TROPHODYNAMICS OF THE BENTHIC AND HYPERBENTHIC COMMUNITIES INHABITING THE SUB-ANTARCTIC PRINCE EDWARD ISLANDS:

STABLE ISOTOPE AND FATTY ACID SIGNATURES

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

by

Elizabeth Louise Allan

January 2011

ABSTRACT

The aim of this study was to investigate spatial changes in the trophic and energy pathways of the benthic community in the shallow shelf waters of the sub-Antarctic Prince Edward Islands (PEI). A combination of stable isotope and fatty acid analyses were used to provide a time-integrated view of the assimilated feeding history of selected components of the PEI benthic community. This study forms part of the larger project entitled "Variability in the Southern Ocean ecosystems" and is a contribution to the South African National Antarctic Programme (SANAP). During austral autumn 2009, benthic specimens were collected from 10 stations (from depths of 70 to 295 m) in different regions around the PEI: inter-island shelf (upstream, between and downstream of the islands) and nearshore. Historical data were combined with new data collected during 2009 to assess the long-term trends in the feeding ecology of the benthos in the region of the islands.

The stable isotope and fatty acid signatures of the benthic suspension- and deposit-feeding organisms generated during this study suggested that these two communities incorporated both phytoplankton and kelp in their diets. Stable isotope, and to a lesser extent fatty acid signatures, indicated that kelp contributed more to the diets of those organisms in close proximity to the kelp beds (nearshore stations) than those from the inter-island region. Overall, however, pelagic phytoplankton was the dominant food source in the diets of all organisms, even for those living near the kelp beds. Notable exceptions were the sponges and bryozoans, in which kelp and phytoplankton contributed similar proportions to their diets, most likely resulting from a size restricted feeding mode. There were, therefore, no distinct spatial differences in the importance of the various food sources. However, fatty acid compositional data indicated increased food quality between and within the lee of the islands compared to upstream. The organisms collected upstream of the PEI had substantially lower quantities of total fatty acids (TFAs) than organisms of the same species collected from nearshore, open shelf or downstream stations. The increased food quality between and within the lee of the islands was likely a result of the "island mass effect", which reflects increased phytoplankton concentrations at the PEI.

The fatty acid profiles of hyperbenthic shrimp *Nauticaris marionis*, a key species in the PEI ecosystem, revealed no distinct ontogenetic or spatial patterns. This result is in contrast to the stable isotope analyses, which detected both spatial and ontogenetic differences in the diet of the shrimp. Nearshore shrimp were more ^{13}C-enriched than those from the inter-island region, suggesting increased kelp entering the food web within these regions. In addition, the shrimps demonstrated enrichment in δ^{13}C and δ^{15}N signatures with an increase in size, resulting in a relatively distinct separation of size classes, thus reflecting niche separation through their diets. The fatty acid profiles revealed that the shrimp all contained large proportions of polyunsaturated fatty acids (PUFAs) and essential fatty acids (EFAs), indicating that the quality of food consumed was similar among size class and region despite the niche separation and variation in carbon sources utilised. In addition, diatom and dinoflagellate fatty acids (20:5ω3 and 22:6ω3, respectively) occurred in the highest proportions in *N. marionis*, highlighting the importance of phytoplankton (indirectly) in their diet. These results represent strong evidence that phytoplankton is an importance food source in the PEI ecosystem.

The temporal investigation of isotope signatures in the benthos at the PEI indicated that *N. marionis* demonstrated an overall depletion in δ^{13}C signatures over the period of 1984 to 2009 (nearshore: -2.55 ‰, inter-island: -2.32 ‰). Overall, the benthic community showed similar depletions in δ^{13}C signatures (from -1.96 to -4.70 ‰), suggesting that shifts have occurred in the carbon signatures at the base of the food web. The depletion in δ^{13}C signatures of the benthos at the PEI most likely reflects increased contributions of smaller slow growing phytoplankton cells (more depleted signatures than large fast growing cells) in the diets of these organisms over time. These diet shifts, in turn, suggest a decrease in productivity has occurred at the islands, likely due to a decreased frequency and intensity of the "island mass effect". Decreased phytoplankton productivity at the PEI likely results from the southward shift in the average position of the sub-Antarctic Front (SAF), most likely in response to climate change, which in turn promotes flow-through conditions rather than retention at the PEI.

