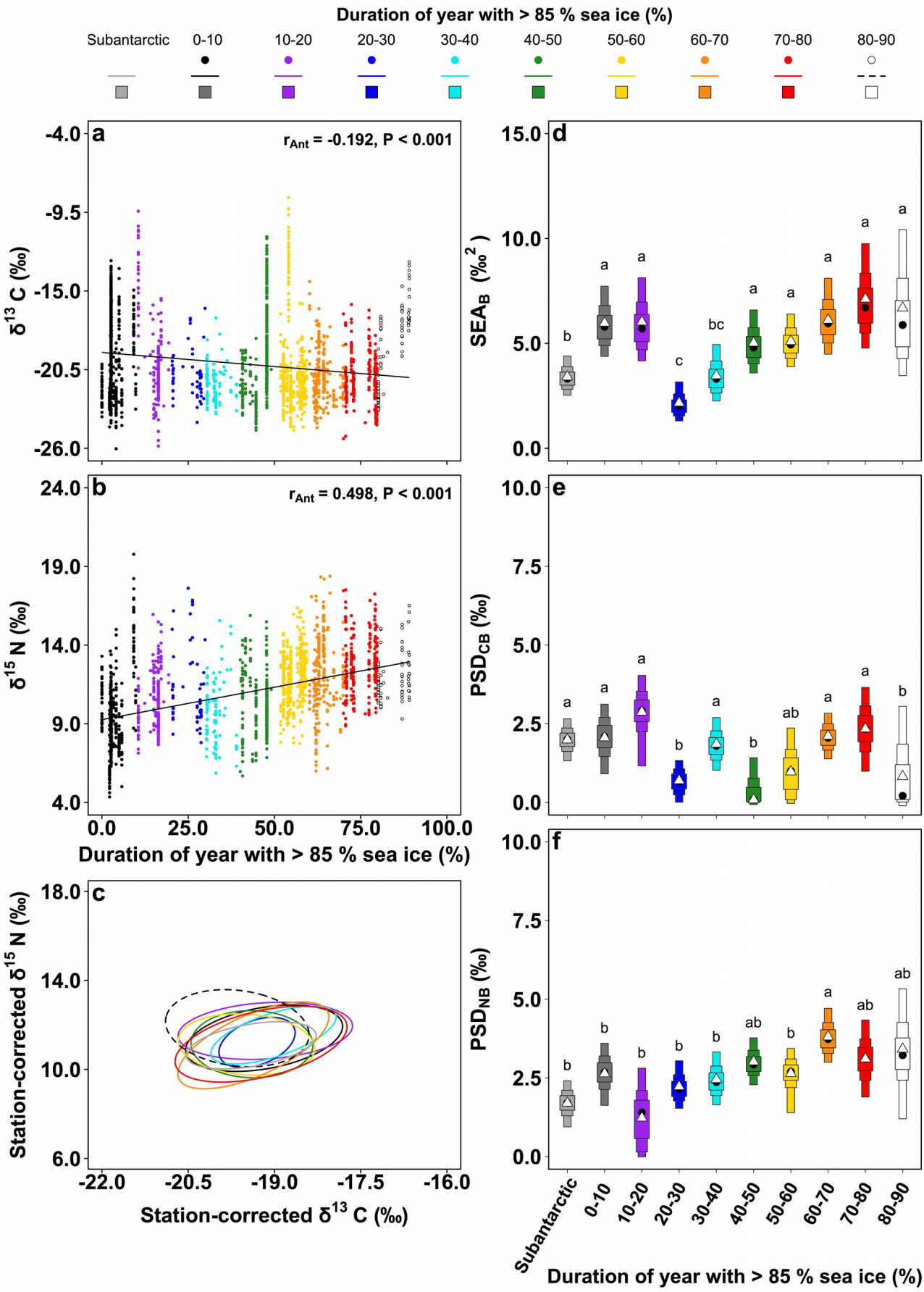

Duration of year with > 85 % sea ice (%)
Subantarctic
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
a
r_{Ant} = -0.192, P < 0.001
δ^{13} C (‰)
b
r_{Ant} = 0.498, P < 0.001
δ^{15} N (‰)
Duration of year with > 85 % sea ice (%)
c
Station-corrected δ^{15} N (‰)
Station-corrected δ^{13} C (‰)
d
SEA_B (‰^{2})
e
PSD_{CB} (‰)
f
PSD_{NB} (‰)
Subantarctic
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
Duration of year with > 85 % sea ice (%)

Fig. 6.11. Effect of sea ice season duration on sea star $\delta^{13}C$ and $\delta^{15}N$ values: relationship of sea ice season duration with a) $\delta^{13}C$ values and b) $\delta^{15}N$ values in Antarctic sea stars only. c) Standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa and subsequent sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of d) standard ellipse area (SEA), e) pseudo-standard deviation for $\delta^{13}C$ values (PSD_C) and f) $\delta^{15}N$ values (PSD_N) for each sea ice season duration interval.

The generation of standard ellipses with the mean station-corrected $\delta^{13}C$ and $\delta^{15}N$ values of sea star taxa (Fig. 6.11.c) and the subsequent computation of SEA_B with $\delta^{13}C$ and $\delta^{15}N$ suggest that Antarctic sea stars had a higher SEA_B (mode range: 3.3-5.8 ‰^{2}) than the Subantarctic ones (mode = 3.3 ‰^{2}, CI_{95} = 2.5-4.4 ‰^{2}), i.e. that Antarctic species had more different $\delta^{13}C$ and $\delta^{15}N$ values than Subantarctic ones (Fig. 6.11.d). However, sea stars sampled in zones covered by ice between 20 and 30 % (mode = 2.0 ‰^{2}, CI_{95} = 1.3-3.2 ‰^{2}) and between 30 and 40 % (mode = 3.4 ‰^{2}, CI_{95} = 2.2-5.0 ‰^{2}) of the year may have lower or similar SEA_B values than those of Subantarctic sea stars. PSD_{CB} inconsistently changed between sea ice season duration intervals (Fig. 6.11.e). PSD_{NB} appeared to slightly increase with the sea ice season duration intervals but this increase did not appear to be meaningful as PSD_{NB} was similar for all sea ice season duration intervals except for the 60-70 % interval that had a higher PSD_{NB} (mode = 3.7 ‰, CI_{95} = 3.0-4.7 ‰) than the interval between 0 and 40 % and the Subantarctic one (mode range: 1.1-2.7 ‰; Fig. 6.11.f).

$\delta^{34}S$ values were not impacted by sea ice season duration in Antarctic sea stars (Table 6.3) and the weak correlation between $\delta^{34}S$ and sea ice season duration may be considered as negligible (Fig. 6.12.a). Similarly, weak but significant relationships between $\delta^{34}S$ and sea ice season duration occurred in the Antarctic Peninsula ($r = 0.103$, $P = 0.023$) and Weddell Sea ($r = 0.261$, $P < 0.001$) but not in Oates ($r = –0.055$, $P = 0.368$). PSD_{SB} appeared to be low between 0 and 40 % of ice season duration (mode range: 0.0-2.5 ‰) and became higher if the ice season duration lasts more than 40 % of the year (mode range: 2.4-3.1 ‰; Fig. 6.8.b).

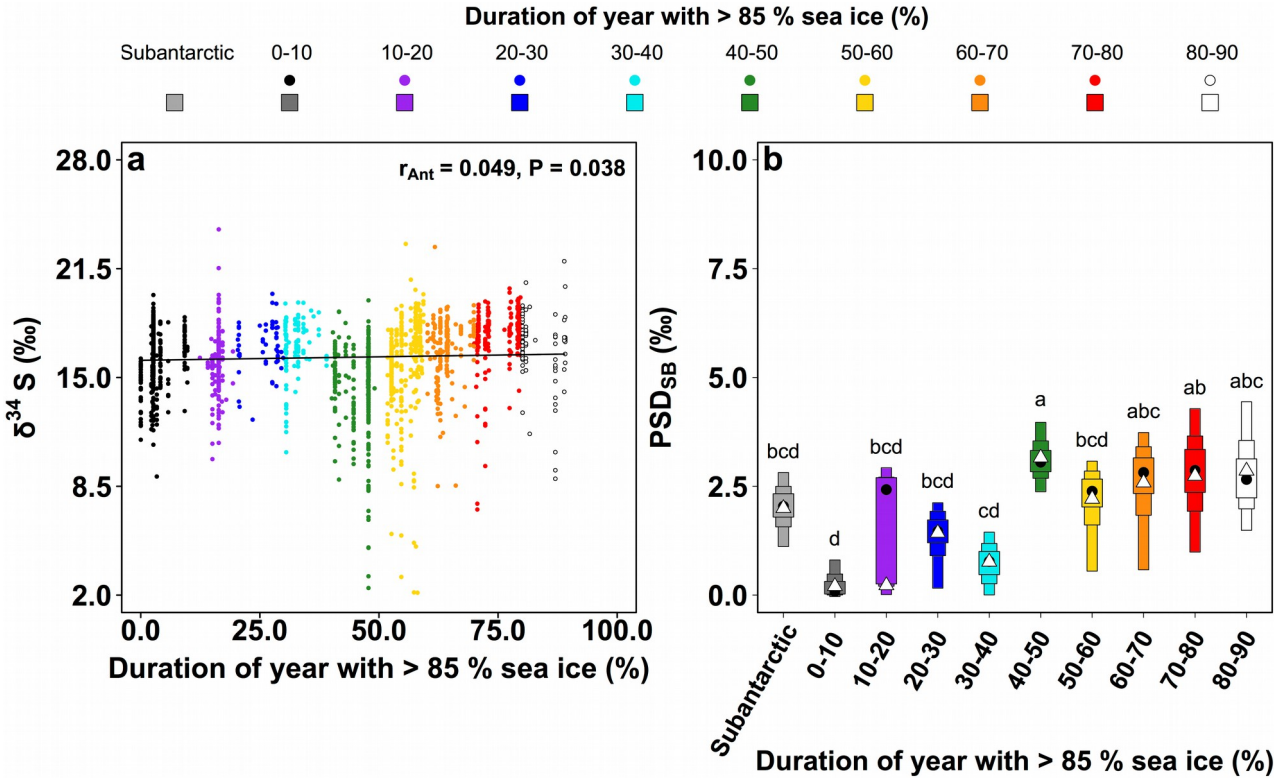


Fig. 6.12. Effect of sea ice season duration on sea star $\delta^{34}S$ values: a) relationships between sea ice season duration and $\delta^{34}S$ values in Antarctic sea stars only. b) Sample-size corrected (white triangles) and Bayesian estimation (boxes: 50 %, 75 % and 95 % credible intervals, black dots: modes) of pseudo-standard deviation for $\delta^{34}S$ values (PSD_S) for standard ellipses generated with the mean station-corrected $\delta^{13}C$ and $\delta^{34}S$ values of sea star taxa for each sea ice season duration interval.

The interaction between sea ice season duration and the trophic group impacted $\delta^{13}C$ and $\delta^{15}N$ values of Antarctic sea stars (Table 6.3). $\delta^{13}C$ values decreased with sea ice season duration for the sediment feeders and the omnivores but increased for the predators of active prey and the pelagos-based omnivores (Fig. 6.13.a). $\delta^{13}C$ values remained stable for the other trophic groups. $\delta^{15}N$ values increased with sea ice season duration for predators of active prey and of sessile prey, omnivores and pelagos-based omnivores, as well as for the sea stars with an unknown trophic group (Fig. 6.13.b). $\delta^{15}N$ values decreased with sea ice season duration only for predators of encrusting prey and remained stable for the other trophic groups. The interaction between sea ice season duration and the trophic group was not significant and thus had no effect on $\delta^{34}S$ values of Antarctic sea stars (Table 6.3). $\delta^{34}S$ values slightly decreased with sea ice season duration for the omnivores, and slightly increased for the sea stars with an unknown trophic group, the predators of active prey, sessile prey and the sediment feeders, but all these effects were weak (Fig. 6.13.c). They remained stable for the other groups.

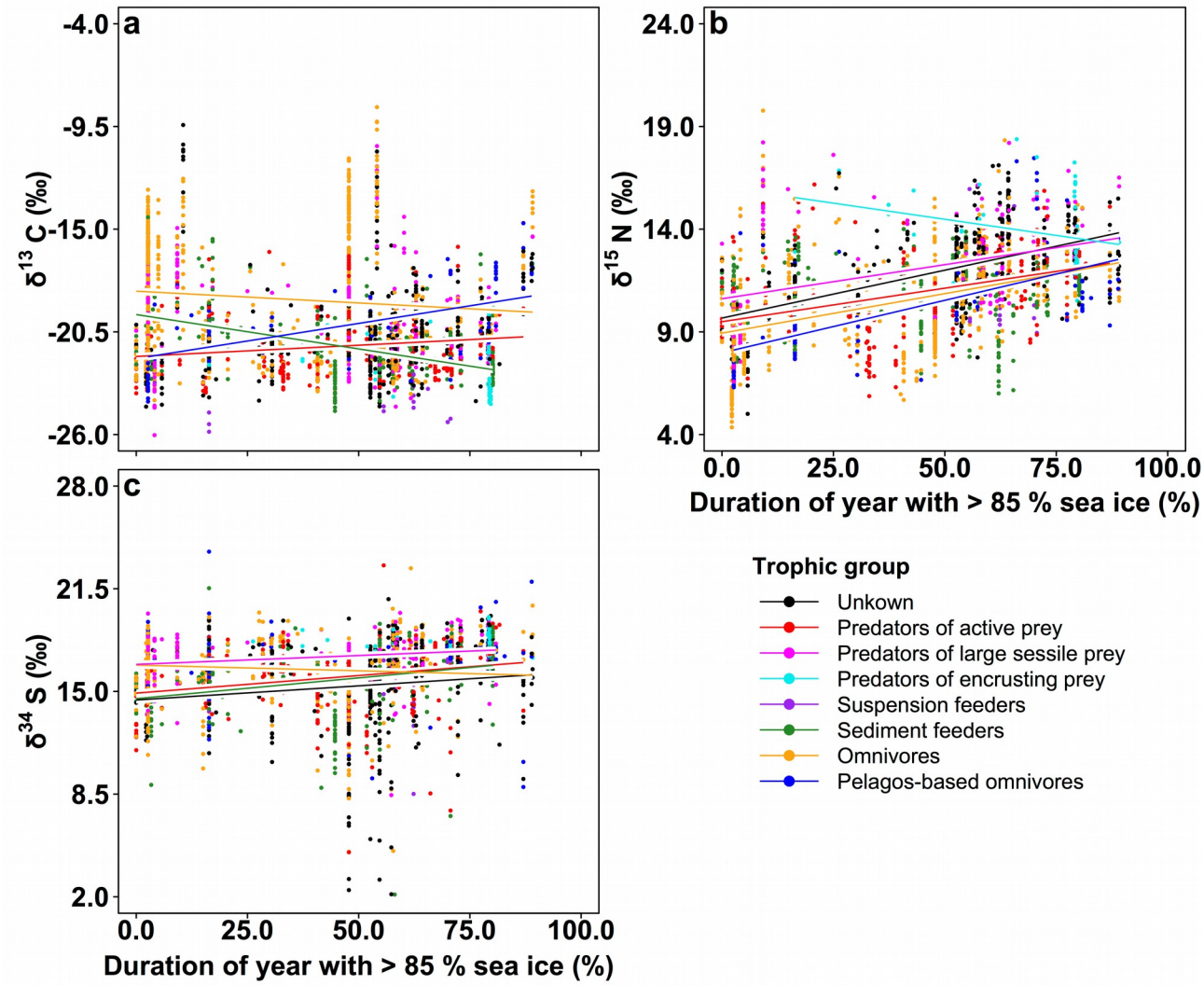


Fig. 6.13. Relationship between sea ice season duration and a) $\delta^{13}C$, b) $\delta^{15}N$ and c) $\delta^{34}S$ values for each trophic group in Antarctic sea stars only. Only significant regressions in each trophic group are shown.

The interaction between sea ice season duration and depth did not impact stable isotope values of Antarctic sea stars (Table 6.3). Indeed, sea ice season duration and $\delta^{13}C$ values were positively correlated in the 3 bathomes, although the correlations can be considered as negligible (Fig. 6.14.a, b and c). However, it should be noted that all sea stars sampled between 500 and 1000 m in zones where sea ice lasts more than 85 % of the year in the Weddell Sea had $\delta^{13}C$ values higher than those predicted by the regression line and ranging from –19.6 to –13.0 ‰ (Fig. 6.14.c). $\delta^{15}N$ values and sea ice season duration were positively correlated in the 3 bathomes (Fig. 6.14.d, e and f). Finally, $\delta^{34}S$ values increased with sea ice season duration between 200 and 1000 m (Fig. 6.14.h and i). A correlation coefficient could not be computed between 0 and 100 m because of insufficient variability of sea ice season duration in this bathome (Fig. 6.14.g).