TABLE OF CONTENTS

ABSTRACT ii
TABLE OF CONTENTS iv
LIST OF TABLES viii
LIST OF FIGURES xi
LIST OF ABBREVIATIONS xvi
ACKNOWLEDGEMENTS xviii
DECLARATION xix

CHAPTER 1: GENERAL INTRODUCTION 1
1.1. THE PRINCE EDWARD ISLANDS 1
1.1.1. Position in the Polar Frontal Zone 1
1.1.2. Hydrodynamics around the islands 4
1.1.3. Ecosystem of the islands 6
1.2. ASSESSING FEEDING RELATIONSHIPS 9
1.2.1. Stable isotopes 10
1.2.2. Fatty acids 11
1.3. GLOBAL CLIMATE CHANGE IN THE SOUTHERN OCEAN 12
1.3.1. Changes in the marine environment around the Prince Edward Islands 13
1.4. THESIS OVERVIEW 15

CHAPTER 2: MATERIALS AND METHODS 16
2.1. STUDY AREA AND SAMPLE COLLECTION 16
2.1.1. Environmental variables and food sources 16
2.1.2. Benthic community 18
2.1.3. Hyperbenthic shrimp *Nauticaris marionis* 18
2.2. SAMPLE TREATMENT 21
2.2.1. Environmental variables and food sources 21
2.2.2. Benthic community 21
2.2.3. Hyperbenthic shrimp *Nauticaris marionis* 22

2.3. STABLE ISOTOPE ANALYSIS 23
2.4. FATTY ACID ANALYSIS 23

CHAPTER 3: REGIONAL VARIATIONS IN THE DIETS OF BENTHIC SUSPENSION- AND DEPOSIT-FEEDING COMMUNITIES AROUND THE PRINCE EDWARD ISLANDS .. 25
3.1. INTRODUCTION 25
3.2. MATERIALS AND METHODS 26
3.2.1. Study area, sample collection and treatment 26
3.2.2. Stable isotope analysis 26
3.2.3. Fatty acid analysis 26
3.2.3.1. Target fatty acids 27
3.2.4. Data analysis 27
3.3. RESULTS 28
3.3.1. Environmental variables and food sources 28
3.3.2. Stable isotopes 28
3.3.2.1. Food sources 28
3.3.2.2. Suspension- and deposit-feeders 30
3.3.3. Fatty acids 35
3.3.3.1. Food sources 35
3.3.3.2. Suspension- and deposit-feeders 37
3.3.4. Diets of suspension- and deposit-feeders using target fatty acids 38
3.3.4.1. Inter-specific variation 38
3.3.4.2. Regional variation 42
3.4. DISCUSSION 46
3.4.1. Environmental conditions 46
3.4.2. Food sources 47
3.4.3. Diets of benthic suspension- and deposit-feeders 47
3.4.3.1. Stable isotopes 47
3.4.3.2. Fatty acids 48
3.4.4. Regional variations in food availability and utilisation by benthic organisms 50
3.5. CONCLUSIONS 54

CHAPTER 4: ONTOGENETIC AND SPATIAL VARIATIONS IN THE DIET OF THE HYPERBENTHIC SHRIMP *NAUTICARIS MARIONIS* AROUND THE PRINCE EDWARD ISLANDS 55

4.1. INTRODUCTION 55

4.2. MATERIALS AND METHODS 57

4.2.1. Study area, sample collection and treatment 57

4.2.2. Stable isotope analysis 57

4.2.3. Fatty acid analysis 57

4.2.3.1. Target fatty acids 58

4.2.4. Data analysis 58

4.3. RESULTS 58

4.3.1. Ontogenetic and spatial variation 59

4.3.1.1. Stable isotopes 59

4.3.1.2. Fatty acids 61

4.3.2. Food sources 63

4.4. DISCUSSION 67

4.4.1. Ontogenetic variation 67

4.4.2. Food sources 69

4.4.3. Spatial variation 71

4.5. CONCLUSION 72

CHAPTER 5: TEMPORAL VARIATION IN STABLE ISOTOPE SIGNATURES OF THE BENTHIC AND HYPERBENTHIC COMMUNITY IN THE VICINITY OF THE PRINCE EDWARD ISLANDS AND POTENTIAL LONG-TERM CHANGES 73

5.1. INTRODUCTION 73

5.2. MATERIALS AND METHODS 74

5.2.1. $\delta^{13}C$ and $\delta^{15}N$ signatures in the hyperbenthic shrimp *Nauticaris marionis* 74

5.2.2. $\delta^{13}C$ and $\delta^{15}N$ signatures in the benthic community: nearshore and inter-island 75

5.2.3. $\delta^{13}C$ signatures of suspended particulate matter at the Prince Edward Islands 76

5.3. RESULTS 76

5.4. DISCUSSION 80

5.5. CONCLUSION 85

CHAPTER 6: GENERAL DISCUSSION 86
6.1. TROPHODYNAMICS OF THE BENTHIC AND HYPERBENTHIC COMMUNITIES 86
6.2. LONG-TERM EFFECTS OF GLOBAL CLIMATE CHANGE 88
6.3. FUTURE STUDIES 91

References 92
Appendix 114

LIST OF TABLES

Table 2.1 Position and information about the 10 benthic stations sampled around the Prince Edward Islands during the 2009 investigation 18

Table 2.2 Spatial distribution of benthic suspension- and deposit-feeding organisms collected around the Prince Edward Islands and the analyses conducted (●: isotope ratios; ○: fatty acid profiles; number indicates sample size)..... 19

Table 2.3 Spatial distribution of detritus, zooplankton and *Nauticaris marionis* collected around the vicinity of the Prince Edward Islands and the analyses conducted (●: isotope ratios; ○: fatty acid profiles; number indicates sample size)..... 20

Table 4.1 $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SD; ‰) of all potential pelagic and/or benthic food sources (zooplankton, detritus and benthic suspension-/deposit-feeders) and *Nauticaris marionis* (consumer) at each station around the Prince Edward Islands 65

Table 5.1 $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SD; ‰) of the zooplankton and benthic organisms collected during April 1999 (Kaehler *et al.*, 2000) and April 2009 (current study) around the Prince Edward Islands. The benthic community is separated into nearshore and inter-island (central) regions 77

Table A1 Fatty acid composition (mean % TFA ± SD) of the surface water suspended particulate matter (SPM) in the vicinity and in the surrounding offshore region of the Prince Edward Islands. Data represent all fatty acids at concentrations >1% TFA in at least one sample (n = 1 per station)..... 114

Table A2 Fatty acid composition (mean % TFA ± SD) of the kelp *Macrocystis laevis*. Fresh and degraded fronds, and degraded kelp particulate organic matter (POM) and the suspended particulate matter (SPM) obtained from within the kelp beds near Marion Island. Data represent all fatty acids at concentrations >1% TFA in at least one sample..... 116

Table A3 Fatty acid composition (mean % TFA ± SD) of the four species of sponge at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 117

Table A4 Fatty acid composition (mean % TFA ± SD) of the two species of bryozoan at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 119

Table A5 Fatty acid composition (mean % TFA ± SD) of the brachiopod *Magellania kerguelenensis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 120

Table A6 Fatty acid composition (mean % TFA ± SD) of the bivalves *Limatula pygmaea* and *Thracia meridionalis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 121

Table A7 Fatty acid composition (mean % TFA ± SD) of the polychaete *Serpula vermicularis vermicularis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 122

Table A8 Fatty acid composition (mean % TFA ± SD) of the holothurians *Pseudocnus laevigatus and Psolus paradubiosus* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 123

Table A9 Fatty acid composition (mean % TFA ± SD) of the hydrozoan *Plumularia insignis*, gorgonian coral *Thouarella variabilis* and the sea pen *Pennatula inflata* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 124

Table A10 Fatty acid composition (mean % TFA ± SD) of the polychaete *Thelepus extensus* at the station where it was collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 125

Table A11 Fatty acid composition (mean % TFA ± SD) of the polychaete *Lanice marionensis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 126

Table A12 Fatty acid composition (mean % TFA ± SD) of the gastropod *Margarella expansa* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample 127

Table A13 Fatty acid composition (mean % TFA ± SD) of the size classes of the hyperbenthic shrimp *Nauticaris marionis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.....128

Table A14 Fatty acid composition (mean % TFA ± SD) of the detritus at the stations where it was collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.....133

Table A15 Fatty acid composition (mean % TFA ± SD) of the three size fractions of zooplankton for the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.....134

LIST OF FIGURES

Figure 1.1 Circumpolar map of the Southern Ocean indicating the average geographical position of the major fontal systems as well as the positions of the islands and archipelagos of the Southern Ocean highlighting the Prince Edward Islands (PEI). STC, subtropical Convergence; SAF, sub-Antarctic Front; APF, Antarctic Polar Front. Figure drawn in the Ocean Data View computer package and position of the fronts was obtained from Orsi *et al.* (1995) 2

Figure 1.2 Hydrodynamics around the Prince Edward Islands when the sub-Antarctic Front (SAF) lies in closer proximity to the islands, resulting in a flow-through system (A) and when the SAF lies far to the north of the islands, resulting in the formation of anticyclonic eddies between and within the lee of the islands (B). Adapted from Pakhomov and Chown (2003)..... 5

Figure 1.3 Theoretical food web indicating the potential carbon flow in the Prince Edward Islands ecosystem. Adapted from Pakhomov *et al.* (2009) 7

Figure 2.1 Survey area around the Prince Edward Islands indicating position of the 10 benthic stations. The benthic stations were divided into inter-island stations: upstream (1, 2 and 3; ■), between (4, 5 and 6; ▲) and downstream (7; ◆) of the islands, and nearshore (8, 9 and 10; ●). Surface water was collected from the surrounding offshore region (○): upstream (i, ii and iii) and downstream (iv, v, vi, vii). * Natal Bank: shallow bank with kelp beds.... 17