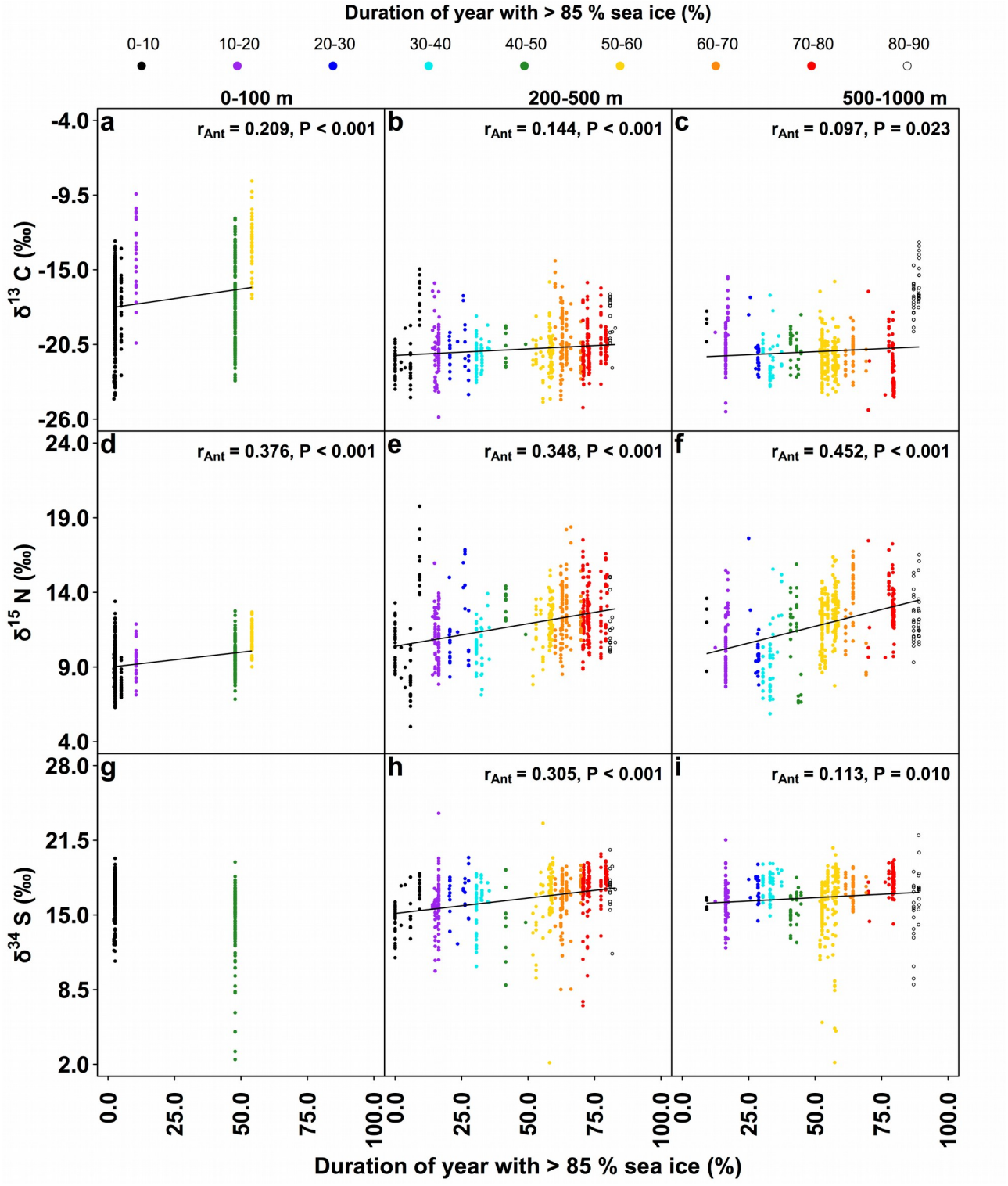


Fig. 6.14. Relationships between sea ice season duration and a, b, c) $\delta^{13}C$, d, e, f) $\delta^{15}N$ and g, h, i) $\delta^{34}S$ values for the a, d, g) 0-100 m, b, e, h) 200-500 m and c, f, i) 500-1000 m bathomes in Antarctic sea stars only. No correlation was computed between $\delta^{34}S$ and sea ice season duration in the 0-100 m bathome because of only two different sea ice season duration values.

6.3.2 Relationships between environmental parameters and stable isotope values within ecoregions

The results of the PCA with the $\delta^{13}C$ and $\delta^{15}N$ values, the log-transformed depth, the sea ice concentration and the sea ice season duration on the whole dataset (Fig. 6.15) reflected several of the results previously reported on the relationships between environmental parameters and stable isotope values. The PCA results notably highlighted the negative link between $\delta^{13}C$ values and depth, with the $\delta^{13}C$ and depth vectors pointing in opposite directions and higher $\delta^{13}C$ values being recorded in sea stars collected in Antarctic ecoregions at depths shallower than 100 m (Antarctic Peninsula, Central Indian-Prydz Bay, Central Indian-Wilkes, Oates), followed by the ones collected at intermediate depths (Amundsen, Pacific Antarctic Ridge, South Atlantic, South Orkney Islands, South Sandwich Islands, Weddell Sea) and finally by the Atlantic Basin where all sea stars were collected below 4000 m (Table 6.1). By contrast, no link between depth and $\delta^{15}N$ values appeared, the depth and $\delta^{15}N$ vectors being orthogonal, similarly to what was observed in the ANCOVAs (Table 6.3). The PCA results also highlighted the higher $\delta^{13}C$ values in the Subantarctic ecoregions, including South Georgia, where no station shallower than 100 m was sampled. The high $\delta^{13}C$ values recorded for South Georgia may suggest that the higher $\delta^{13}C$ values recorded in sea stars from the Subantarctic ecoregions cannot be explained only by the high proportion of shallow water samples (*ca* 38 %) in these ecoregions. Several Antarctic regions (Central Indian-Wilkes, Antarctic Peninsula) appeared to be very similar to Subantarctic ecoregions. This is mostly linked to their high $\delta^{13}C$ values. In Central Indian-Wilkes, this trend concerned only coastal sea stars, as no deep samples were available. In the Antarctic Peninsula, however, a significant proportion (39.5 %) of sea stars were sampled below 100 m, suggesting this trend was true regardless of sampling depth. The relationship between sea ice concentration and $\delta^{13}C$ values did not appear in the PCA results as $\delta^{13}C$ value tend to increase with sea ice concentration but are also higher in Subantarctic ecoregions where sea ice is absent. Similarly, no relationships between sea ice season duration and $\delta^{13}C$ or $\delta^{15}N$ value were highlighted.

When PCAs were performed within the ecoregions (Fig. 6.16), the negative correlation between depth and $\delta^{13}C$ values was still observed in all ecoregions except South Georgia (Fig. 6.16.e), where the smallest range of depths was sampled (Table 6.1). No relationships between depth and $\delta^{15}N$ values were observed in 4 of the 5 investigated ecoregions. The relationship between $\delta^{13}C$ values and sea ice concentration appeared in Oates (Fig. 6.16.b) and Weddell Sea (Fig. 6.16.e), where large ranges of sea ice concentration values (5-84 % for Oates and 0-90 % for Weddell Sea; Table 6.1)

were sampled, but not in Antarctic Peninsula, where there was a lower range (0-36 %; Table 6.1). Negative relationships between sea ice season duration and $\delta^{13}C$ values were observed in Antarctic Peninsula (Fig. 6.16.a) and Oates (Fig. 6.16.b). However, the previously reported positive relationship between sea ice season duration and $\delta^{13}C$ values in Weddell Sea did not appear (Fig. 6.16.c). No clear relationships of $\delta^{15}N$ values with sea ice concentration and sea ice season duration were observed in the 3 Antarctic ecoregions.

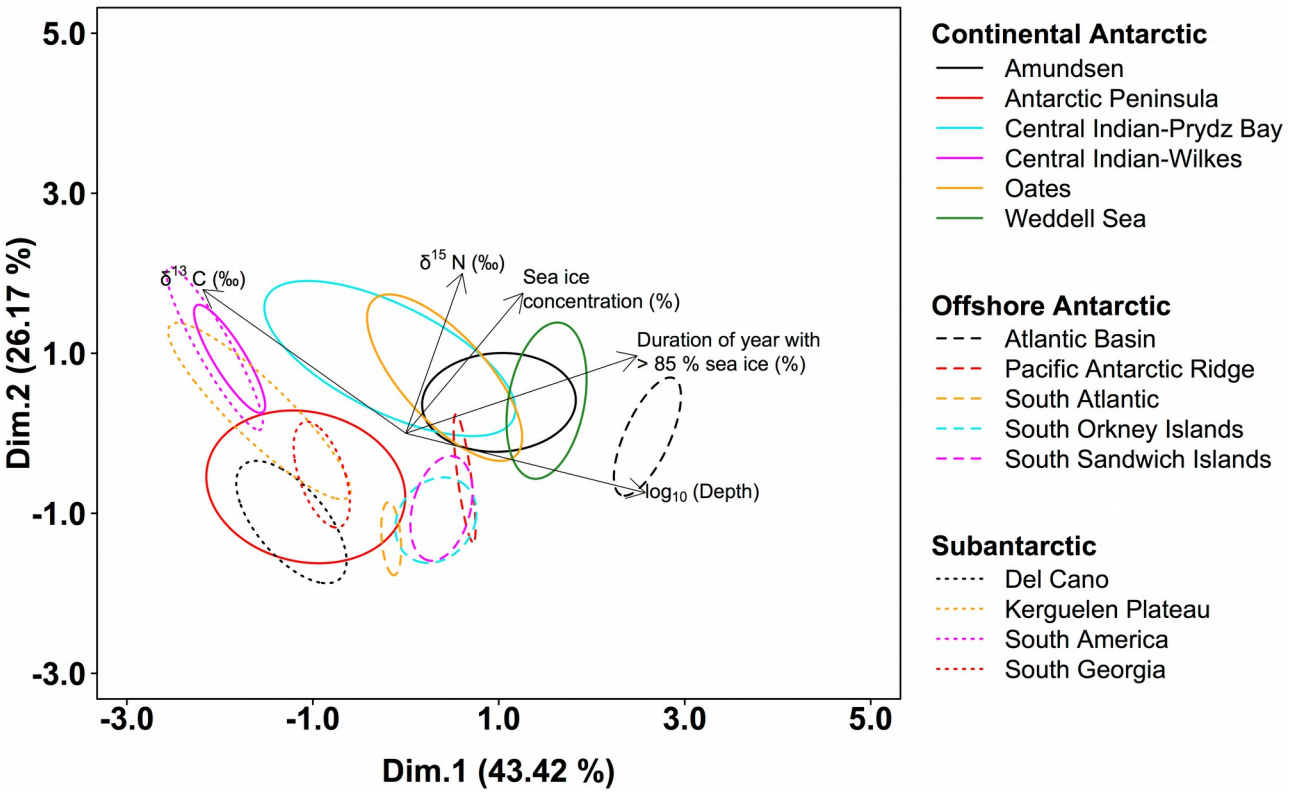


Fig. 6.15. Principal Component Analyses (PCA) on the relationships between environmental parameters (depth, sea ice concentration, sea ice season duration) and $\delta^{13}C$ and $\delta^{15}N$ values and their variability between and within ecoregions (ellipses).

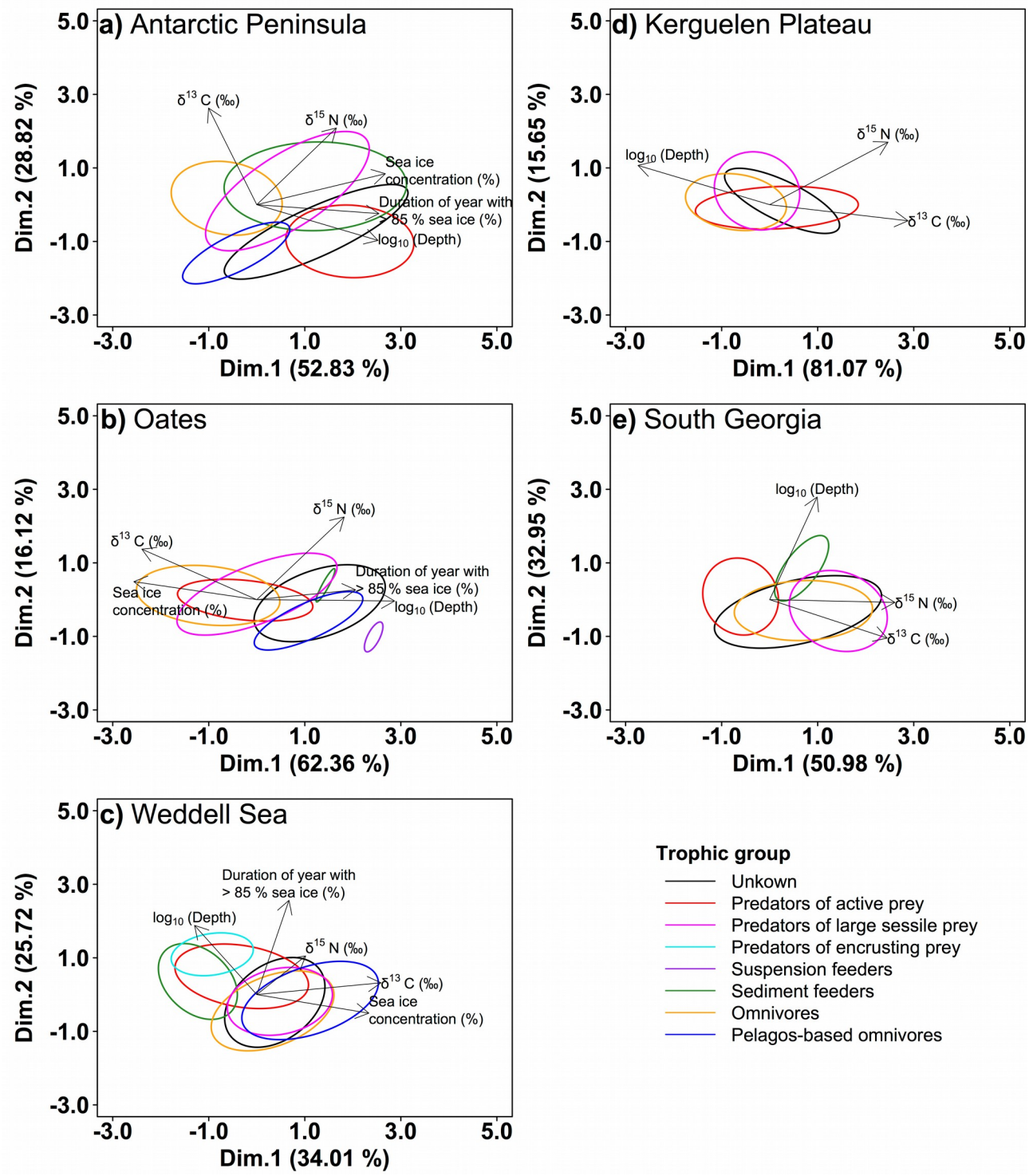


Fig. 6.16. Principal Component Analyses (PCA) on the relationships between environmental parameters (depth, sea ice concentration, sea ice season duration for Antarctic ecoregions, depth only for Subantarctic ecoregion) and $\delta^{13}C$ and $\delta^{15}N$ values within selected Antarctic (a, b, c) and Subantarctic (d, e) ecoregions and their variability between and within trophic groups with $n \geq 5$ (ellipses).

6.4 Discussion

This chapter assessed the influence of environmental parameters on the trophic ecology of sea stars from the global Southern Ocean. To do so, the relationships of stable isotope values in sea star tissues with trophic groups and environmental parameters were assessed.

$\delta^{13}C$ values may help to identify the food sources supporting sea stars (France, 1995). Low $\delta^{13}C$ values characterise pelagic particulate organic matter (POM) from Antarctic waters (from ca –25 to ca –30 ‰, Rau et al., 1991b; Espinasse et al., 2019; Michel et al., 2019). Intermediate $\delta^{13}C$ values characterise benthic primary producers (from *ca* –25 ‰ to *ca* –10 ‰; Gillies et al., 2012; 2013; Michel et al., 2019) and/or POM from Subantarctic waters (from *ca* –21 to *ca* –23 ‰; Rau et al., 1991b; Espinasse et al., 2019). Coastal Antarctic POM may also sometimes have intermediate $\delta^{13}C$ values (*ca* –20 ‰; Gillies et al., 2012; 2013). High $\delta^{13}C$ values characterise the sea ice microbial community (from *ca* –20 ‰ in offshore areas to *ca* –8 ‰ in coastal areas; Rau et al., 1991a; Minck et al., 2008; Gillies et al., 2012; 2013; Michel et al., 2019). $\delta^{15}N$ values are generally used to estimate the trophic level of consumers (Michener and Kauffman, 2007) but may also be used to discriminate between fresh and degraded organic matter sources as high $\delta^{15}N$ values may be expected in organic matter following bacterial degradation (Saino and Hattori, 1980; Wada, 1980). High $\delta^{15}N$ values may also highlight the consumption of sponges by sea stars. Indeed, sponges have higher $\delta^{15}N$ values than other suspension feeding taxa (Mintenbeck et al., 2007) and are thus expected to induce higher $\delta^{15}N$ values in their consumers. Sponges may assimilate degraded organic matter after it has been further metabolised by symbiotic bacteria, which may explain the particularly high $\delta^{15}N$ values in sponge tissues (Iken et al., 2001). $\delta^{34}S$ may be used to refine the discrimination between food sources supporting sea stars (Fry et al., 1982; Machás and Santos, 1999; Connolly et al., 2004) as pelagic sulfates with high $\delta^{34}S$ values are the main source of inorganic sulfur for both phytoplankton and phytobenthos at the baseline of food webs (Giordano and Raven, 2014), while sulfides with low $\delta^{34}S$ values are present in sediment because of the activity of sulfate reducing bacteria (Fry et al., 1982).

The generation of standard ellipses for each trophic group with the mean station-corrected stable isotope values of sea star taxa and the subsequent computation of isotopic niche metrics allows to determine if the relative position of each taxon in the isotopic space changes within each trophic group or depending on environmental conditions. These results may be used either to investigate trophic diversity between taxa of a given trophic group or to validate the species composition of this trophic group, or to determine if the trophic diversity between sea star taxa varies according to

environmental conditions. In particular, PSD_{CB}, PSD_{NB} and PSD_{SB} may be used to assess, respectively, the differences of average relative $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values between taxa. PSD_{CB} and $PSD_{S\,B}$ may then help to assess differences of resource utilisation while PSD_{NB} may be used to determine the trophic position variability between taxa.

6.4.1 Potential bias to consider

The sea stars were sampled in many places with various methods, and a cautious attitude may be needed when analysing the results.

Stable isotopes were analysed in sea stars from various sources, including population genetic studies (Moreau, 2019; Moreau et al., 2019) or collections stored in museums or partner institutions. Stable isotope data found in the literature (Gillies and Stark, 2008; Michel et al., 2019; Zenteno et al., 2019) or unpublished data shared by colleagues were also included in this study. Consequently, species identification methods and results may differ depending on the institution that provided the samples.

Around 12 % of the individuals have been identified only using genetic methods, allowing them to be separated into clades but without giving them an exact species name as these clades are not presently described (Moreau, 2019; Moreau et al., 2019). The other ones were identified using anatomical features, sometimes together with genetic analysis, and could be assigned to a described species. Furthermore, some sea stars were either identified down to the species, to the genus, or down to the family. This pleads for more taxonomic studies on sea stars, a group which is one of the dominant taxa found in Southern Ocean.