Figure 3.1 Surface water total chlorophyll-*a* (chl-*a*; µg L^{-1}) and suspended particulate matter (SPM; mg L^{-1}) concentrations in the vicinity (A and B, respectively) and in the offshore region (C and D, respectively) of the Prince Edward Islands 29

Figure 3.2 $\delta^{13}C$ signatures (‰) of the surface water suspended particulate matter in the vicinity (A) and in the offshore region (B) of the Prince Edward Islands .. 30

Figure 3.3 $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of the benthic suspension-feeding organisms collected at all regions around the Prince Edward Islands and $\delta^{13}C$ signatures (‰) of the potential primary producers contributing to their diets. Phytoplankton signatures were obtained from previous studies in the region (Kaehler *et al.*, 2006; Pakhomov *et al.*, 2009); range of $\delta^{13}C$ values for various phytoplankton communities is indicated by the black line with community composition indicated at each end (mixed: mixture of small diatoms, dinoflagellates and coccolithophorids; diatom bloom: a phytoplankton community dominated by large chain-forming diatoms); error bars represent standard deviations 31

Figure 3.4 $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of the benthic deposit-feeding organisms collected at all regions around the Prince Edward Islands and $\delta^{13}C$ signatures (‰) of the potential primary producers contributing to their diets. Phytoplankton signatures were obtained from previous studies in the region (Kaehler *et al.*, 2006; Pakhomov *et al.*, 2009); range of $\delta^{13}C$ values for various phytoplankton communities is indicated by the black line with community composition indicated at each end (mixed: mixture of small diatoms, dinoflagellates and coccolithophorids; diatom bloom: a phytoplankton community dominated by large chain-forming diatoms); error bars represent standard deviations 32

Figure 3.5 $\delta^{15}N$ signatures (‰) of the benthic suspension- and deposit-feeding organisms in the different regions around the Prince Edward Islands. Error bars indicate standard deviations 33

Figure 3.6 $\delta^{13}C$ signatures (‰) of the benthic suspension- and deposit-feeding organisms in the different regions around the Prince Edward Islands. Estimated 100% diet lines were calculated using an average trophic enrichment of 1.00 ‰ for carbon (Fry and Sherr, 1984; Peterson *et al.*, 1985); signatures for diatom blooms from a similar region were obtained from Pakhomov *et al.* (2009); error bars represent standard deviations 34

Figure 3.7 Concentration (µg FA mg^{-1} DM) of total fatty acids (TFAs) in the surface water suspended particulate matter in the vicinity (A) and in the offshore region (B) of the Prince Edward Islands 36

Figure 3.8 Proportions (% TFA) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the benthic suspension-feeding organisms among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island - upstream and downstream of the islands (A), inter-island - between the islands (B) and nearshore (C). Error bars indicate standard deviations 40

Figure 3.9 Proportions (% TFA) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the benthic deposit-feeding organisms among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations 41

Figure 3.10 Quantities (µg FA mg DW^{-1}) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the suspension-feeding bryozoan sp. 1 (A), brachiopod *Magellania kerguelenensis* (B), bivalve *Limatula pygmaea* (C) and the deposit-feeding polychaete *Lanice marionensis* (D) among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations; note y-axis consists of different scales starting from smallest (A) to largest (D) quantities 43

Figure 3.11 Quantities (µg FA mg DW^{-1}) of total fatty acids (TFAs) in the suspension-feeding bryozoan sp. 1 (A), brachiopod *Magellania kerguelenensis* (B), bivalve *Limatula pygmaea* (C) and the deposit-feeding polychaete *Lanice marionensis* (D) among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations; note y-axis consists of different scales starting from smallest (A) to largest (D) quantities 44

Figure 3.12 Proportions (% TFA) of polyunsaturated fatty acids (PUFAs) and essential fatty acids (EFAs) in the deposit-feeding polychaete *Lanice marionensis* at the seven stations from where it was collected around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations 45

Figure 3.13 Changes in the quantities (µg FA mg DW^{-1}) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the gorgonian coral *Thouarella variabilis* between upstream (inter-island Station 2) and downstream (inter-island Station 7) areas of the Prince Edward Islands. Error bars indicate standard deviations 45

Figure 4.1 $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of *Nauticaris marionis* collected at each station (A to I) around the Prince Edward Islands. Size classes: 4.0 – 5.0 mm (I); 5.5 – 6.5 mm (II), 7.0 – 8.0 mm (III), 8.5 – 9.5 mm (IV) and 10.0 – 11.0 mm (V); inter-island: upstream (○), between (◇) and downstream (∆) of the islands; nearshore (■); error bars represent standard deviations 60

Figure 4.2 $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) for each size class of *Nauticaris marionis* (A to D) collected around the Prince Edward Islands. Regions: inter-island upstream (1 and 3), between (4, 5 and 6) and downstream (7) of the islands, and nearshore (8, 9 and 10); error bars represent standard deviations 61

Figure 4.3 Principal component analysis (PCA) of transformed proportional data of *Nauticaris marionis* collected around the Prince Edward Islands. Convex hulls indicate size classes (A) and stations (B). Arrows running parallel to each axis denote the influence of the specified fatty acids that have loading values >0.2 62

Figure 4.4 Proportion (% TFA) of essential fatty acids (EFAs; A) and quantity (μg FA mg^{-1} DM) of total fatty acids (TFAs; B) in the various size class of *Nauticaris marionis* at the nine stations it was collected from around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations 63

Figure 5.1 Temporal shifts in $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of *Nauticaris marionis* collected from nearshore (A) and inter-island (B) regions around the Prince Edward Islands during April/May between 1984 and 2009. Data (mean ± SD) for *N. marionis* from 1984, 1985, 1987, 1999 and 2000 were obtained from Pakhomov *et al.* (2004). Nearshore: near kelp beds (Station 8); inter-island: [a] central shelf (Station 4), [b] south of Natal Bank (Station 6) and [c] downstream (Station 7). Note that the $\delta^{13}C$ and $\delta^{15}N$ signatures of *N. marionis* from 1984, 1985, 1987 and 1997 were corrected for preservation according to Pakhomov *et al.* (2004) 76

Figure 5.2 $\delta^{13}C$ signatures (‰) of zooplankton and benthic organisms collected from the nearshore and inter-island regions during April 1999 (Kaehler *et al.*, 2000) and April 2009 (current study) around the Prince Edward Islands..... 78

Figure 5.3 $\delta^{13}C$ signatures (‰) of the surface water suspended particulate matter (SPM) collected during March/April 2003 (Kaehler *et al.*, 2006; A) and April 2009 (current study; C) around the Prince Edward Islands. The sea-surface temperature data were derived from monthly averages (MODIS-Terra.R1.1, NASA Giovanni) for March/April 2003 (B) and April 2009 (D) in the vicinity of the Prince Edward Islands. The position of the sub-Antarctic Front was identified by the 8.0 to 8.5°C isotherms, as described by Uddstrom and Oien (1999)..... 79

LIST OF ABBREVIATIONS

ACC	Antarctic Circumpolar Current
ai-	*anteiso-*
APF	Antarctic Polar Front
BAFA	bacterial fatty acid (s)
BHT	butylated hydroxytoluene
C	carbon
chl-*a*	chlorophyll-*a*
CL	carapace length
CV	coefficient of variation
DM	dry mass
EFA	essential fatty acid (s)
FA	fatty acid
FAME	fatty acid methyl ester
FSW	filtered seawater
GC	gas chromatography
GC-MS	gas chromatography-mass-spectrometry
HPFA	higher plant fatty acid (s)
i-	*iso-*
IAEA	International Atomic Energy Agency
IRMS	Isotope Ratio Mass Spectrometer
MUFA	monounsaturated fatty acid (s)
N	nitrogen
NMI	nonmethylene interrupted
PC	principal component (s)
PCA	principal component analysis
PEI	Prince Edward Islands
PFZ	Polar Frontal Zone
POM	particulate organic matter
PUFA	polyunsaturated fatty acid (s)

SAF	sub-Antarctic Front
SANAP	South African National Antarctic Programme
SD	standard deviation
SFA	saturated fatty acid (s)
SPM	suspended particulate matter
STC	subtropical Convergence
TFA	total (identified) fatty acid (s)

ACKNOWLEDGEMENTS

I would like to thank the South African Department of Environmental Affairs and Tourism (DEAT), National Research Foundation (NRF) and Rhodes University for providing the funding and facilities for this study. My appreciation also goes to the Andrew Mellon Foundation and Deutscher Akademischer Austausch Dienst (DAAD) for their financial support during my PhD.

There are many people that I would like to express my gratitude to. Firstly, I would like to thank my supervisors William Froneman and Nicole Richoux for their support and guidance during my PhD. Thank you for all your enthusiasm and for helping me to develop as a scientist.

I would also like to thank the officers and crew of the MV *S.A. Agulhas* (Voyage 145) for their invaluable assistance at sea. Thanks also to Nicole Richoux, Mathilde Schapira, Fynn McQuaid, Jeremy Plass-Johnson, Ryan Young and Sole Tarantelli for all their assistance with data collection around the Prince Edward Islands. My sincere gratitude goes to the members of the Lipid Lab for a great working environment and to Sven Kaehler at IsoEnvironmental cc, Department of Botany, Rhodes University for isotope analysis.