Similarly, trophic groups were assigned to taxa depending on the knowledge available in the literature on their diet. However, this information may sometime be limited. Furthermore, trophic groups were frequently assigned to taxa depending on the diet of their congeners when no knowledge on the diet of the species was available. In such conditions, misattribution of a given taxa to a trophic group cannot be excluded.

However, the number of taxa and individuals per trophic group, bathome, sea ice concentration or ice season duration interval is usually high. The wrong attribution of several individuals to given taxa or of several taxa to a trophic group is thus unlikely to strongly modify the results.

Another potential bias could be the impact of the mean correction of stable isotope values in each sampling station on the relative position of taxa in the isotopic space. Indeed, this method allows to correct spatial variations of stable isotope values of the primary food sources or the effects

of the environmental parameters on stable isotope values prior to isotopic niche computation. However, as all stations are given the same mean of stable isotope values, sea star individuals or taxa from stations with either a low number of individuals, a low diversity of taxa or of stable isotope values, are at risk of their stable isotope values being over or underestimated in comparison to sea stars from stations with higher features, as their corrected stable isotope values would become close to the general mean (see Fig. 2.5 in chapter 2).

6.4.2 Trophic ecology of sea star trophic groups

$\delta^{13}C$ and $\delta^{15}N$ values differed between trophic groups, highlighting the difference of trophic ecology between these groups.

Predators of encrusting prey and suspension feeders were characterised by the lowest $\delta^{13}C$ values, reaching –24.2 ± 1.0 ‰ in suspension feeders and –22.3 ± 1.7 ‰ in predators of encrusting prey. As predators of sessile and encrusting prey consume suspension feeding prey such as encrusting sponges or bryozoa (Mauzey et al., 1968), their low $\delta^{13}C$ values may highlight their reliance on the suspension feeder communities. Similarly, direct consumption of suspended organic matter and zooplankton by suspension feeders (Howell et al., 2003) would explain their low $\delta^{13}C$ values. These trophic groups then are likely part of the suspension feeder food webs in the Southern Ocean. Furthermore, these two trophic groups had the lowest proportions of individuals samples in the 0-100 m bathome (0.0 % for suspension feeders and 1.4 % for predators of encrusting prey), which may contribute to their low $\delta^{13}C$ values as sea stars from deeper environment are generally supported by pelagic production (see section 6.4.3.1). $\delta^{15}N$ values differed between these two trophic groups, confirming that sea star taxa from two different trophic levels may be components of the suspension feeder food web, i.e. by exploiting directly the organic matter as suspension feeders, or as predator of suspension feeders. Predators of encrusting prey had the highest $\delta^{15}N$ values. Such high $\delta^{15}N$ values in sea stars feeding on primary consumers such as sponges and bryozoa may be explained by the characteristics of the organic matter consumed by suspension feeders. Indeed, suspension feeders such as sponges or bivalves rely on fine slowly sinking or resuspended organic matter (Gutt, 2007; Mintenbeck et al., 2007) and therefore depend on small particles resulting from the fragmentation and degradation of larger phytodetritus. Consequently, high $\delta^{15}N$ values may be expected in the organic matter consumed by suspension feeders (Saino and Hattori, 1980; Wada, 1980), and then in the suspension feeders (Mintenbeck et al., 2007) and finally in their predators. The particularly high $\delta^{15}N$ values in sponges may also be linked to bacterial

symbiosome (Mintenbeck et al., 2007) and may further contribute to induce higher $\delta^{15}N$ values in the predators of encrusting prey.

Despite having different feeding behaviours, pelagos-based omnivores and sediment feeders had similar $\delta^{13}C$ values, that were higher than those of predators of encrusting prey and suspension feeders. Pelagos-based omnivores had $\delta^{15}N$ values similar to those of suspension feeders, suggesting that they feed on prey with similar trophic position. Indeed, pelagos-based omnivores feed on suspension feeding sponges or bivalves, but are hypothesised to also consume suspended matter (Dearborn, 1977; Brueggeman, 1998; chapter 5). Consequently, it would have been expected that they have $\delta^{13}C$ values similar to those of predators of encrusting prey and suspension-feeders. A higher proportion of individuals sampled in the 0-100 m bathome (17.8 %) may contribute to the higher $\delta^{13}C$ values in pelagos-based omnivores. Furthermore, high PSD_{CB} (mode higher than 2.0 ‰) were recorded for this trophic group, showing a high diversity of relative average $\delta^{13}C$ values between taxa. This may indicate that several taxa may preferentially rely on benthic or sympagic food sources in several locations. The pelagos-based omnivores also had high PSD_{NB} (mode higher than 2.0 ‰), meaning a high diversity of relative average $\delta^{15}N$ values between taxa. The different $\delta^{15}N$ values between taxa may be the result of the contrasted amount of basal organic matter or of other organisms in their omnivore diet. It may also indicate reliance on organic matter at different states of degradation. Finally, it may indicate the preferential consumption of sponges in several taxa since sponges are characterised by higher $\delta^{15}N$ values than other suspension feeding taxa (Mintenbeck et al., 2007). Indeed, the pelagos-based omnivore trophic group contains 2 taxa from the genus *Henricia*, recorded to feed on sponges (Mauzey et al., 1968; Sheild and Witman, 1993), and 8 taxa from the genus *Notasterias*, reported to feed on bivalves but not on sponges (Dearborn, 1977; Brueggeman, 1998). The combination of high PSD_{CB} and high PSD_{NB} in the pelagos-based omnivores resulted in high SEA_B for this trophic group which is therefore relatively trophically diverse.

Sediment feeders ingest sediment containing organic matter. This organic matter may come from local benthic primary production in shallow areas but more likely from pelagic and sea surface primary production (including from the sea ice microbial community). The variability of $\delta^{13}C$ values in their tissues may indicate variability of primary production sources but also of the degradation state of this matter. Indeed, degradation processes may affect $\delta^{13}C$ values of organic matter (Savoye et al., 2003). Similarly to suspension feeders and predators of sessile prey, a low proportion of sediment feeders were collected in the 0-100 m bathome (4.6 %). Consequently, their

higher $\delta^{13}C$ values may indicate reliance on more degraded organic matter. A low PSD_{CB} (mode lower than 0.5 ‰) was recorded in sediment feeders. Sediment feeders also had $\delta^{15}N$ values similar to those of suspension feeders, which may indicate reliance on the fine and degraded fraction of organic matter for both trophic groups. However, high PSD_{NB} values were recorded for sediment feeders (mode higher than 2.0 ‰), suggesting high variations of relative $\delta^{15}N$ values between taxa. High variations of relative $\delta^{15}N$ values may indicate variability of the degradation state of the organic matter retrieved from ingested sediment (Saino and Hattori, 1980; Wada, 1980) with several taxa being able to select non-degraded organic matter. In particular, deep sea sediment feeders may assimilate heterotrophic bacterias living in the sediment (Howell et al., 2003). Differences of $\delta^{15}N$ values between sediment feeder taxa may also indicate differences of the importance of the organic matter or of the infaunal organisms between taxa, and thus differences of trophic level. Indeed, previous studies have shown that sediment feeder sea stars may ingest bulk sediment in order to consume its organic matter (Howell et al., 2003; 2004) and/or its infauna (Howell et al., 2003; Gale et al., 2013).

Like the pelagos-based omnivores, predators of sessile prey had higher $\delta^{13}C$ values than predators of encrusting prey and suspension feeders despite their feeding on sessile organisms (Dayton et al., 1974). A higher proportion of predators of sessile prey sampled in the 0-100 m bathome (22.0 %) may explain the difference of $\delta^{13}C$ values between predators of sessile and of encrusting prey. Furthermore, like the pelagos-based omnivores, predators of sessile prey have also a high PSD_{CB} (mode higher than 2.0 ‰), indicating high variability of relative $\delta^{13}C$ values between taxa of this trophic group, i.e. preferential reliance on pelagic, benthic or sympagic food sources for several taxa in several locations. Predators of sessile prey had the second highest $\delta^{15}N$ values after those of predators of encrusting prey. Taxa included in this trophic group are mostly sessile sponge consumers (Dayton et al., 1974), which may explain their high $\delta^{15}N$ values as Antarctic sponges have higher $\delta^{15}N$ values than other suspension feeding taxa (Mintenbeck et al., 2007).

Predators of active prey and omnivores had the highest $\delta^{13}C$ values. High proportions of individuals were sampled in the 0-100 m bathome (28.0 % for predators of active prey and 52.7 % for omnivores), which may explain their high mean $\delta^{13}C$ values. High PSD_{CB} for predators of active prey (mode higher than 2.0 ‰) may indicate preferential reliance on pelagic, benthic or sympagic food sources for several taxa in several locations. $\delta^{15}N$ values of predators of active prey were higher than those of omnivores, in agreement with their higher trophic positions. The inclusion of organic matter or unicellular organisms in the diet of omnivores (Pearse, 1965; Dearborn, 1977;

Michel et al., 2019) can explain that they have a lower trophic level than predators of active prey. However, high PSD_{NB} for omnivores (mode higher than 2.5 ‰), like for the pelagos-based omnivores, may result from a different importances between these taxa of basal organic matter and of other organisms, and reliance on organic matter at different state of degradation.

$\delta^{34}S$ values differed slightly between trophic groups and were close to the $\delta^{34}S$ values of seawater sulfates (Fry et al., 1982). This suggests that sulfates from the surface photosynthetic zone are likely the main source of nutrients for the primary producers at the baseline of the food webs exploited by all trophic groups. The PSD_{SB} was similar for all trophic groups, meaning that none of the trophic groups were characterised by higher or lower differences of $\delta^{34}S$ values between taxa.

6.4.3 Environmental drivers of the trophic ecology of sea stars

6.4.3.1 Influence of depth on the trophic ecology of sea stars

Depth appeared to influence stable isotope values and their variability in sea stars from the Southern Ocean. The characteristics and the diversity of food sources supporting benthic food webs may explain this effect of the depth. Indeed, $\delta^{13}C$ values decreased with depth for all trophic groups, except for pelagos-based omnivores. The link between depth and $\delta^{13}C$ values also appeared to explain most of the variability of stable isotope data between and within ecoregions, except in South Georgia, where a small range of depths was sampled and no sea stars were sampled in the coastal and/or shallow environment. Similarly, ecoregions where a significant number of sea stars were collected in the coastal and/or shallow environment had higher $\delta^{13}C$ values. Furthermore, the highest PSD_{CB} was observed between 0 and 100 m. Below 100 m, PSD_{CB} was lower, even if the 500-1000 and 1500-2000 m depths had only slightly lower PSD_{CB} values than the 0-100 m bathome, meaning that the variability of $\delta^{13}C$ values between taxa decreased from shallow to deeper waters. Changes of $\delta^{15}N$ values with depth depended on the trophic group but the PSD_{NB} continuously increased with depth, with the lowest PSD_{NB} being observed between 0 and 100 m, indicating that the variability of $\delta^{15}N$ values between sea star taxa increased with depth.

Studies on the food web functioning of coastal Antarctic have shown that these communities are supported by a wide range of primary carbon sources, including pelagic production (Zenteno et al., 2019) and detritus (Dunton, 2001), but also local production of micro (Gillies et al., 2012) and macrophytobenthos (Dunton, 2001; Gillies et al., 2012; Zenteno et al., 2019). The sea ice microbial community may also be an important food source (Norkko et al., 2007; Rossi et al., 2019) especially in case of sea ice persistence (Wing et al., 2012; 2018; Michel et al., 2019). Micro and

macrophytobenthos and the sea ice microbial community have usually higher $\delta^{13}C$ values than the pelagic production (Gillies et al. 2012; 2013; Michel et al., 2019; Zenteno et al., 2019) in accordance with the discrimination of pelagic (lower $\delta^{13}C$ values) and benthic primary producers (higher $\delta^{13}C$ values) usually observed in $\delta^{13}C$ values (France, 1995). Similarly, studies on the coastal Subantarctic food webs suggest that these communities are supported by at least two food sources, i.e. benthic organic matter from both macrophytobenthos and sediment (Andrade et al., 2016; Riccialdelli et al., 2017), or pelagic organic matter and phytobenthos (Kaehler et al., 2000; chapter 4). The food sources are consumed by specific feeding guilds while higher trophic level organisms feed on a mix of these feeding guilds (Gillies et al., 2012; 2013; Zenteno et al., 2019). In sea stars, this phenomenon may be highlighted by several species from Windmill Islands having intermediate $\delta^{13}C$ values between the food sources with highest and lowest $\delta^{13}C$ values (Gillies et al., 2012). However, in the same study, two other species were characterised by higher $\delta^{13}C$ values (Gillies et al., 2012), suggesting a preferential exploitation of one of the food sources for several species and thus potentially inducing higher variability of $\delta^{13}C$ values between species. Consequently, in coastal areas, the inclusion of both pelagic production and local benthic primary production, and possibly of the sea ice microbial community, as food sources in the food web, may induce higher and more variable $\delta^{13}C$ values in the organisms, and thus in sea stars. Furthermore, the high diversity and availability of food sources would promote trophic redundancy with limited competition risks (Costa-Pereira et al., 2019) between benthic organisms, and thus sea star taxa, in coastal and shallow water environments. As a result, sea star taxa may have similar trophic levels in coastal areas. That would explain the low variability of $\delta^{15}N$ values between sea star taxa in coastal communities. Furthermore, the high productivity and resource availability in coastal ecosystems may also promote omnivore diet and shorter food chains (Ward and McCann, 2017; Doi and Hillebrand, 2019). In particular, the higher resource diversity or abundance in coastal Antarctic communities may promote the existence of the trophic continuums observed in these communities (Gillies et al., 2012; 2013), or the reduction of the trophic level of benthic organisms by consuming directly primary producers (Michel et al., 2019; Rossi et al., 2019). In particular, the abundant omnivore sea stars such as *Odontaster validus* and *Diplasterias brucei* may feed directly on sea ice-derived particles when they are available in abundance (Michel et al., 2019).

By contrast, continental shelves and deeper marine food webs from the worldwide ocean are usually only supported by surface-derived primary production sinking to the bottom, which is either consumed directly or as detritus (Le Loc'h et al., 2008; Gontikaki et al., 2011; Valls et al., 2014).

Export of the oceanic surface production to the bottom is generally low worldwide (< 5-10 %) but can reach 10 % in Antarctic (Buesseler, 1998; Buesseler et al., 2010). The export of the surface production in Antarctic is seasonally driven, alternating periods of minimum particle fluxes during periods of sea ice cover and those of maximum particles fluxes following sea ice melting and phytoplankton blooms (Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015). These particles are either pelagic producers sedimenting directly or being exported to the bottom in the faecal pellets of grazing zooplankton and krill (Abelmann and Gersonde, 1991). Important particle fluxes may result in the accumulation of thick phytodetritus layers on the seabed in areas with low current speed (Gutt et al., 1998; Mincks et al., 2005; Smith et al., 2012), and these detritus may be selected as the main source of organic matter for the benthic deposit feeders of the Antarctic continental shelf (Moens et al., 2007; Mincks et al., 2008; Purinton et al., 2008; Würzberg et al., 2011). The decrease of $\delta^{13}C$ values and of their variability in sea stars from the deeper Southern Ocean in comparison to shallower or more coastal areas may thus emphasise the transition from food webs supported by a mixture of benthic and pelagic food sources to food webs supported by sinking pelagic production only. However, the pelagos-based omnivore sea stars may already specialise on the pelagic food sources in coastal areas as their $\delta^{13}C$ values increased with depth instead of decreasing. The importance of particle fluxes decreases with depth (Berelson, 2001; Suzuki et al., 2001) and the availability of the pelagic production exported from the surface may then become more limited in deeper environments. More limited resource availability would promote trophic segregation (Barger and Kitaysky, 2012; Juncos et al., 2015) between sea star taxa to avoid competition, and thus a higher diversity of trophic levels. This higher diversity of trophic levels would then explain the higher diversity of $\delta^{15}N$ values between sea star taxa in deeper environments. However, this higher diversity of $\delta^{15}N$ values in sea stars from deeper environments may also result from a better segregation of the suspension and deposit feeder food chains.

Degradation processes in sedimenting or deposited organic matter would result in an increase with depth of $\delta^{15}N$ values in the organic matter (Saino and Hattori, 1980; Wada, 1980), and thus in an increase of $\delta^{15}N$ values of its consumers. Yet, mean $\delta^{15}N$ values in sea stars did not linearly change with depth. Instead, the effect of depth on $\delta^{15}N$ values differed among trophic groups.

$\delta^{15}N$ values decreased with depth in predators of active prey, sediment feeders and predators of encrusting prey. This may indicate a decrease of their mean trophic levels. Conversely, the absence of increase of $\delta^{15}N$ values with depth suggests that these trophic groups are not supported by degraded organic matter in deeper environments whose $\delta^{15}N$ values generally increase compared to

fresh detritus. Instead, these trophic groups may rely on food webs whose primary consumers are able to select the least degraded organic matter. Indeed, the deposit feeding organisms associated with soft bottoms on the Antarctic continental shelf are able to select organic matter deposited at the bottom, according to their nutritive quality. Selection of freshly deposited phytodetritus was observed in several mobile deposit feeding taxa (Suhr et al., 2003; Moens et al., 2007; Purinton et al., 2008; Würzberg et al., 2011) and fresh phytodetritus appeared as one of the main food sources for deep benthic food webs of the WAP continental shelf (Mincks et al., 2008). Consumption of fresh and poorly degraded phytodetritus would thus not induce strong increases of $\delta^{15}N$ values with depth in mobile deposit feeders (Mintenbeck et al., 2007), including sea stars, and their predators, such as predatory sea stars targeting active prey. Formation of cell aggregates or inclusion of phytoplankton into fast sinking faecal pellets (Abelmann and Gersonde, 1991; Belcher et al., 2017) would induce higher and faster sinking rates of phytoplankton cells during summer blooms. Higher quantities of fresh materials could then reach the bottom and be available for the benthos, as suggested by the higher particle fluxes to the bottom during summer (Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015) or differences of $\delta^{15}N$ values between surface plankton and sediment trap materials occurring only in winter (Mincks et al., 2008). The seasonality of particle fluxes would suggest that the consumption of fresh phytodetritus by the mobile deposit feeding benthos from the continental shelf is a seasonal phenomenon. However, consumption of freshly deposited phytodetritus by the benthos of the Antarctic continental shelf is actually a year-round phenomenon (Mincks et al., 2008; Purinton et al., 2008), thanks to the limited degradation of organic matter in the Antarctic continental shelf due to low water temperatures (Mincks et al., 2005; Smith et al., 2012).