I am also grateful to my friends for their continual encouragement and providing welcome distractions. Most importantly, I am grateful to Kendall Crous and Tim Richardson for all their help, especially during the final stages.

I would also like to thank the people closest to me. Firstly, to my parents for all their love and support, and for always believing that I can achieve anything I try to do. Finally I would like to thank my husband Ben. Your continual love and support has helped me to become the best that I can be and for this I cannot thank you enough. You are my one constant and for that I am very grateful!

DECLARATION

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author unless otherwise stated.

"Twenty years from now
you will be more disappointed
by the things that you didn't do
than by the ones you did do.
So throw off the bowlines.
Sail away from the safe harbour.
Catch the trade winds in your sails.
Explore. Dream. Discover."

~

Mark Twain

1 GENERAL INTRODUCTION

Coastal regions, oceanic islands and ice-edge zones are typically characterised by elevated levels of primary production compared to the surrounding open ocean region (Subba Rao and Platt, 1984; Smith and Nelson, 1986; Boden, 1988; Perissinotto and Duncombe Rae, 1990). Due to the enhanced primary production within these ecosystems they generally support diverse and abundant benthic communities, usually dominated by suspension-feeders, through pelagic-benthic coupling (Grebmeier and Barry, 1991; Arntz *et al.*, 1994; Clarke *et al.*, 1996; McQuaid and Froneman, 2004; Tatián *et al.*, 2008). Despite the moderate to low production rates recorded in the polar regions, these systems have diverse, biomass-rich benthic communities (Dayton and Oliver, 1977; Branch *et al.*, 1993a; Clarke *et al.*, 1996; Sahade *et al.*, 1998; Pakhomov and Froneman, 1999a; Jacob *et al.*, 2006; Tatián *et al.*, 2008). These benthic communities, in turn, support organisms occupying higher trophic levels, and therefore play a vital role in the functioning of these ecosystems (Perissinotto and McQuaid, 1990; Hirons *et al.*, 2001; Moore *et al.*, 2003; Simpkins *et al.*, 2003; Corbisier *et al.*, 2004; Smith *et al.*, 2006). It is therefore important to understand how benthic communities utilise alternative trophic sources, especially in regions experiencing irregular fluctuations in primary productivity.

1.1. THE PRINCE EDWARD ISLANDS

1.1.1. Position in the Polar Frontal Zone

The sub-Antarctic Prince Edward Islands (PEI) are situated in the Indian sector of the Southern Ocean and are comprised of Marion Island and Prince Edward Island (Fig. 1.1). These two islands are 22 km apart and separated by a shallow (mean depth ~180 m) inter-island shelf that falls off rapidly to 3000 m (Fig. 1.1; Pakhomov and Froneman, 1999a). The PEI are situated in the direct path of the easterly flowing Antarctic Circumpolar Current (ACC), between the sub-Antarctic Front (SAF) to the north, and the Antarctic Polar Front (APF) to the south (Fig. 1.1), in the transition zone known as the Polar Frontal Zone (PFZ; Valentine and Lutjeharms, 1983; Lutjeharms and Valentine, 1984; Lutjeharms, 1985;

Duncombe Rae, 1989a, b). The ACC approaches the PEI at an average speed of 0.35 m s^{-1} (Lutjeharms *et al.*, 1988), with a mean surface speed that varies between 0.15 and 0.67 m s^{-1} (Allanson *et al.*, 1985).

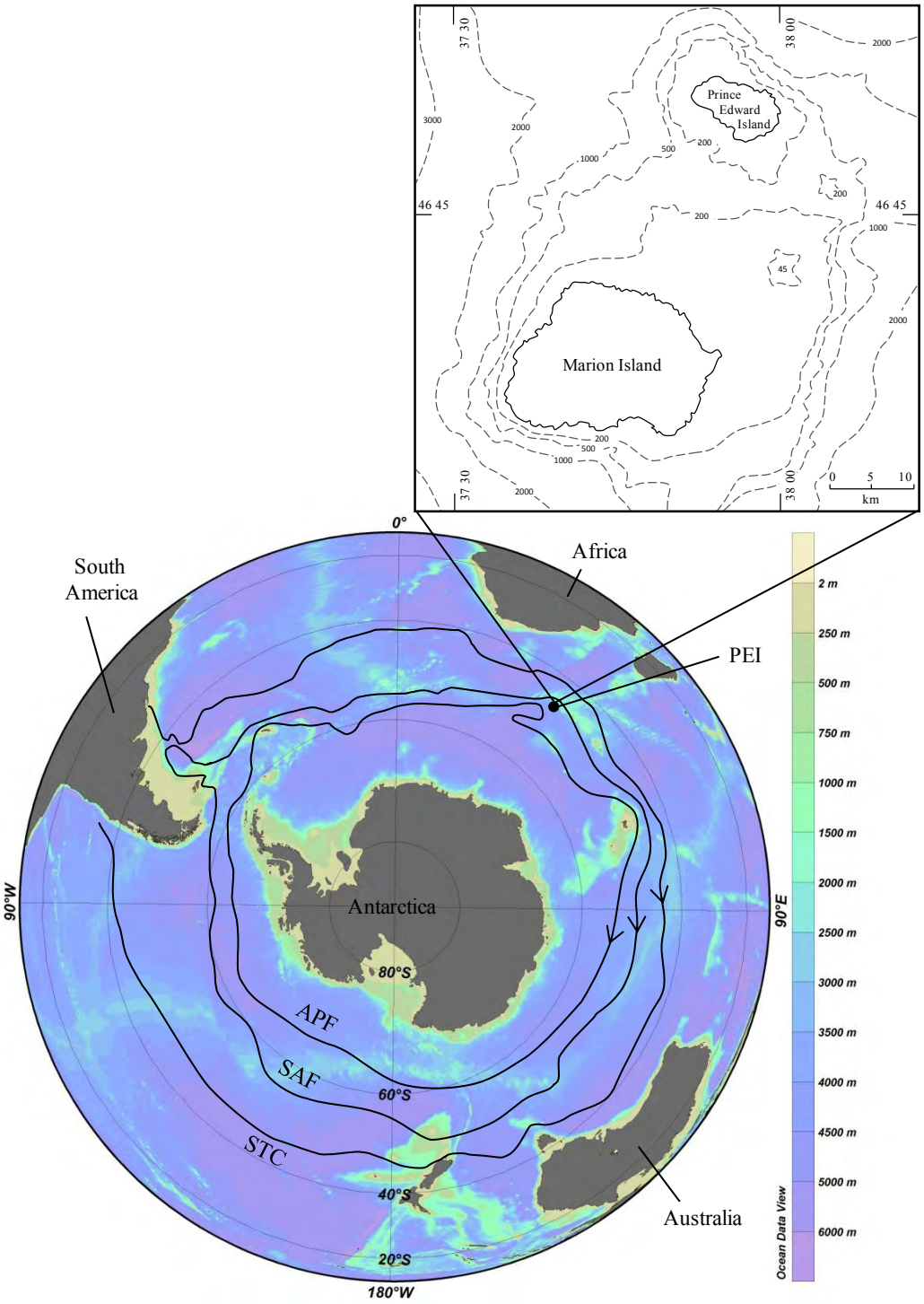

Figure 1.1. Circumpolar map of the Southern Ocean indicating the average geographical position of the major fontal systems as well as the positions of the islands and archipelagos of the Southern Ocean highlighting the Prince Edward Islands (PEI). STC, subtropical Convergence; SAF, sub-Antarctic Front; APF, Antarctic Polar Front. Figure drawn in the Ocean Data View computer package and position of the fronts was obtained from Orsi *et al.* (1995).

The PFZ demonstrates a high degree of spatial and temporal mesoscale variability in oceanographic conditions (Ansorge *et al.*, 1999; Pakhomov and Froneman, 1999a), including shifting cold-core eddies, changes in the geographic position of the major frontal zones that delimit the PFZ and meanders in both frontal systems (Legeckis, 1977; Bryden, 1983; Lutjeharms, 1990; Ansorge *et al.*, 1999). In particular, the positions of the SAF and APF are highly variable in the region of the PEI (Valentine and Lutjeharms, 1983; Lutjeharms and Valentine, 1984; Nagata *et al.*, 1988; Duncombe Rae, 1989a, b; Lutjeharms, 1990). The variability in the flow rates and position of the PFZ results from the interaction of the ACC with the prominent bottom topography (Nowlin and Klinck, 1986; Park *et al.*, 1993; Ansorge *et al.*, 1999). The surface waters of the PFZ are characterised by highly variable concentrations of nutrients such as nitrate (9.5 to 97.5 mmol m^{-3}), silicate (0.2 to 16.5 mmol m^{-3}) and phosphate (<0.1 to 16.6 mmol m^{-3}; Allanson *et al.*, 1985; Duncombe Rae, 1989a; Ismail, 1990; Balarin, 2000). The intrusion of Antarctic surface and sub-Antarctic surface waters into the PFZ, as well as eddies generated from either frontal systems or the interaction between the ACC and the South-West Indian Ridge, contribute to changes in nutrient concentrations in this region (Ansorge *et al.*, 1999; Froneman *et al.*, 1999; Ansorge and Lutjeharms, 2002, 2003; Ansorge *et al.*, 2004).