$\delta^{15}N$ values increased with depth in trophic groups known to be supported by resuspended matter, i.e. the suspension feeders, the predators of sessile prey feeding on suspension feeders such as sponges, and the pelagos-based omnivores feeding on both suspended matter and sessile prey. $\delta^{15}N$ values also increased more slightly with depth in omnivores. Contrary to mobile deposit feeders, sessile suspension feeders such as sponges or bivalves rely on fine slowly sinking or resuspended organic matter (Gutt, 2007; Mintenbeck et al., 2007) and therefore depend on small particles resulting from the fragmentation and degradation of larger phytodetritus. Consequently, increasing of $\delta^{15}N$ values with depth in the organic matter they consume may be expected and would thus explain the increasing $\delta^{15}N$ values observed with depth in suspension feeders, including sea stars (Mintenbeck et al., 2007), but also in their predators such as sea star species consuming

sponges. Consequently, the increase of $\delta^{15}N$ values with depth in the organisms relying on the suspension feeder communities and its stability in the organisms relying on the deposit feeder communities may further contribute to the higher diversity of $\delta^{15}N$ values in deeper waters. The slight increase with depth of $\delta^{15}N$ values in omnivores may also suggest a higher contribution of degraded phytodetritus to their trophic ecology, because of a less selective feeding behaviour. It may also indicate an increase of trophic level with the limitation of resource availability in deeper environments promoting carnivore diet.

There was no effect of depth and a negligible effect of the interaction between depth and trophic group on $\delta^{34}S$ values. Furthermore, $\delta^{34}S$ values were close to the $\delta^{34}S$ values of seawater sulfates (Fry et al., 1982). Consequently, sulfates from the surface photosynthetic zone still remain the main source of nutrients for primary producers at the base of the food web, and the absence of effect of depth on $\delta^{34}S$ values further illustrates the dependence of the benthos of the continental shelf and deep-sea environment on the surface pelagic production in the Southern Ocean.

6.4.3.2 Influence of sea ice concentration on the trophic ecology of sea stars

Photosynthetic organisms from the sea ice habitat have higher $\delta^{13}C$ values than phytoplankton (Rau et al., 1991a; Leventer, 2003; Mincks et al., 2008; Wing et al., 2018; Michel et al., 2019). Variation of sea star $\delta^{13}C$ values with sea ice concentration and ice season duration may thus provide an indication of the inclusion of fresh ice-derived materials among the food sources of the food webs exploited by sea stars. After taking into account the differences between Subantarctic and Antarctic environments and the influence of other environmental parameters on stable isotope values, $\delta^{13}C$ values actually increased with sea ice concentration. However, this increase is slow. Furthermore, the link between sea ice concentration and $\delta^{13}C$ values appeared in Oates and Weddell Sea, where sea ice concentration values could reach 90 % at most, but not in Antarctic Peninsula, where sea ice concentration was 36 % at a maximum, indicating that the increase of $\delta^{13}C$ values likely resulted from the stations with the highest values of sea ice concentrations.

Contrasting effects of sea ice on benthic food web functioning were observed in coastal areas. Ice-derived materials are either a secondary (Gillies et al., 2012; 2013) or major food source (Norkko et al., 2007; Wing et al., 2012; 2018; Michel et al., 2019; Rossi et al., 2019). In particular, coastal sea stars were observed to feed directly on ice-derived materials in case of sea ice persistence (Michel et al., 2019). Consequently, ice-derived materials may be one of the carbon sources supporting shallow water sea stars and food webs. However, more limited studies are

available regarding the use of sea ice-derived materials as a food source by the benthos of the continental shelf.

The interaction between depth and sea ice concentration influenced $\delta^{13}C$ values, with the increase of $\delta^{13}C$ values with sea ice concentration being less important in the 0-100 m bathome than in the deeper 200-500 and 500-1000 m. In particular, sea stars sampled in the Weddell Sea between 500 and 1000 m in areas with high sea ice concentrations may have $\delta^{13}C$ values higher than –18.5 ‰ and, for several individuals, even higher than –15 ‰. Such high $\delta^{13}C$ values in offshore areas cannot be explained by the integration of phytoplankton with very low $\delta^{13}C$ values. Consequently, the high $\delta^{13}C$ values in sea star tissues from areas of the continental shelf with high sea ice concentration are likely the result of the integration of isotopic signatures from the sea ice microbial community. Similarly, the increase of $\delta^{13}C$ values with sea ice concentration occurred in sea stars from the Weddell Sea, that were mostly sampled below 200 m and where maximum concentrations of sea ice were sampled. These results indicate that the sea ice microbial community is potentially a resource for sea stars and their associated food webs on the Antarctic continental shelf. Potential use of sea ice-derived particles as a food source by nematodes has been highlighted in several sites of the continental shelf of Weddell Sea (Moens et al., 2007). Furthermore, sediment trap studies showed that sea ice materials may be an important contributor to the total mass of materials exported to the bottom in several locations (Kim et al., 2019; Abelman and Gersonde, 1991).

No major change of SEA_B, PSD_{CB} and PSD_{NB} values occurred between sea ice concentration intervals. In particular, sea ice did not induce higher or lower variability of $\delta^{13}C$ values, which indicates that sea stars are still supported by a same diversity of food sources even if there is a high sea ice concentration. Furthermore, $\delta^{13}C$ values did not increase with sea ice concentration in the predators of sessile prey and sediment feeders, as well in the suspension feeders but this was because of the low range of sea ice concentration values being available for this trophic group. Sea ice may prevent light transmission to the water column and/or shallow water bottoms and thus inhibits the growth of phytoplankton and phytobenthos if it persists (Hegseth and Von Quillfeldt, 2002; Clark et al., 2015). As a result, the sea ice microbial community is expected to become the main food source for sea stars, and thus for the benthic communities, if other food sources are reduced because of a too high concentration of sea ice. However, several benthic taxa were observed to still rely on other food sources, such as POM or phytobenthos in locations where sea ice persists (Michel et al., 2019). In particular, resuspended and horizontally transported POM contribute to the presence of suspension feeder communities under ice-covered areas (Gutt et al.,

2011; Jansen et al., 2018) and may thus contribute to maintain trophic diversity in these areas. Consumption of sponges that feed on resuspended organic matter may then explain the particularly low $\delta^{13}C$ values observed in predators of sessile prey from a coastal station with high sea ice concentration from the Oates ecoregion as this trophic group includes mostly taxa consuming suspension feeding sponges (Dayton et al., 1974). These low $\delta^{13}C$ values may then explain the absence of a relationship between sea ice concentration and $\delta^{13}C$ values in the predators of sessile prey. Furthermore, the photosynthetic biomass in sea ice has a patchy distribution influenced by other parameters than sea ice concentration, such as snow depth over the ice, sea ice thickness and sea ice freeboard levels (Meiners et al., 2017). Similarly, limited particle fluxes usually occur during periods of ice cover (Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015), suggesting limited availability of the surface production for the benthos in case of high sea ice cover. Consequently, the sea ice microbial community may not be available in high quantity for benthic organisms even in case of high sea ice concentration, resulting in the reliance on alternative food sources for several taxa in several locations. This may occur in the sediment feeders that were collected under 84 % of sea ice concentrations, whose $\delta^{13}C$ values reached –23.2 ± 1.0 ‰. Furthermore, these individuals were collected at more than 5000 m and may thus not receive sufficient sea ice materials from the surface, resulting in the low $\delta^{13}C$ values of these individuals and the absence of a relationship between $\delta^{13}C$ values and sea ice concentration in sediment feeders. Investigations of trophic diversity in benthic food webs in relation with sympagic biomass instead of sea ice concentration would provide more information on the impact of sea ice on trophic diversity.

$\delta^{34}S$ values slightly decrease with sea ice concentration. $\delta^{34}S$ values from the sea ice microbial community have rarely been investigated but Michel et al. (2019) reported an average value of 5.6 ± 2.7 ‰ in Terre Adélie. $\delta^{34}S$ values reported in sea stars are way above the $\delta^{34}S$ values reported by Michel et al. (2019) in sympagic organisms. Furthermore, no consistent pattern appeared when investigating the relationship between $\delta^{34}S$ values and sea ice concentration in Antarctic Peninsula, Oates or Weddell Sea, indicating that sea ice concentration may actually have a limited impact on $\delta^{34}S$ values.

6.4.3.3 Influence of sea ice dynamics on the trophic ecology of sea stars

The impact of the sea ice season duration on stable isotope values may have been modulated by those of the other covariates and of the trophic groups factor. Nevertheless, the sea ice season

duration, as well as its interaction with depth, did not appear to influence stable isotope values. In particular, high $\delta^{13}C$ values that may indicate the integration of isotopic signatures from the sea ice microbial community were recorded for several low or intermediate values of sea ice season duration. When analysing the relationship between $\delta^{13}C$ values and sea ice season duration within ecoregions, increasing $\delta^{13}C$ values with sea ice season duration were observed in Weddell Sea only, where sea stars sampled in zones where sea ice lasts more than 85 % of the year have $\delta^{13}C$ values that may be close or higher than –15 ‰. However, no increase of $\delta^{13}C$ values with sea ice season duration occurred in the bathome corresponding to these samples. Consequently, the sea ice season duration does not appear as a good predictor of the reliance on the sea ice microbial community by sea stars. The reliance on the sea ice microbial community that may be observed at low or intermediate values of sea ice season duration likely results from the sampling of sea stars specifically during or following the sea ice season when the sea ice microbial community may be more available and thus be consumed by the benthos.

$\delta^{15}N$ values seemed to increase with sea ice season duration. On the whole, the effect of sea ice season duration on $\delta^{15}N$ values was only marginally significant but the increase actually occurred in four of the seven identified trophic groups. Higher $\delta^{15}N$ values with longer sea ice season duration may indicate that sea stars from areas with long sea ice season duration have higher trophic levels than those from areas with a shorter one. Conversely, sea stars may rely on communities that supported by more degraded phytodetritus in areas with long sea ice season duration, the high $\delta^{15}N$ values then resulting from the degradation processes in the basal organic matter (Saino and Hattori, 1980; Wada, 1980).

Like for sea ice concentration, no consistent or meaningful change of SEA_B, PSD_{CB} and PSD_{NB} occurred between sea ice season duration intervals. Sea ice season duration also did not impact $\delta^{34}S$ values. PSD_{CB}, and thus the variability of $\delta^{34}S$ values between taxa, became higher when the sea ice season duration lasts more than 40 % of the year.

Sea ice dynamics may have a more indirect impact on the trophic ecology of sea stars. Sea ice dynamics influence the importance of particle fluxes in the Southern Ocean. Minimal fluxes during periods of pack ice cover (Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015) imply that the release of the sea ice microbial community and its massive sedimentation to the bottom likely occur only during the sea ice break up. During periods of minimal fluxes, more limited resource availability induced by long sea ice presence may promote predatory behaviours, resulting in higher mean trophic levels in organisms sampled in persistently ice-covered areas (Wing et al., 2012) or

during periods of ice cover (Rossi et al., 2019). Conversely, the communities from persistently ice-covered areas may rely on more degraded phytodetritus to dampen the impacts of sea ice persistence on the resource availability (Norkko et al., 2007).

Increasing particle fluxes occur following sea ice break up (Thomas et al., 2001; Kim et al., 2019). The sea ice microbial community is estimated to account for 2 to 24 % of the annual primary production in the areas of the Southern Ocean covered by ice at least a part of the year, but there are spatial and seasonal variations of production (Meiners et al., 2012; 2017; Arrigo, 2017). Most of ice-derived materials thus become an important component of the sinking particles during sea ice break up, resulting in brief increases of $\delta^{13}C$ values in sinking particles (Bathmann et al., 1991; Henley et al., 2012). In coastal areas, this results in sea ice-derived materials becoming available for the benthos and inducing an increase of their $\delta^{13}C$ values (Rossi et al., 2019). However, continuous sinking of the sea ice-derived materials may also occur when high biomass is available following sea ice persistence, as highlighted by the consumption by the benthos of sea ice derived materials despite the lack of sea ice break up (Michel et al., 2019) and as suggested by the high $\delta^{13}C$ values recorded in sea stars sampled in areas with high sea ice concentration and season duration. Furthermore, the transient or persistent high availability of sea ice-derived materials induces a simplification of coastal benthic food webs, with reduction of the mean trophic level (Michel et al., 2019), of intraguild predation and of competition (Rossi et al., 2019).

Following the release of ice-derived materials, the sea ice break up then induces the summer phytoplankton blooms (Garibotti et al., 2005; Rozema et al., 2017), resulting in decreasing $\delta^{13}C$ values in POM (Bathman et al., 2011; Henley et al., 2012) and an important and more continuous flux of sinking particles (Fischer et al., 1988; Honjo et al., 2000) that become the main resource for benthic organisms from the continental shelf (Mincks et al., 2008). However, almost perennial sea ice season may prevent or reduce phytoplankton blooms (Hegseth and Von Quillfeldt, 2002; Mendes et al., 2013), resulting in the particle fluxes to the seabed to occur during partial melting events and to be mostly composed by the sea ice microbial community throughout the year (Kim et al., 2019). Consequently, sea ice primary production may support the benthic organisms from the continental shelf or of the deep sea in areas where the surface has an almost perennial sea ice cover, which would explain the high $\delta^{13}C$ values recorded in sea stars sampled in these areas.

6.4.4 Biogeographic variations of the trophic ecology of sea stars: differentiation between Subantarctic and Antarctic sea stars

The investigation of the relationship between stable isotope values and environmental parameters with PCAs showed that sea stars from the Subantarctic ecoregions had higher $\delta^{13}C$ values than those from the Antarctic ones. Sea stars from Subantarctic continental shelves or deep sea likely depend on sinking pelagic particles, as dependence of deep benthic communities on the surface primary production is a worldwide phenomenon (Le Loc'h et al., 2008; Gontikaki et al., 2011; Valls et al., 2014). Consequently, differences of $\delta^{13}C$ values between Subantarctic and Antarctic sea stars may reflect different primary production properties at the surface of the ocean. Actually, a southward decrease of $\delta^{13}C$ values in surface POM occurs from Subantarctic to Antarctic waters (Rau et al., 1991b; Francois et al., 1993; Espinasse et al., 2019). Higher availability of dissolved carbon dioxide (CO_2) in Antarctic waters, induced by higher CO_2 solubility at lower temperatures, and its utilisation by photosynthetic organisms with a low growth rate is a mechanism that may explain the lower $\delta^{13}C$ values of POM in the Antarctic waters (Rau et al., 1991b; Francois et al., 1993) and then in Antarctic sea stars.

Sea stars from the Antarctic Peninsula appeared to have high $\delta^{13}C$ values, similar to those of Subantarctic ones. However, this similarity is partly explained by the sampling of a high number of sea stars with high $\delta^{13}C$ values in the coastal and enclosed Ezcurra Inlet, in Admiralty Bay. It is also explained by local reliance on the sea ice microbial community for sea stars sampled in the inner Marguerite Bay, where the maximum sea ice concentration values were sampled in this ecoregion, resulting in high $\delta^{13}C$ values in these sea stars despite being sampled in deep water (between 180 and 591 m). The high $\delta^{13}C$ values in the coastal ice-free Ezcurra Inlet and in the inner Marguerite Bay in Antarctic Peninsula also explain the absence of relationship between $\delta^{13}C$ values and sea ice concentration in this ecoregion.

6.4.5 Conclusions

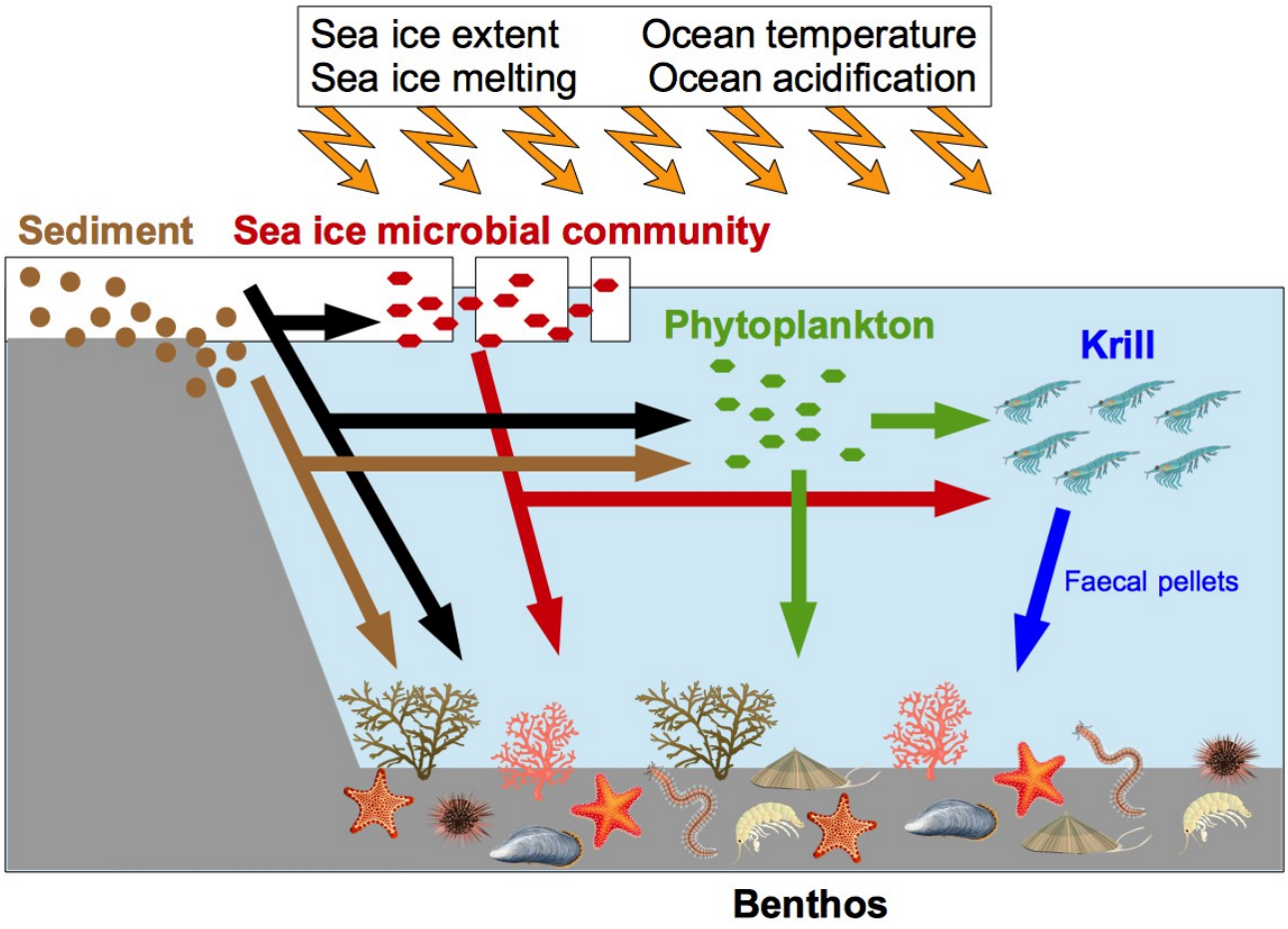
Depth had a major effect on $\delta^{13}C$ values and their variability, both at the scale of the whole Southern Ocean and within its ecoregions, highlighting the transition from sea star assemblages supported by a mixture of local benthic, sympagic and pelagic primary production in coastal and/or shallow water areas, to sea stars mostly supported by the sinking pelagic production on continental shelves and deeper areas. Furthermore, the increasing variation of $\delta^{15}N$ values between sea star species with depth highlighted the increasing diversity of trophic levels and thus of feeding

strategies of sea stars in deeper areas.

A significant but weak effect of sea ice concentration on $\delta^{13}C$ values was observed. Particularly high $\delta^{13}C$ values were recorded in sea stars sampled in areas of the deep continental shelf where high sea ice concentration were present and long sea ice season duration occur. These results indicate that the sea ice microbial community may be a food source for Antarctic sea stars, even in deep waters. $\delta^{15}N$ values increased with sea ice season duration for several trophic groups, which may indicate their increasing reliance on degraded phytodetritus during longer periods of sea ice cover to dampen the impacts of sea ice presence on resource availability.

$\delta^{13}C$ values of sea stars differed between ecoregions. In particular, the differences of $\delta^{13}C$ values between surface POM from Subantarctic and Antarctic waters were reflected in $\delta^{13}C$ values of benthic sea stars, notably in South Georgia where no sea stars were sampled in coastal and/or shallow waters. Consequently, this result further emphasises the importance of pelagic production for deeper sea stars, and thus for deeper benthic food webs.

Chapter 7: General discussion



Environmental conditions impacting the benthos in the Southern Ocean.

This thesis is part of the vERSO (Ecosystem Responses to global change: a multiscale approach in the Southern Ocean; BR/132/A1/vERSO) and RECTO (Refugia and Ecosystem Tolerance in the Southern Ocean; BR/154/A1/RECTO) projects funded by the Belgian Science Policy Office (BELSPO). The goals of these projects were to assess the impact of environmental modifications induced by climate change on benthic Antarctic ecosystems and the adaptive capacities of key benthic taxa to cope with these environmental changes. Both projects included a component on the study of sea stars from the Southern Ocean to assess their diversity and origin, the impact of their reproductive strategy (brooding *versus* broadcasting) on their distribution (Moreau, 2019), their trophic role in ecosystems and the impacts of environmental features on their trophic ecology to estimate how their modifications may impact sea stars in the context of climate change (this thesis).

Sea stars, or asteroids, are an important group of the Southern Ocean benthos in terms of diversity (235 species, i.e. around 12 % of all known sea star species, Danis et al., 2014), abundance and biomass (Gerdes et al., 1992; Pabis et al., 2011) and ecology (Dayton et al., 1974). The knowledge on the qualitative diet of sea stars, mostly based on scattered observations (Jangoux, 1982; Dearborn, 1977; McClintock, 1994), suggested the existence of diverse feeding behaviours and strategies.

Here, we aimed to investigate the trophic ecology of sea stars, as well as its relationship with environmental features, and to provide new insights on the food web and ecosystem functioning in this region. Ultimately, the interplay between trophic ecology and environmental dynamics may contribute to determine how sea stars and the food webs they exploit could be impacted by future environmental changes linked to climate change.

The results of this thesis show that a combination of intrinsic and environmental factors appeared to be the main drivers of sea star feeding ecology in the Southern Ocean.

7.1 Using sample from archived collections in trophic ecology studies

The work presented in this thesis is the result of the analysis of stable isotope values in 2454 sea star specimens (to which stable isotope values from 204 specimens retrieved from the literature or shared by colleagues were added), sampled over numerous Antarctic and Subantarctic regions. Analysing stable isotope values in such a large number of individuals on a widespread study area has been made possible by using samples from archived institution and museum collections. Consequently, this work shows how such samples may be an interesting cost-effective tool to conduct global trophic ecology investigations in remote locations. More generally, these samples

may represent a readily accessible source of data for food web studies. They can help to fill gaps in the knowledge of the ecology of organisms coming from data-poor regions or ecosystems, or may be used to study the past trophic ecology of organisms if they were collected during periods of more pristine environmental conditions. However, as the preservative fluids may alter stable isotope values, it was necessary to preliminarily assess how the preservation methodology impacts stable isotope values in sea stars to take into account the potential biases of preservation methods in the following studies (chapter 3; Le Bourg et al., 2020).

Future research on large-scale patterns of trophic ecology of organisms and of food web functioning may be eased by the use of archived samples. These studies have to be done in conjunction with continued research on the impacts of preservation methodology on stable isotope values, as some taxa still remain underrepresented (e.g. only one study for sipunculids, several echinoderm taxa not studied, no studies for tunicates) in the abundant literature available on this topic.

7.2 Feeding behaviours of sea stars in the Southern Ocean

7.2.1 Sea star trophic groups in the Southern Ocean

Even if sea stars are usually viewed as generalist predators in marine ecosystems, they can exhibit trophic specialisation and/or dietary preferences and exploit a wide variety of food items through diverse feeding modes (Jangoux, 1982). Here, the compilation of studies using stomach content analyses, field observations (Dearborn, 1977; Jangoux, 1982; McClintock, 1994) and/or other methods (e.g. Howell et al., 2003; 2004; Gale et al., 2013), as well as the studies on sea stars from Kerguelen Island (chapter 4) and Admiralty Bay (chapter 5), allowed to make a preliminary classification of sea star taxa from the Southern Ocean into trophic groups (Table 6.2 in chapter 6), ranging from suspension feeders to predators of large prey. The variability of observed stable isotope values in some of these trophic groups suggested a considerable diversity of food sources and/or of feeding strategies. For example, the variability of $\delta^{15}N$ values between sediment feeding taxa may indicate selectivity on the ingested organic matter depending on sediment characteristics (grain size, degradation state of the organic matter, presence of buried fauna). The variability of $\delta^{15}N$ values between pelagos-based omnivore taxa may reflect preferential consumption of sponges with higher $\delta^{15}N$ values (Mintenbeck et al., 2007) in several taxa when other taxa may preferentially feed on bivalves. Finally, differences of $\delta^{15}N$ values between taxa from the pelagos-based omnivore and the omnivore trophic groups may reflect different relative importance of predatory and/or

scavenging behaviour and more direct consumption of basal organic matter between taxa. All these results show the potential trophic diversity existing between taxa apparently exhibiting similar feeding behaviours in the Southern Ocean.

The differences of trophic ecology between and within sea star taxa may also be subject to variability as the trophic ecology of sea stars likely results from a combination of intrinsic and environmental factors. Consequently, the research effort on individual taxa, with various methods, should be continued to refine the classification of trophic groups. In particular, the trophic ecology of several sea star taxa has not been studied so far and these taxa could thus not be assigned to trophic groups.

7.2.2 What could sea stars not assigned to a trophic group feed on?

When no information on the diet of a sea star taxon was available, its trophic group was assigned according to the known diet of congeners (Table 6.2 in chapter 6). This information may sometimes be limited and, thus, misattribution of a given taxa to a trophic group cannot be excluded. Furthermore, several taxa could not be assigned to a trophic group because no information were available on their diet or that of their congeners. These sea stars represent 16.9 % of the individuals and 22.5 % of the taxa. To include a maximum number of individuals in the data analyses on the impacts of environmental features on the stable isotope values, these taxa were classified in an unknown trophic group.

The method of inferring the trophic group of a taxon according to the diet of its congeners may have limitations as the diet may differ between species in a same genus. For example, *Odontaster meridionalis* is considered a spongivore, and thus was assigned to the predators of sessile prey, while *Odontaster validus* is considered an omnivore (Dearborn, 1977). Similarly, the *Bathybiaster* sp. individual was assigned to the unknown trophic group (Table 6.2 in chapter 6) because of *Bathybiaster loripes* and *Bathybiaster vexillifer* being respectively assigned to sediment feeders (Dearborn, 1977) and predators of active prey (Tyler et al., 1993). Several sea stars were also assigned to the unknown trophic group as a result of their incomplete identification. They include all undetermined taxa but more notably the unidentified Pterasteridae (n = 63, i.e. 14.0 % of the sea stars with an unknown trophic group). Indeed, identified genera in the Pterasteridae family include *Hymenaster* and *Pteraster*, which were included in two different trophic groups, i.e. the omnivores and the predators of encrusting prey respectively. Because the trophic ecology may strongly differ between genera of a same family, the method of inferring the trophic group of a taxa according to

the diet of its congeners should not be further extended by assigning to taxa a trophic group according to the diet of other genera included in the same family. For example, sea stars with an unknown trophic group include taxa from the Goniasteridae family, i.e. the genus *Chitonaster* and the species *Notioceramus anomalus* (n = 85, i.e. 18.9 % of the sea stars with an unknown trophic group). Feeding on deep sea corals has been recorded in 7 Goniasteridae genera (Mah, 2018), which may indicate that *Chitonaster* and *Notioceramus anomalus* are predators of sessile prey. However, two sediment feeding and one predatory genera have also been recorded in this family (Mah, 2016; 2018).

Hypotheses may be formulated on the diet of sea stars according to their morphology and body shape. For example, sturdiness may provide protection against predators and impacts but would reduce flexibility and thus predatory ability (Blake, 1989). High number of arms may be associated to feeding on organisms from the water column (Dearborn et al., 1991; Emson and Young, 1994; Lauerman, 1998; Lawrence, 2012).

The disc size may also be linked to the feeding ecology (chapter 5). Sea stars do no extend their stomach beyond the edge of the disc, and a larger disc therefore allows to extend the stomach over a larger area, resulting in a capacity to feed on larger prey or surface when feeding on biofilms and colonial organisms (Lawrence, 2012; 2013). Furthermore, the ratio between the arm length R and the disc radius r (R/r; Lawrence, 2013; Martinez et al., 2017) may provide preliminary hints on the diet. Sea stars with a large disc and short arms, and thus a small R/r, may consume sediment, biofilms, large or encrusting colonial sessile prey and even display herbivory. Their large disc allows them to extend their stomach over a large area, but they could have reduced dexterity and flexibility, probably because the arms are widened at their base (Blake, 1989; Lawrence, 2012; 2013; Martinez et al., 2017). Comparatively, sea stars with the same arm length than the previous ones but with a smaller disc, and thus a larger R/r, would extend their stomach over a smaller surface. However, their arms may be more flexible (Blake, 1989) for prey manipulation, or for feeding on the water column in multi-armed sea stars (Lawrence, 2012).

Here, predators of encrusting prey had the lowest R/r (2.03 ± 0.71), followed by predators of large sessile prey (3.57 ± 1.36), sediment feeders (4.37 ± 1.40) and omnivores (4.65 ± 3.94). Predators of active prey (6.82 ± 3.90), pelagos-based omnivores (7.66 ± 2.64) and suspension feeders (11.56 ± 12.82) had the highest R/r. The R/r of sea stars with an unknown trophic group (3.74 ± 2.42) was similar to those of predators of sessile prey and those of omnivores (Fig. 7.1).

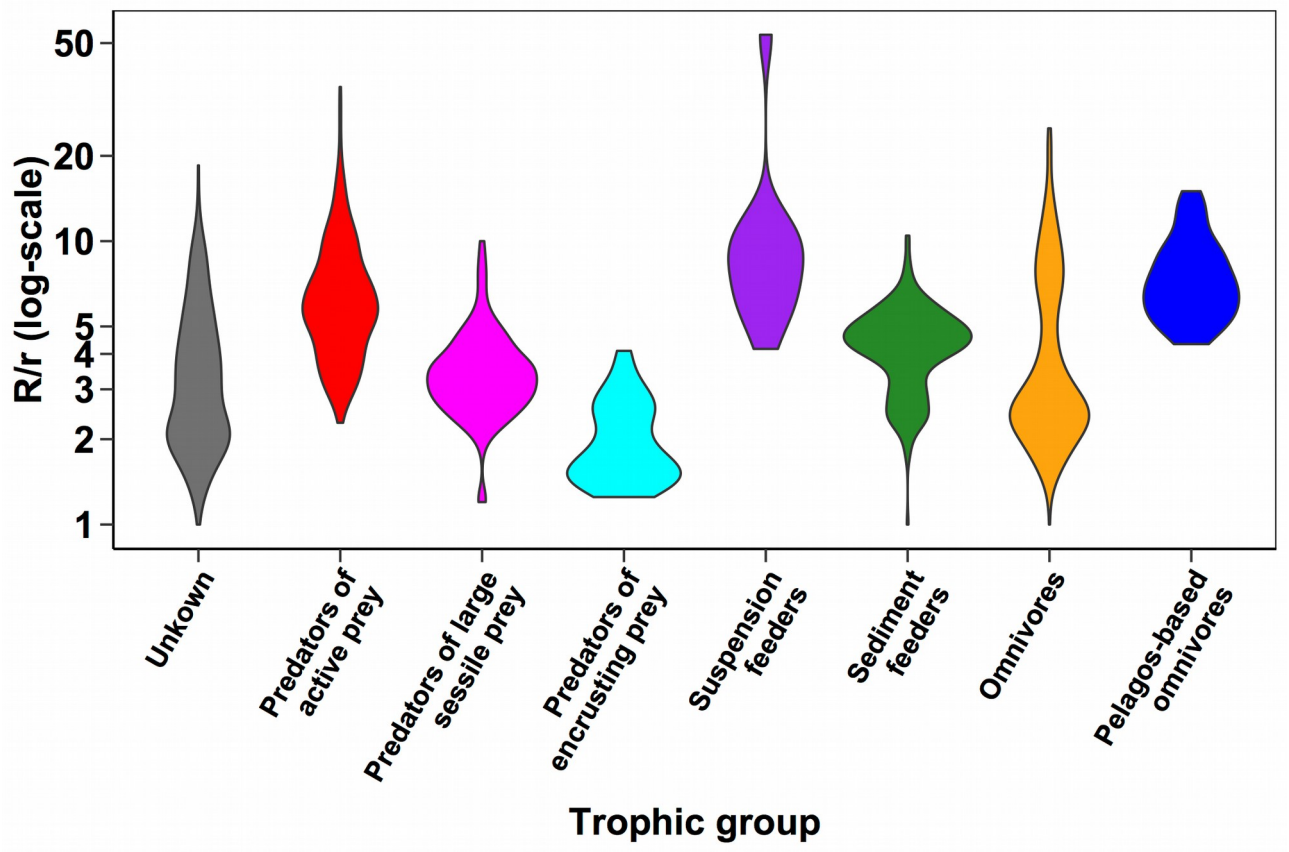


Fig. 7.1. Distribution of arm length R and disc radius r ratios (R/r) in each sea star trophic group.

High variability of the R/r values occurred in the predators of active prey and the omnivores. This could be caused by more imprecise arm length and disc radius measurements in the smallest sea stars, but is more probably linked with inclusion of taxa characterised by different R/r within the same trophic group, as the R/r also depends on the taxa. For example, the omnivores include Odontasteridae with small R/r and Asteriidae with large R/r (Fig. 7.1). The suspension feeders also had a high variability of the R/r because of the extreme value in a single individual of *Freyella attenuata* (R/r = 53.50) in comparison to the mean R/r of *Odinella nutrix* (8.07 ± 2.46; Fig. 7.1). Consequently, caution is necessary when inferring the trophic ecology of sea stars according to their R/r values. Similarly, taxa with no trophic group may have different R/r values, with a minimum of 1.73 ± 0.43 for *Kampylaster incurvatus* and a maximum of 11.00 for *Anteliaster scaber*.

Sea stars with an unknown trophic group include diverse taxa for which no information on the diet was available, and likely comprise taxa from several trophic groups. Nevertheless, their $\delta^{13}C$ values (–20.3 ± 2.7 ‰) were similar to those of sediment feeders (–21.1 ± 2.1 ‰) and pelagos-based omnivores (–20.5 ± 1.9 ‰). Their $\delta^{15}N$ values (12.0 ± 2.0 ‰) were similar to those of the predators of sessile prey (12.1 ± 2.4 ‰, chapter 6). Moreover, it seemed to increase with depth, like for several other groups ultimately depending at least partly on suspended organic matter (suspension feeders, predators of sessile prey, pelagos-based omnivores and omnivores). Their R/r values are similar to those of predators of sessile prey and omnivores. Overall, it seems likely that the sea stars with no known trophic groups include taxa from several, if not all, of the aforementioned trophic groups.

In an effort to assign unknown taxa to one or several trophic groups (Table 7.1), we ran a principal component analysis (PCA) using ecological ($\delta^{13}C$, $\delta^{15}N$) and morphological (R/r values) parameters (Fig. 7.2). Using this PCA, we tried to determine to which trophic group(s) each unknown taxon was the most similar, therefore allowing a preliminary eco-functional classification. This analysis confirmed that most of the taxa were most similar to the predators of sessile prey and omnivores, although they were also to sediment feeders (Fig. 7.2). It also indicated that several taxa may be predators of encrusting prey. However, the Forcipulatida taxa are more likely predators of active prey than of sessile prey, with the exception of *Psalidaster mordax*, that may be a pelagos-based omnivore, or even a suspension feeder, as suggested by its low $\delta^{13}C$ and $\delta^{15}N$ values, and thanks to its large pedicellariae (0.7-0.9 mm length), similar to those of *Notasterias* species, and its multiarmed morphology (11 arms; Fisher, 1940), although the adaptiveness of a number of arms included between 5 and 15 has not yet been demonstrated (Lawrence, 2013).

The PCA thus provided a preliminary assessment of the trophic groups of taxa whose trophic ecology is unknown. However, as previously stated, caution is necessary when inferring the trophic ecology of sea stars according to their R/r values. Actually, $\delta^{13}C$ and $\delta^{15}N$ values are not correlated to R/r and sea star taxa could rarely be assigned to a single trophic group because of several trophic groups having similar $\delta^{13}C$, $\delta^{15}N$ and R/r values (Fig. 7.2; Table 7.1). Identification of food items consumed remains necessary to assign individual taxa to trophic groups.

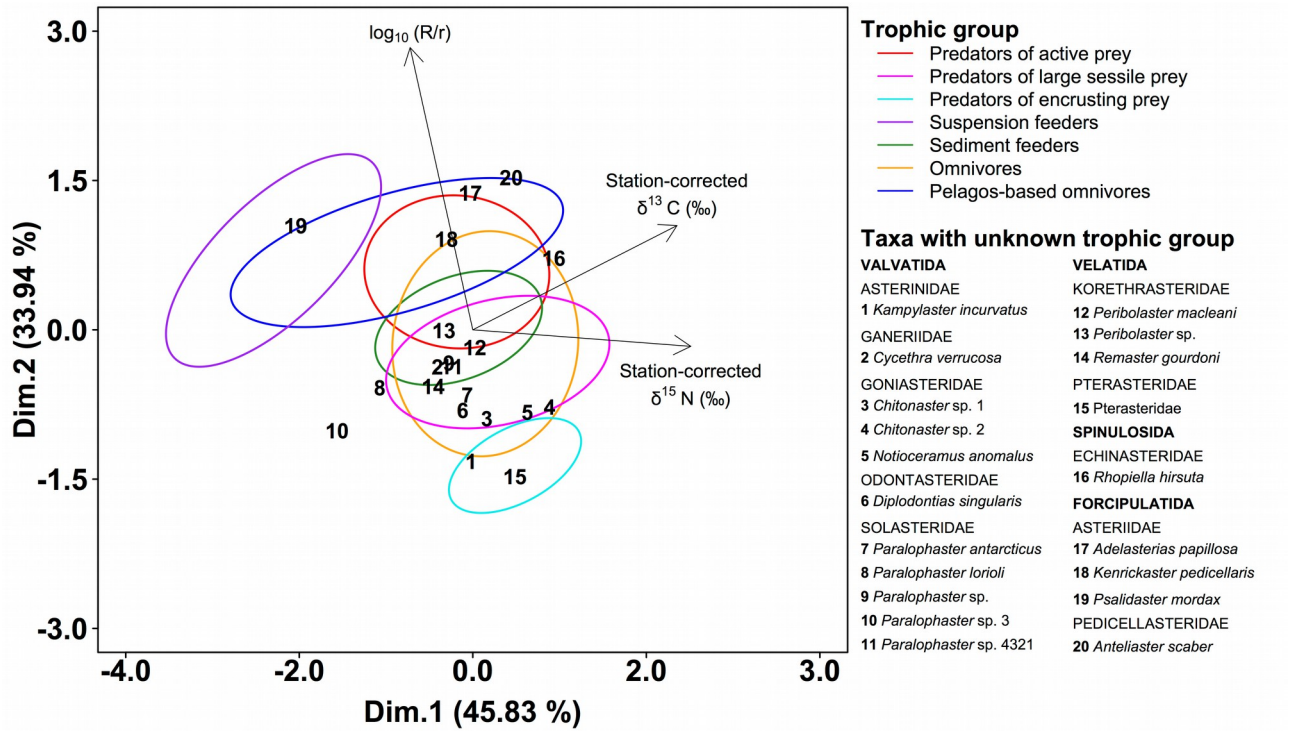


Fig. 7.2. Principal component analysis (PCA) assessing the relationships between station-corrected $\delta^{13}C$ and $\delta^{15}N$ values, and log-transformed R/r values and their variability within identified trophic groups (ellipses). Numbers are identified taxa with no known trophic group (sea stars with no determined taxa are not shown) and their position on the plot are their mean principal component (PC) values. $\delta^{13}C$ and $\delta^{15}N$ values were mean-corrected for each station according to the procedure described in the section 2.4 of the chapter 2 to remove the potential impact of environmental parameters (e.g. depth) or spatial variations of stable isotope values of the primary food sources at the baseline of the food webs.

Table 7.1. Potential trophic groups that may be assigned to taxa with no known trophic group following the principal component analysis (PCA) from the figure 7.2. Most likely trophic groups are trophic groups whose ellipses encompass the mean principal component (PC) values of taxa with no known trophic groups. Other possible trophic groups are trophic groups whose ellipse borders are close to the mean PC values of taxa with no known trophic groups.

Taxa	Most likely trophic groups	Other possible trophic groups	Note
VALVATIDA			
ASTERINIDAE			
1 *Kampylaster incurvatus*	Predators of encrusting prey	Omnivores; predator of sessile prey	
GANERIIDAE			
2 *Cycethra verrucosa*	Predators of sessile prey; omnivores; sediment feeders	Predators of active prey	
GONIASTERIDAE			
3 *Chitonaster* sp. 1	Predators of sessile prey; omnivores	Predators of encrusting prey	
4 *Chitonaster* sp. 2	Predators of sessile prey; omnivores	Predators of encrusting prey	
5 *Notioceramus anomalus*	Predators of sessile prey; omnivores	Predators of encrusting prey	
ODONTASTERIDAE			
6 *Diplodontias singularis*	Predators of sessile prey; omnivores	Sediment feeders	
SOLASTERIDAE			
7 *Paralophaster antarcticus*	Predators of sessile prey; omnivores	Sediment feeders	
8 *Paralophaster lorioli*		Predators of sessile prey; sediment feeder; omnivores	
9 *Paralophaster* sp.	Predators of sessile prey; sediment feeders; omnivores	Predators of active prey	
10 *Paralophaster* sp. 3			No trophic group highlighted by the PCA
11 *Paralophaster* sp. 4321	Predators of sessile prey; sediment feeders; omnivores	Predators of active prey	
VELATIDA			
KORETHRASTERIDAE			
12 *Peribolaster macleani*	Predators of active prey; predators of sessile prey; sediment feeders; omnivores		

13 *Peribolaster* sp.	Predators of active prey; predators of sessile prey; sediment feeders; omnivores		
14 *Remaster gourdoni*	Predators of sessile prey; sediment feeders; omnivores		
PTERASTERIDAE			
15 Pterasteridae	Predators of encrusting prey	Omnivores	
SPINULOSIDA			
ECHINASTERIDAE			
16 *Rhopiella hirsuta*		Predators of active prey; omnivores; pelagos-based omnivores	
FORCIPULATIDA			
ASTERIIDAE			
17 *Adelasterias papillosa*	Pelagos-based omnivores	Predators of active prey	
18 *Kenrickaster pedicellaris*	Predators of active prey; omnivores; pelagos-based omnivores		
19 *Psalidaster mordax*	Suspension feeders; pelagos-based omnivores		Multiarmed morphology and large pedicellariae (Fisher, 1940)
PEDICELLASTERIDAE			
20 *Anteliaster scaber*	Pelagos-based omnivores	Predators of active prey	

7.2.3 Role of sea stars in Southern Ocean food webs

In temperate zones, the feeding behaviour of sea stars may have important effects on ecosystems by impacting abundances of their prey but also of organisms associated with their prey (i.e. top-down control; Paine, 1966; Kayal et al., 2012; Schultz et al., 2016; Burt et al., 2018). In particular, the 2013 sea star wasting disease on Pacific American coast, and the subsequent mass mortality of sea stars, emphasised their importance in the functioning of the food web of kelp forests. Predation on sea urchins by sea stars in kelp forests from Pacific American coast contributes to prevent kelp overgrazing by sea urchins and thus prevents major community shifts, i.e. from kelp forests to urchin barrens (Schultz et al., 2016; Burt et al., 2018). As a result, the predation of sea stars on kelp grazers appears to contribute to the maintenance of the potential ecosystem services provided by kelp forests in temperate environments (Smale et al., 2013; Bertocci et al., 2015). Kelp forests dominated by *Macrocystis pyrifera* are a major ecosystem of coastal areas of temperate Pacific American coast, but also of subantarctic islands and Patagonia (Teagle et al., 2017), and the impact

of sea stars on these communities may be similar in temperate and Subantarctic regions.

In the chapter 4, stable isotope analyses (SIA) in flora and fauna, including sea stars, from Kerguelen Island, and subsequent food web reconstruction with mixing models could provide new insights regarding the food web functioning in Subantarctic kelp forests, as well as on the trophic role of sea stars in this type of ecosystems. However, no major kelp grazers were identified by mixing models. Instead, two main trophic pathways were highlighted. The first one was a bentho-pelagic food chain supported by both pelagic particulate organic matter (POM) and maybe resuspended macrophytobenthos detritus. The second one, a phytobenthos-based food chain, was characterised by micro and non-kelp macrophytobenthos supporting grazers or epifauna. These results suggest that kelp is less likely to be removed by overgrazing in Subantarctic regions than in more temperate ones. As a result, the feeding behaviour of sea stars is unlikely to impact large kelp populations in Subantarctic regions. However, they may ease the settlement and growing of kelp by consuming organisms feeding on kelp spores and sporelings (Blankley and Branch, 1985). Our results suggest a higher functional diversity than previously thought for sea stars in coastal Subantarctic ecosystems. Indeed, earlier studies on the Patagonian kelp forests food webs considered most sea stars species as apex predators relying on multiple production pathways (Castilla, 1985; Adami and Gordillo, 1999). Yet, the stable isotope values and the mixing model results may indicate that the studied sea star species display different feeding behaviours or exploit different trophic pathways. Indeed, the Echinasteridae taxon had a lower trophic level and may partly feed on primary producers or detritus. Furthermore, although the Echinasteridae, *Diplasterias meridionalis* and *Leptychaster kerguelenensis* appeared to variably feed on both the bentho-pelagic and phytobenthos-based food chains, *Anasterias perrieri* appeared to rely mostly on the phytobenthos-based food chain. Finally, the distinct stable isotope values of *Anasterias* sp. for which no food sources were highlighted may indicate that they exploit other trophic pathways than the two ones observed in the chapter 4.

In Antarctic waters, predation by sea stars has important impacts on the structure of coastal sponge assemblages (Dayton et al., 1974). In these assemblages, two predators of sessile prey (*Acodontaster conspicuus* and *Perknaster fuscus*) may consume fast-growing sponges, preventing them to dominate the space resource or to grow over slow-growing sponges. *Acodontaster conspicuus* also consumes significant amounts of slow-growing Rosselid sponges and may potentially reduce their population. However, the omnivore sea star *Odontaster validus* may prevent the growth of *Acodontaster conspicuus* populations by consuming their larvae or settled juveniles

through suspension or deposit feeding, but also through direct grouped predation on adult individuals. To summarise, consumption of fast-growing sponges by the predators of sessile prey and consumption of slow-growing sponge predators by omnivore sea stars prevent fast growing sponges to dominate the community and permit the development of slow growing sponge species, resulting in the presence of a diverse sponge community (Dayton et al., 1974). Similar top-down processes may occur in other sea star trophic groups or taxa. They could be mediated by reduction of predator and/or competitor recruitment by suspension feeders, sediment feeders and/or omnivores, through consumption of larvae. Other possible mechanisms include reduction of competition for space through consumption of sessile organisms, and reduction of predation pressure through consumption of predators by predatory or omnivore taxa.

7.3 Ontogenetic and morphologic variations of the trophic ecology of sea stars

Ontogenetic changes in trophic ecology are of a common occurrence. Indeed, changes of morphological features or of habitat during growth would induce modifications in prey size or prey categories targeted by organisms (Luczkovich et al., 1995; Scharf et al., 2000; Sánchez-Hernández et al., 2019). Ontogenetic changes of prey size in sea stars have been observed both experimentally (Sommer et al., 1999; Gooding and Harley, 2015) and in field studies (Baeta and Ramón, 2013; Fernandez et al., 2017). Assessment of ontogenetic changes in the trophic ecology of organisms is frequently assessed by linking stable isotope values to organism sizes (e.g. Hussey et al., 2011; Polito et al., 2013; Linzmaier et al., 2018). This method was notably used in sea stars from the Gulf of Saint Lawrence, and ontogenetic changes of $\delta^{15}N$ values of *Leptasterias polaris* (Nadon and Himmelman, 2010) were linked to increasing contribution of predatory gastropods to its diet during growth (Himmelman and Dutil, 1991).

The chapter 5 showed that stable isotope values were linked to body size in a sea star assemblage from Ezcurra Inlet (King George Island, South Shetland Islands). In this study, the influence of two size measurements on stable isotope values was investigated: the arm length and the disc radius. The results of this study not only allowed to determine if ontogenetic changes of trophic ecology of Antarctic sea star occurred, but also if one of these two measured morphological features had more influence on sea star feeding than the other. Changes of stable isotope values with size were observed in sea stars, but not in all species, suggesting that some change their feeding habits while growing while others do not. Furthermore, after taking into account the effect of other factors, ontogenetic changes of stable isotope values were mostly observed when linking the disc radius

with $\delta^{13}C$ and $\delta^{15}N$ values. By contrast, the arm length appeared to be linked only to $\delta^{34}S$ values, and this change of $\delta^{34}S$ values with the arm length appeared to occur very slowly in two species. The influence of the disc radius on $\delta^{13}C$ and $\delta^{15}N$ values was interpreted as being the result of ontogenetic changes of the trophic ecology as larger sea stars may be able to extend their cardiac stomach over a larger area below the disc, resulting in a capacity to feed on larger prey, or on larger surfaces when consuming biofilms or encrusting organisms (Lawrence, 2012).

Ontogenetic changes of the trophic ecology of organisms frequently result in an increase of the size range of consumed prey, with small prey still being consumed while large prey are progressively added to the diet (Scharf et al., 2000). This phenomenon was notably observed in sea stars (Baeta and Ramón, 2013; Fernandez et al., 2017) and may indicate that organisms may increase the diversity of consumed prey and widen their prey spectrum throughout growth. This wide prey spectrum may then promote trophic plasticity, with organisms able to switch to alternative prey categories or size classes when availability of commonly consumed items is limited. As a result, ontogenic changes in trophic ecology could contribute to increase the tolerance of adult sea stars to modifications of prey availability following environmental disturbance.

7.4 Environmental drivers of the feeding ecology of sea stars in the Southern Ocean

Various habitat characteristics impact prey availability, that would then impact the trophic ecology of organisms and trophic interactions between them. The variability in prey availability resulting from environmental conditions could, through bottom-up control, modulate processes such as interspecific competition, trophic redundancy and resource segregation (Fig. 7.3). Sufficient prey availability may result in the consumption of the same prey by all organisms without competitive interaction (Costa-Pereira et al., 2019), but limited prey availability may induce a range of feeding behaviours and interactions. Among them are the increase of the trophic niche width by adding new kinds of prey to the diet to satisfy the energy requirements if the prey diversity is sufficient (optimal foraging; Stephen and Krebs, 1986; e.g. Svanbäck and Bolnick, 2007; Costa-Pereira et al., 2019), the trophic competition between organisms that would lead to trophic specialisation and/or reduction of the trophic niche width (niche partitioning; Schoener, 1974; e.g. Mason et al., 2008; Juncos et al., 2015; Tran et al., 2015; Jackson et al., 2016; Costa-Pereira et al., 2019), or the exclusion of several organisms from the food web (competitive exclusion; Hardin, 1960; e.g. Bøhn et al., 2008).

The distribution of known biotic and abiotic environmental parameters and their combination allow to classify geographic regions into ecoregions. The presence or absence of matching abiotic environmental conditions within ecoregions could then condition their primary production, and ultimately the presence or absence of specific organisms or communities. As a result, food web functioning may be expected to differ between ecoregions because of the impacts of environmental parameters on primary production and thus on resource and prey availability.

In the chapter 5, the spatial differentiation of stable isotope values in sea stars collected in nearby stations from Ezcurra Inlet indicated that the mobility of sea stars of the Southern Ocean is likely limited. This suggests that the trophic ecology and trophic diversity for this taxon in a given area may be linked to local environmental conditions. As a result, investigating the trophic ecology of sea stars may also provide insights regarding the functioning of benthic ecosystems in the different types of environment in the Southern Ocean.

The chapter 6 investigated the relationship between environmental parameters and sea star trophic ecology at the scale of the global Southern Ocean. Sea stars were sampled in 14 of the 23 ecoregions identified by Douglass et al. (2014b; 2014c), and a supplementary ecoregion, i.e. South America, comprising Falkland Islands and Patagonia was also investigated. The differences of stable isotope values between ecoregions and the link with their environmental conditions were investigated in this chapter through an exploratory analysis to investigate biogeographic differences in the trophic ecology of sea stars. This analysis notably highlighted the separation between Antarctic and Subantarctic environments, with the difference of $\delta^{13}C$ values in surface water POM between Subantarctic and Antarctic waters (Rau et al., 1991b; Francois et al., 1993; Espinasse et al., 2019) being reflected in benthic sea stars. Furthermore, the relationship between environmental parameters and stable isotope values within ecoregions was assessed. As the sampling effort was uneven between ecoregions, with two of them comprising 51.6 % of the samples (Weddell Sea and Antarctic Peninsula), the assessment of the relationship between environmental parameters and stable isotope values within ecoregions was done only in those for which a sufficient variability of sampled environmental parameters values was available, i.e. three Antarctic (Antarctic Peninsula, Oates and Weddell Sea) and two Subantarctic ecoregions (Kerguelen Plateau and South Georgia).

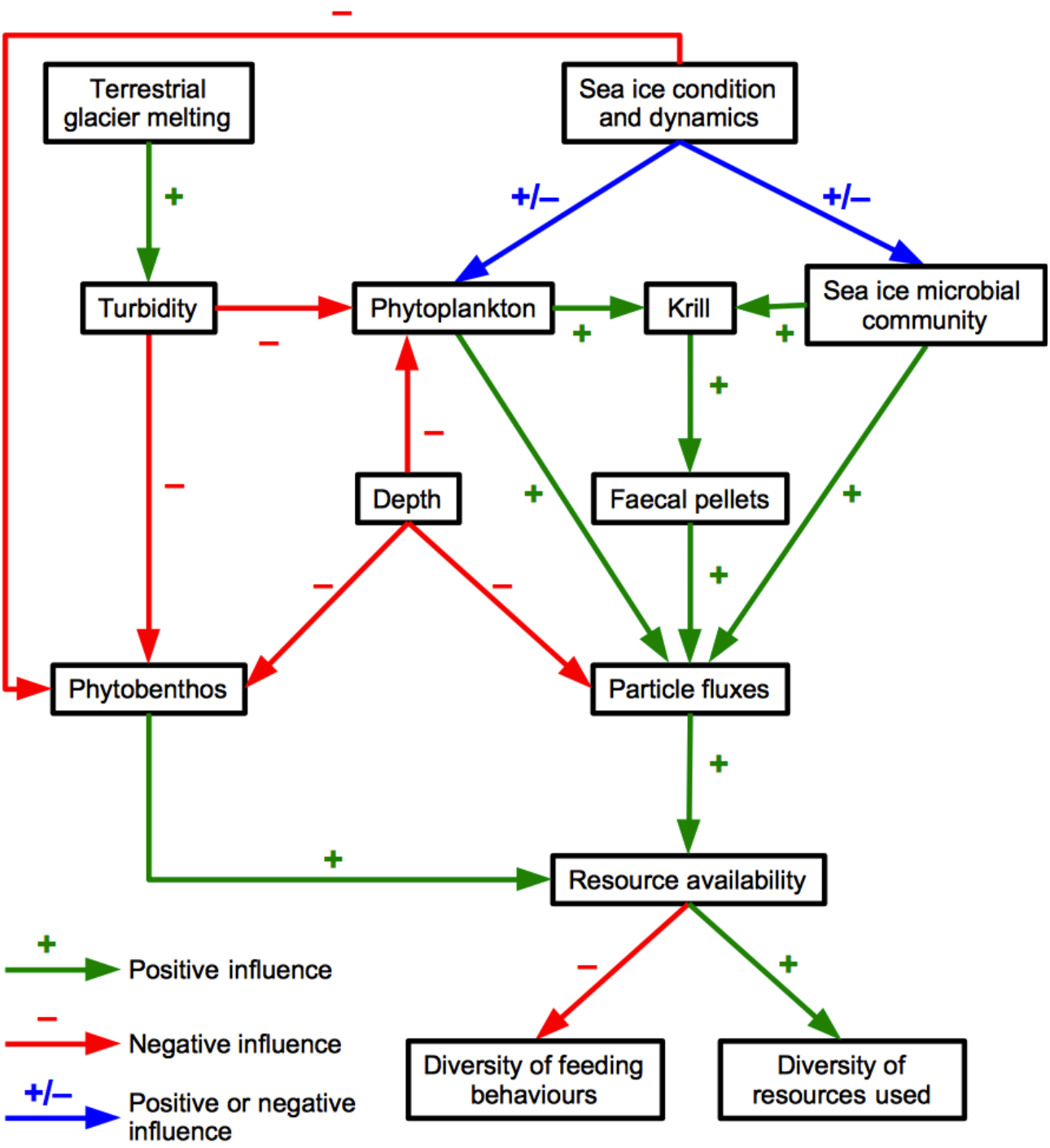


Fig. 7.3. Summary of the impacts of environmental parameters (depth, turbidity, sea ice condition and dynamics, terrestrial glacier melting) on primary production (phytoplankton, sea ice microbial community, phytobenthos) and subsequent krill and faecal pellet production, particle fluxes, resource availability, diversity of resource used and of feeding behaviours between sea stars. Arrows represent positive (+) or negative (–) influence of a parameter on another one (e.g. terrestrial glacier melting increases turbidity; turbidity decreases phytoplankton abundance).

7.4.1 Differences of feeding ecology between coastal and deeper sea stars

Depth has important impacts on the functioning of benthic communities, notably by covarying with various environmental parameters. In particular, light penetration in shallow benthic areas allows the development of abundant and varied photosynthetic communities, both in the water column, on sea ice and on the sea floor, that become the baseline food sources of shallow benthic communities. By contrast, light absorption in deep water results in reduction or absence of primary production (Fig. 7.3). Benthic communities from continental shelves and deeper areas then usually depend on the sedimenting phytoplankton (Le Loc'h et al., 2008; Gontikaki et al., 2011; Valls et al., 2014), including in the Southern Ocean (Mincks et al., 2008; Purinton et al., 2008).

The study of the relationship between environmental parameters and stable isotope values showed that trophic ecology of sea stars strongly differed between coastal and deeper areas, with decreasing $\delta^{13}C$ values and modifications of the variability of stable isotope values with depth. The exploratory analyses further highlighted the important influence of depth, the relationship between depth and $\delta^{13}C$ values occurring in all ecoregions except South Georgia, where a small range of depths was sampled, and with no sampled sea star in the coastal and/or shallow environment.

Sea stars from the coastal areas appeared to be supported by a mixture of pelagic, sympagic and benthic food sources, i.e. phytoplankton, sea ice microbial community and/or phytobenthos. Furthermore, a limited diversity of trophic levels was observed in coastal areas. Conversely, sea stars from deeper areas appeared to mostly rely on a single pelagic organic matter source, i.e. the fluxes of sinking phytoplankton from the surface. The intensity of these fluxes generally decreases with depth (Berelson, 2001; Suzuki et al., 2001), due to the consumption of sinking particles by pelagic fauna and to remineralisation processes. Furthermore, sea stars from deeper areas appeared to exhibit a higher diversity of $\delta^{15}N$ values, suggesting a higher diversity of trophic levels, and thus a higher diversity of feeding strategies and behaviours. This difference of food source and trophic level diversity between coastal and deeper waters could be linked to the depth-dependent diversity and abundance of primary production. Sea stars from coastal areas could feed at similar trophic levels with limited risks of competition, thanks to the exploitation of different food sources and/or to the fact these food sources are very abundant (even if drastic seasonal/spatial variability occurs). On the other hand, the more limited food source diversity and availability in deeper water (Fig. 7.3) could promote the diversity of feeding behaviours (e.g. omnivory, active predation, scavenging, or a combination thereof) and of associated trophic levels in sea stars, therefore reducing competition risks.

The relationship between depth and the associated food source availability and diversity of trophic levels may reflect a potential relationship between food source availability and food chain length, i.e. the maximum trophic position in a community, and thus the number of trophic levels in the communities. The factors influencing the food chain length in ecosystems have been regularly assessed (Post, 2002; Doi, 2012; Ward and McCann, 2017) and several hypotheses were formulated about it. The productivity and availability hypotheses predict that greater resource productivity and/or availability, respectively, would result in longer food chains (Doi, 2012), but this relationship has seldom been observed in natural ecosystems (Post, 2002). Instead, the food chain length may increase with productivity until a threshold is reached and then decrease as high productivity may promote omnivory and thus shorter food chains (Ward and McCann; 2017). In particular, organisms with trophic plasticity such as omnivores may switch their diet to lower trophic levels in case of high food source availability (Kondoh and Ninomya, 2009; Doi and Hillebrand, 2019) as it may have occurred for sea stars from Terre Adélie which directly consumed sympagic materials following sea ice persistence (Michel et al., 2019). Consequently, reduced diversity of feeding behaviours and of trophic levels in sea stars from coastal ecosystems could be linked to higher food source availability resulting from the high diversity and/or the high quantity of primary production pathways in these areas. Conversely, increased diversity of feeding behaviours and higher number of trophic levels in sea stars from deeper ecosystems could be linked to low food availability resulting from a single primary production pathway indirectly supporting deep communities through sedimentation from the surface and whose availability decreases with depth.

Besides food chain length, the higher variability of $\delta^{15}N$ values may also result from the co-existence of multiple food chains supported by different organic matter sources with distinct $\delta^{15}N$ values. Those could notably include a deposit feeder food chain supported by large and poorly degraded particles (Mincks et al., 2008) with low $\delta^{15}N$ values, and a suspension feeder food chain supported by fine resuspended particles (Gili et al., 2001; Mintenbeck et al., 2007) characterised by high $\delta^{15}N$ values because of the bacterial degradation and fractionation prior to their resuspension (Saino and Hattori, 1980; Wada, 1980; Mintenbeck et al., 2007). Those two aforementioned hypotheses (greater food chain length and co-existing food chains) are not mutually exclusive and could co-occur.

7.4.2 Effects of chronic glacier meltwater inputs on the trophic ecology of coastal sea stars

Marine communities are not closed systems, and the functioning of their associated food webs

may result from the influence of nearby areas. The influence of allochthonous river and terrestrial inputs on food web functioning is a well-studied phenomenon. Allochthonous inputs may include nutrients, organic matter or sediment, which, in turn, affect primary production, diversity and biomass of organisms in the food web (e.g. Gaudy et al., 2003; Giberto et al., 2004).

In polar coastal ecosystems, and notably fjords, freshwater and terrestrial inputs mostly result from the melting of glaciers, with the meltwater reducing the salinity in the adjacent area and providing mineral particles that increase turbidity. Sediment inputs are a chronic disturbance for benthic communities by inducing an increase of water turbidity and muddy bottom sediment in these areas. In turn, high turbidity reduces pelagic and benthic primary production by reducing light transmission in the water (Fig. 7.3; Thrush et al., 2004; Donohue and Garcia Molinos, 2009; Hoffmann et al., 2019). Furthermore, primary consumers may be directly impacted by the turbidity and the sediment characteristics resulting from meltwater input, that may notably clog feeding structures of filter feeders (Thrush et al., 2004; Bell et al., 2015). Lower salinity may also impact respiration, reproduction, recruitment and feeding of various benthic taxa (Ingels et al., 2012). Nevertheless, gradients of community structure, with lower benthic diversity and biomass in inner fjords than in outer fjords, are usually associated with the gradients of turbidity (Wlodarska-Kowalczuk and Pearson, 2004; Wlodarska-Kowalczuk et al., 2005; Pasotti et al., 2015a), even if increased turbidity does not necessarily result in reduced trophic diversity in areas affected by ice disturbance. Instead, inner and outer fjords appear to have similar trophic diversity (Włodarska-Kowalczuk et al., 2019).

The chapter 5 studied the spatial variation of stable isotope values in sea stars collected in nearby stations from Ezcurra Inlet, a fjord of the Admiralty Bay in King George Island. This study provided information on the food web functioning under varying degrees of turbidity resulting from glacier meltwater run-off. The differences of meltwater inputs and turbidity likely impacted the trophic ecology of sea stars of the area. Decreasing $\delta^{13}C$ values from inner to outer sampling stations of Ezcurra Inlet were linked to the higher importance of matter of terrestrial origin provided by glacier meltwater in inner stations and to the autochthonous production in outer stations.

Furthermore, the variation of the trophic diversity of sea stars from the inner to the outer fjord was assessed by investigating isotopic niche overlap in *Diplasterias brandti* and *Odontaster validus*, two omnivore species that were frequently sampled together. Isotopic niche overlap between the two species was higher in the outer stations than in the inner ones, in relation with more similar $\delta^{13}C$ values in the outer part of the fjord. This result suggests resource partitioning between species in the

inner fjord affected by higher meltwater inputs and higher turbidity. Moreover, *Odontaster validus* showed a gradual decrease in isotopic niche size from the outer to the inner Ezcurra Inlet. This species consumes a wide spectrum of prey (Pearse, 1965; Dayton et al., 1974; reviewed in Dearborn, 1977 and McClintock, 1994) which allows it to constrict its trophic niche size as the limited availability of several size class or categories of prey in a given environment may be dampened by the consumption of other ones. The wide prey spectrum and its associated trophic plasticity could help *Odontaster validus* to thrive in multiple environmental settings.

Consequently, a hypothesis to explain the increased resource segregation between sea stars in areas impacted by meltwater and turbidity could be the lower diversity and abundance of prey, that would cause species with trophic plasticity to focus on different prey items, resulting in the constriction of their trophic niches and the reduction of their overlap. This decrease in niche overlap would reduce risks of competition between sea stars, allowing their coexistence in areas with limited prey availability. By contrast, higher diversity and abundance of prey in non-disturbed areas would allow sea stars to exploit the same prey with limited risk of competition.

7.4.3 Impacts of sea ice on the trophic ecology of sea stars and food web functioning

Sea ice is a major ecological driver in the Southern Ocean. Sea ice winter formation and summer melting influence the occurrence of summer diatom blooms, with its absence during winter or persistence during summer preventing it (Hegseth and Von Quillfeldt, 2002; Garibotti et al., 2005; Montes-Hugo et al., 2009; Mendes et al., 2013; Rozema et al., 2017). Similarly, sea ice influences the intensity of benthic-pelagic coupling (Fig. 7.3; Fischer et al., 1988; Honjo et al., 2000; Kim et al., 2015; 2019). In coastal areas, sea ice also influences phytobenthos production, with its persistence reducing the light transmission to the bottom and thus preventing phytobenthos survival and production (Fig. 7.3; Clark et al., 2015). Finally, sea ice hosts a specific microbial community (i.e. sympagic communities; Arrigo, 2017) that may be an important food source for pelagic communities (Fig. 7.3; Brierley and Thomas, 2002; Leventer, 2003; Kohlbach et al., 2017; 2019).

7.4.3.1. The sea ice microbial community as a food source

The sea ice microbial community can be a food source for benthic communities, mostly in coastal ecosystems (Moens et al., 2007; Norkko et al., 2007; Wing et al., 2012; 2018; Michel et al., 2019; Rossi et al., 2019). It is characterised by higher $\delta^{13}C$ values than than those of phytoplankton (Rau et al., 1991a; Leventer, 2003; Mincks et al., 2008; Wing et al., 2018; Michel et al., 2019).

High $\delta^{13}C$ values in benthic organisms in relation with sea ice condition may thus provide an indication of the direct use of sympagic organisms as a food source in benthic communities.

The chapter 6 highlighted a slow but significant increase of $\delta^{13}C$ values in sea star tissues in conjunction with higher sea ice concentration in surface waters. In particular, sea stars sampled on the Antarctic continental shelf in areas with high sea ice concentrations may have high $\delta^{13}C$ values that likely result from the assimilation of the sea ice microbial community. Consequently, sea ice-derived materials produced in surface waters may be a food source for sea stars on the deeper continental shelf. However, the increase of $\delta^{15}N$ values with sea ice season duration in several trophic groups may also indicate increasing reliance on degraded phytodetritus during longer periods of sea ice cover to dampen the impacts of sea ice presence on the resource availability.

A more variable influence of sea ice concentration on $\delta^{13}C$ values was observed within the three Antarctic ecoregions. Indeed, while the global relationship between $\delta^{13}C$ values and sea ice concentration occurred in Oates and Weddell Sea, it did not in the Antarctic Peninsula. This may indicate biogeographic variation of the importance of the sea ice microbial community for sea stars, which could result from different sea ice condition and dynamics in the three ecoregions.

However, the absence of relationship between $\delta^{13}C$ values and sea ice concentration in the Antarctic Peninsula could result from a high range of $\delta^{13}C$ values being measured at a 0 % sea ice concentration. This may be the result of the high number of sea stars sampled in the coastal and enclosed Ezcurra Inlet in Admiralty Bay and in the offshore area of South Shetland Islands. Furthermore, high $\delta^{13}C$ values were measured in the inner Marguerite Bay despite these sea stars being sampled below 100 m and at sea ice concentrations lower than 40 %. However, the sea ice concentration in these stations may be underestimated because of the presence of nearby landmasses requiring to assign to these stations the sea ice concentration values from the closest area where no landmass was present. The high $\delta^{13}C$ values may indicate reliance on the sea ice microbial community by sea stars from the inner Marguerite Bay. Conversely, in the more northern and open waters near Anvers Island, the benthos of the continental shelf was not observed to rely on ice-derived materials in summer, these materials not being an important part of the deposited materials in the sediment (Mincks et al., 2008). Instead, phytodetritus derived from the phytoplankton bloom are the main food source for benthic organisms from this region. Consequently, the importance of the sea ice microbial community as a food source for sea stars may differ between locations within the Antarctic Peninsula ecoregion.

Sea stars from Oates were sampled in Terre Adélie, where sea ice has a seasonal presence,

although periods of local sea ice persistence recently occurred. Reliance on the sea ice microbial community and direct consumption of sea ice materials by omnivore sea stars have been observed in the coastal zone of this region with mixing model and trophic level computations (Michel et al., 2019), showing that sea ice derived materials may be a significant food source for coastal sea stars from this ecoregion. However, particularly low $\delta^{13}C$ values observed in predators of sessile prey in the same area during a period of high sea ice concentration show that other food sources such as planktonic items may support several taxa in the food webs of the Oates ecoregion (Michel et al., 2019). The Ross Sea is another ecoregion where reliance on the sea ice microbial community as a food source by coastal benthic communities has been highlighted (Norkko et al., 2007; Wing et al., 2012; 2018; Rossi et al., 2019). However, sea ice appears to have different impacts on the trophic levels of sea stars. Omnivore sea stars from Oates have lower trophic levels (Michel et al., 2019) than those from ice-covered areas in Ross Sea (Wing et al., 2012), maybe because different sea ice condition induce different availability and/or supply of the sea ice microbial community in both ecoregions. Contrary to Oates and Ross Sea, the sea ice microbial community was considered to be a secondary carbon source in the coastal food webs from the Prydz Bay and Wilkes ecoregions (Gillies et al., 2012; 2013). Instead, these studies considered epiphytic and microphytobenthic diatoms as more likely food sources with high $\delta^{13}C$ values (Gillies et al., 2012) for benthic organisms of these ecoregions.

The Weddell Sea has a long sea ice season duration, with a large permanently ice-covered area in its western part (Raymond, 2012; Douglass et al., 2014b). In this ecoregion, sea stars may have high $\delta^{13}C$ values in several stations with high sea ice concentration and long sea ice season duration, despite being sampled between 500 and 1000 m. These high $\delta^{13}C$ values in offshore areas are likely the result of the integration of isotopic signatures from the sinking sea ice microbial community. High $\delta^{13}C$ values recorded in nematodes and meiofauna in several locations from the Weddell Sea were similarly considered as resulting from the integration of sea ice-derived materials (Moens et al., 2007). Sea ice-derived materials may thus be a significant food source for sea stars and other benthic organisms living on the continental shelf of this ecoregion.

7.4.3.2. The multiple impacts of sea ice on resource availability

Sea ice concentration and sea ice season duration did not appear to directly impact the trophic diversity of sea stars (chapter 6), as high or low sea ice concentrations and season duration did not induce either an increase or a reduction of the variability of $\delta^{13}C$ or $\delta^{15}N$ values. This may suggest

that sea ice has no impact on the number of food sources supporting sea stars or on the trophic level diversity in sea star assemblages. As a result, the isotopic niche area did not appear to consistently change between sea ice concentration and sea ice season duration intervals.

The availability of the sea ice microbial community is probably not directly correlated to sea ice concentration and season duration. Firstly, the patchy distribution of this community is influenced by other factors than sea ice concentration (snow depth over the ice, sea ice thickness and sea ice freeboard levels; Meiners et al., 2017). Secondly, in some instances, its transfer to the benthos may be a discrete event that follows sea ice break up (Kim et al., 2019). By contrast, limited particle fluxes from the surface to the benthos usually occur during periods of sea ice cover (Fischer et al., 1988; Kim et al., 2015; 2019). Consequently, sea ice microbial community availability to the benthos might be highly variable even in case of important sea ice presence. This would make that benthic organisms rely on alternative sources in addition to or in place of the sea ice microbial community to prevent competition and/or dampen the impacts of sea ice presence on the resource availability. Furthermore, while sea ice may promote the development and the availability of the sea ice microbial community, its melting in summer may promote other primary production processes such as phytoplankton blooms (Hegseth and Von Quillfeldt, 2002; Garibotti et al., 2005; Montes-Hugo et al., 2009; Mendes et al., 2013; Rozema et al., 2017) that may be more available for the benthos than the sea ice microbial community, and then become major food items supporting benthic food webs.

The resource availability linked to sea ice presence may also have different impacts on the feeding behaviours and trophic levels of sea stars and of other benthic organisms. Indeed, limited particle fluxes to the bottom may promote predatory behaviours, resulting in higher mean trophic levels in organisms sampled in persistently ice-covered areas (Wing et al., 2012) or during periods of ice cover (Rossi et al., 2019). Conversely, the high availability of sea ice-derived materials may induce a simplification of benthic food webs in coastal Antarctic, with reduction of the mean trophic level, of intraguild predation or of competition (Rossi et al., 2019). However, the high availability of sea ice-derived materials and subsequent reduction of the mean trophic level may occur both following sea ice break up (Rossi et al., 2019) or in case of sea ice persistence (Michel et al., 2019).

Consequently, higher or lower sea ice concentration and sea ice season duration values may not be good predictors of food source availability and thus of the relationship between resource availability and trophic diversity in sea stars.

7.4.3.3. Perspectives for future assessments on the impact of sea ice on food webs

New studies on the impact of sea ice on resource availability and subsequent food web functioning are needed. They would help to determine if important and/or perennial sea ice cover may locally induce reliance on sympagic communities by the Antarctic benthos, and/or if it limits or induces the consumption of other food sources. In particular, sampling of benthic organisms during winter, i.e. period of maximal sea ice extent and of minimum intensity of primary production and of particle fluxes, would provide new insights on the impact of limited resource availability induced by sea ice on the feeding behaviours and trophic interactions between organism groups. Other methods should be combined with stable isotope ratios in these studies to confirm the use of sea ice-derived particles as a food source by benthic communities. Indeed, the high $\delta^{13}C$ values of sympagic POM in coastal areas may be confounded with those of epiphytic diatoms (Gillies et al., 2012) and discrete, or time-limited, reliance on a given food source may result in limited integration of the stable isotope values of this food source in organism tissues.

Highly branched isoprenoids (HBI) are a group of lipids found in diatoms. Among them, the Ice Proxy with 25 carbon atoms (IP_{25}, or HBI I) and the Ice Proxy for the Southern Ocean with 25 carbon atoms ($IPSO_{25}$, or HBI II) are specific to diatom species present in sea ice from Arctic and Antarctic, respectively. There is also another marker reflecting phytoplankton production in the marginal ice zone (HBI III). The presence of HBIs in sediment represents a measure of past seasonal sea ice and is thus used for palaeo sea ice reconstruction (Belt, 2018). However, HBIs may also be used as a proxy for the reliance on the sea ice microbial community by organisms, and they have been analysed in various tissues of consumers from multiple trophic levels. HBIs have been measured in krill stomach contents, tissues and faecal pellets (Schmidt et al., 2018), and in muscle and liver of coastal teleosts in Antarctic (Goutte et al., 2014). Similarly, in Arctic, HBIs have been measured in the liver of polar bears (Brown et al., 2018) and notably in whole benthic organisms (Brown and Belt, 2012). As $IPSO_{25}$ is poorly degraded in the water column (Rontani et al., 2019) and since deposit feeders from the Antarctic continental shelf can select fresh phytodetritus (Moens et al., 2007; Würzberg et al., 2011), it should be possible to analyse HBIs in tissues of correctly preserved (Brown, 2018) benthic organisms, including sea stars, from the Southern Ocean, despite the degradation of $IPSO_{25}$ in the sediment (Rontani et al., 2019). Investigations based on multiple integrative trophic markers therefore hold great potential to determine whether the sea ice microbial community is a major carbon source for benthic food webs in the Southern Ocean, or if it may become so through future environmental modifications.

7.5 Potential impacts of climate change on the trophic ecology of sea stars and their associated food webs

Modification of environmental conditions are currently happening in the Southern Ocean as a result of the climate change. Higher ocean temperatures and ocean acidification will directly affect growth and survival of organisms (Peck et al., 2004; 2009; 2010; Kroeker et al., 2013; reviewed in Morley et al., 2019). Conversely, higher ocean temperatures in the Southern Ocean will ease the arrival of exotic species (Aronson et al., 2009) such as durophagous litholid crabs (Thatje et al., 2008; Aronson et al., 2015), mussels (Cárdenas et al., 2020) or Subantarctic kelp species (Fraser et al., 2018). Adult Antarctic sea stars may have higher tolerance to temperature changes and ocean acidification than other benthic ectotherm taxa (Peck et al., 2008; Morley et al., 2012; Dell'Acqua et al., 2019). Higher temperatures increase metabolic rate and thus oxygen demand, with muscle being the major tissue in terms of oxygen demand, and may induce death when this demand exceeds the animal capacity for oxygen uptake and supply. The thermal tolerance of sea stars may result from low muscle mass relative to whole body mass, and thus lower oxygen demand than in other ectotherm invertebrates living at similar temperatures (Peck et al., 2008). However, early development stages may be more sensitive to temperature and pH changes (Stanwell-Smith and Peck, 1998; Gonzalez-Bernat et al., 2013; Karelitz et al., 2017), which may then impact sea star recruitment and population size in the long term.

The modification of environmental conditions, the potential disappearance of native organisms and the arrival of exotic organisms will likely induce modifications of the food web functioning of Antarctic marine ecosystems.

The decrease in sea ice cover and ice season duration in WAP (Stammerjohn et al., 2008a; 2008b), and more recently in other Antarctic regions (Parkinson, 2019), is one of the most visible phenomena induced by climate change in the Southern Ocean, and is expected to impact the functioning of food webs. Indeed, sea ice impacts the dynamic of the phytoplankton communities on which benthic communities on the Antarctic continental shelf and deeper waters depend. The retreat of the seasonal sea ice resulted in shifts in the phytoplankton communities in the northern Antarctic Peninsula, from highly productive communities dominated by large diatoms during summer blooms, to less productive communities, dominated by smaller photosynthetic organisms (Montes-Hugo et al., 2009; Rozema et al., 2017), with lower export rates to the benthos (Anadón et al., 2002). Indeed, fast sinking of diatom aggregates would not occur. Furthermore, krill populations would be displaced to the new areas of phytoplankton blooms and replaced by salps in the formerly

seasonally ice-covered areas (Loeb et al., 1997; Nicol et al., 2000; Montes-Hugo et al., 2009; Gutt et al., 2011). This absence of krill would then result in a reduction of its contribution to the export of pelagic primary production to the bottom in faecal pellets in these areas (Belcher et al., 2017; 2019). Consequently, a reduction of particle fluxes to the benthos may be expected in case of retreat of seasonal sea ice (Fig. 7.3). Considering the relationship between particle fluxes and benthic biomass in deep environments (Galéron et al., 2000; Johnson et al., 2007; Sweetman and Witte, 2008), a reduction of the biomass of benthic organisms on the Antarctic continental shelf and in the deeper environment would be expected in the Antarctic Peninsula, although the presence of "food banks" may temporarily delay this change. As a result, more limited resource and prey availability on the Antarctic continental shelf and deeper environment may induce competitive interaction between sea stars in this ecoregion, as well as the reduction of their biomass. The competitive interactions would eventually result in trophic niche segregation and/or competitive exclusion. However, this phenomenon may be counterbalanced by the lateral transport of biogenic particles from coastal areas to the continental shelf (Isla et al., 2006) that may contribute to maintain a significant resource availability.

Conversely, sea ice retreat over the Antarctic continental shelf would contribute to an increase of primary production in formerly permanently ice-covered areas (Arrigo et al., 2008), as shown by the southward relocation of phytoplankton blooms in areas that were previously ice-covered most of the year in WAP (Montes-Hugo et al., 2009). This would result in increased particle fluxes to the seabed and thus higher quantity of primary production being available to the benthos as cell aggregates or faecal pellets. These modifications of pelagic production linked to sea ice retreat and its subsequent availability for the benthos would then have consequences on the benthic communities of continental shelves. For example, the collapse of the Larsen ice shelf in the western Weddell Sea was followed by a rapid colonisation of the pelagic environment by krill while the benthic communities appeared to shift, although more slowly, from an impoverished suspension feeder community to a deposit feeder community (Gutt et al., 2011; 2013). The retreat of permanent sea ice or the reduction of the sea ice season duration may also induce increasing production of suspension feeder taxa (Fillinger et al., 2013; Barnes, 2015). Increasing resource availability and production of the benthos in formerly ice-covered areas may then provide new feeding grounds for sea stars in the western Weddell Sea. However, sponge-eating sea stars were seldom observed in the growing sponge community under the Larsen ice shelf following its collapse and the subsequent increase of sponge production. This may indicate that recruitment and colonisation of the area by

sea stars has not yet begun or is limited by the impacts of environmental changes on sea star larvae (Fillinger et al., 2013).

Contrary to WAP, sea ice tended to persist or increase its cover in the other Antarctic regions (Stammerjohn et al., 2008b; Parkinson and Cavalieri, 2012) until recently (Parkinson, 2019). As sea ice persistence may prevent phytoplankton growth (Hegseth and Von Quillfeldt, 2002; Mendes et al., 2013) and is associated with reduced particle fluxes (Fischer et al., 1988; Kim et al., 2015), a reduction of the resource availability for the benthos may be expected like for areas where seasonal sea ice disappears. More limited resource availability may then reduce the benthos biomass, and then prey availability for sea stars, which may in turn result in reduced sea star biomass and increasing competitive interactions between sea star taxa. Furthermore, resuspension of particles may provide a more regular food source than phytoplankton blooms for the benthos of areas permanently covered by sea ice, which may result in a higher importance of suspension feeder communities as the one that was present below the Larsen Shelf before its collapse (Gutt et al., 2011).

The sea ice microbial community may also be expected to become a more important food source for benthic communities in newly ice-covered areas, and its high availability may result in benthic organisms to consume it directly with limited competition (Rossi et al., 2019). However, the presence and the availability of the sea ice microbial community depends on various factors, resulting in regional, vertical and seasonal variation of its distribution (Meiners et al., 2012; 2017), which may then result in regional variation of the impact of increased sea ice cover on the benthos and thus on sea stars. In Terre Adélie, in the Oates ecoregion, benthic organisms, including omnivore sea star species, were observed to have low trophic positions, and thus to consume directly sea ice materials, in case of permanent sea ice cover (Michel et al., 2019), suggesting that non-melting sea ice may provide sufficient biomass of food source to the benthos. Conversely, in Ross Sea, benthic organisms, including sea stars, were observed to maintain similar or higher trophic level under permanently ice-covered areas than in seasonally ice-covered areas (Wing et al., 2012). These differences may result from different availability and/or supply of the sea ice microbial community in the ice-covered areas in both ecoregions, maybe as a result of different sea ice condition.

The impact of climate change on Antarctic terrestrial glaciers and ice sheets may also have consequences on the marine ecosystem functioning. The recession of terrestrial glaciers in WAP (Braun and Gossmann, 2002; Cook et al., 2005) would increase turbidity (Sahade et al., 2015),

freshwater pulses (Dierssen et al., 2002) and iceberg scouring frequency (Barnes and Souster, 2011). On one hand, the increased freshwater inputs resulting from the melting of terrestrial glaciers and ice sheet would contribute to summer phytoplankton blooms by providing iron and inducing stratification and may then fill the role of seasonal sea ice in phytoplankton dynamics if sea ice has retreated (Dierssen et al., 2002; Death et al., 2014). Increased terrestrial inputs and then more important lateral transport of particles, including biogenic ones, to the deeper continental shelf (Isla et al., 2006) may also be expected. On the other hand, increased turbidity and iceberg scouring frequency would reduce the intensity of benthic primary production (Hoffmann et al., 2019) and the diversity and abundance of coastal benthic communities in the area (Smale and Barnes, 2008; Sahade et al., 2015). Reduction of primary production and prey abundance in relation to turbidity was observed to induce trophic niche segregation between the omnivores *Diplasterias brandti* and *Odontaster validus* in Ezcurra Inlet, and thus to reduce competitive interaction, notably thanks to the constriction of the trophic niche of *Odontaster validus* (chapter 5). A similar phenomenon may be expected for sea stars in areas where terrestrial inputs and turbidity would increase because of stronger glacier melting. Several sea star taxa may be excluded following the increasing turbidity, like those depending on the pelagic food chains, as the biomass of pelagic primary producers and of the suspension feeders they consume may be reduced. However, in the long term, reduced glacier surface could diminish terrestrial inputs and open new areas for benthic colonisation, leading to more diverse benthic assemblages in the formerly disturbed areas (Pasotti et al., 2015a). Primary production may then increase, inducing higher food source and then prey availability for sea stars. Increasing trophic redundancy between sea star taxa may then occur with limited risks of competition. Finally, reduced turbidity may induce a recolonisation by suspension feeders and their predatory sea stars.

Future impacts of climate change in the Southern Ocean or other regions remain difficult to predict due to the variable effects of environmental conditions on ecosystems and food web functioning (e.g. Fig. 7.3). Similarly, predicting the impacts of reduced or increased abundance of a given taxon on communities following environmental changes is challenging as it may lead to trophic cascades that not only impact the prey consumed by this taxon, but also other organisms. Knowledge on the trophic ecology of organisms is thus necessary to determine how food web may be affected by community modifications.

7.6 Conclusions and perspectives

This thesis provide new information on the trophic ecology of sea stars in the Southern Ocean. Sea star taxa from this ocean display a variety of trophic strategies and behaviours but their trophic ecology is also driven by both intrinsic (e.g. body size) and environmental factors (e.g. depth, turbidity, sea ice). Environmental factors may condition the characteristics and availability of the organic matter sources supporting sea stars and thus impact their trophic diversity. Turbidity and depth impacted trophic diversity by inducing, respectively, trophic niche constriction and/or niche partitioning, and a decrease of the diversity of organic matter sources and thus a possible increase of trophic level diversity. Sympagic communities may be a food source in some contexts. However, sea stars are more likely to be indirectly impacted by changes in sea ice cover and dynamics, because of their impact on the dynamics of phytoplankton on which sea stars may rely, than directly because of changes in the availability of sympagic-derived material for consumers.

Studies on the trophic ecology of marine organisms and on food web functioning are usually restricted to a given location or region, more global studies being scarce except for mobile vertebrates (e.g. Bird et al., 2018; Pethybridge et al., 2018; Hayden et al., 2019). This thesis includes one of the first studies at a continent level on the trophic ecology of a benthic invertebrate taxon in relation to environmental parameters. The relationships between these parameters and the trophic diversity of sea stars were hypothesised to result from the impacts of these parameters on primary production and subsequent resource availability. However, as all sea stars were sampled during summer, seasonal changes of their trophic ecology could not be investigated. Future studies on seasonal variations should regularly sample pre-selected stations with known environmental conditions. In seasonally ice-covered stations, this sampling strategy may notably help to determine whether cyclic shifts in food sources of sea stars occur throughout the year in relation to sea ice condition and subsequent food source availability. An example of seasonal variation of food sources may be the reliance on the “food bank”, degraded phytodetritus and/or continuously sinking sea ice-derived materials during periods of sea ice cover, followed by sea ice-derived materials during and shortly after sea ice break up and then freshly deposited phytodetritus provided by phytoplankton blooms during ice-free periods. Similarly, the impact of seasonal variations of resource availability on the diversity of feeding behaviours may be investigated. Last but not least, studies on other invertebrates, in other regions and/or in areas with diverse environmental gradients, would tell us if the relationships between environmental parameters and trophic ecology highlighted in this thesis are specific to sea stars from the Southern Ocean or if they are a general ecological phenomenon.

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