The high degree of variability in the oceanic environment of the PFZ is reflected in the biology of the ecosystem as the plankton community is comprised of a mixture of subtropical, sub-Antarctic and Antarctic species (Boden and Parker, 1986; Perissinotto and Boden, 1989; Froneman and Pakhomov, 1998; Froneman *et al.*, 1999; Pakhomov and Froneman, 1999a). The open waters of the PFZ are characterised by low phytoplankton stocks (generally <0.3 µg L^{-1}), which are generally dominated by the pico- (<2.0 µm) and nanophytoplankton size fractions (2.0 – 20.0 µm; Laubscher *et al.*, 1993; Froneman *et al.*, 2001). The predominance of the smaller phytoplankton reflects the prevailing high wind activity and deep water column mixing within this region (Laubscher *et al.*, 1993; Froneman *et al.*, 2001; Gurney *et al.*, 2002; Froneman and Bernard, 2004). Additionally, low macronutrient availability may contribute to the predominance of small phytoplankton cells generally recorded in the open waters of the PFZ (McQuaid and Froneman, 2008).

The zooplankton community of the PFZ is dominated numerically and by biomass by mesozooplankton (200 – 2000 µm), comprising mainly of copepods (Perissinotto and Boden, 1989; Hunt *et al.*, 2001; Bernard and Froneman, 2002, 2003), but at times macrozooplankton

(>2000 μm) contributes substantially to the community (Pakhomov and Froneman, 1999b). Overall, the species composition of zooplankton as well as the abundance and biomass of zooplankton in the open waters of the PFZ exhibit a high degree of spatial variability (Froneman and Balarin, 1998; Hunt *et al.*, 2001; Bernard and Froneman, 2002, 2003). Changes in the zooplankton community composition and abundance/biomass appear to be coupled with the periodic intrusion of the warmer sub-Antarctic surface waters (lowest zooplankton abundance and biomass) and the colder Antarctic surface waters into the PFZ (elevated zooplankton abundance and biomass; Hunt *et al.*, 2001). The frontal regions that delimit the PFZ support elevated biological activity such as enhanced total chlorophyll-*a* (chl-*a*) concentrations and zooplankton abundances (Froneman and Pakhomov, 1998; Pakhomov and Froneman, 1999b; Bernard and Froneman, 2003).

1.1.2. Hydrodynamics around the islands

The PEI periodically experiences localised enhanced phytoplankton production within the immediate vicinity of the islands, a phenomenon known as "island mass effect" (El-Sayed *et al.*, 1979; Allanson *et al.*, 1985; Boden, 1988; Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 1990; Kaehler *et al.*, 2006). During these periods, the total chl-*a* concentrations often exceed 1.5 μg L^{-1} and at times reach 3.0 μg L^{-1}, while the phytoplankton concentrations may be as high as 10^6 to 10^9 cells m^{-3} (Boden, 1988; Perissinotto and Duncombe Rae, 1990). The phytoplankton blooms are generally dominated (80%) by the chain-forming diatom, *Chaetoceros radiacans* (>20 μm), which are only present during blooms forming rapidly sinking resting spores (Perissinotto and Duncombe Rae, 1990). In the PFZ, in the vicinity of the PEI, the most common microphytoplankton species is *Chaetoceros neglectus*, followed by *Dactyliosolen antarcticus*, *Chaetoceros atlanticus* and *Fragilariopsis* spp. (Froneman and Pakhomov, 1998). In the absence of the phytoplankton blooms, total chl-*a* concentrations in the region of the islands are equivalent to those found in the open waters of the PFZ (Boden, 1988; Van Ballegooyen *et al.*, 1989; Balarin, 2000; Perissinotto *et al.*, 2000). It is generally accepted that the occurrence of the "island mass effect" in the vicinity of the PEI is largely determined by prevailing hydrodynamics around the islands (Pakhomov and Froneman, 1999a; Perissinotto *et al.*, 2000; McQuaid and Froneman, 2008).

The position of the SAF relative to the PEI is a critical component that determines if and when phytoplankton blooms occur between the islands. When the SAF is far to the north of

the islands, the flow rate of the ACC past the PEI is slow enough that increased frictional forces between it and the islands cause the formation of trapped anticyclonic eddies between and within the lee of the islands (Fig. 1.2B; Perissinotto and Duncombe Rae, 1990; Ansorge and Lutjeharms, 2002). In contrast, when the SAF lies close to the islands the frictional forces are less, as flow rates of the ACC are higher closer to the frontal systems, thus creating a flow-through system that prevents eddies from forming between the islands (Fig. 1.2A; Perissinotto *et al.*, 2000).

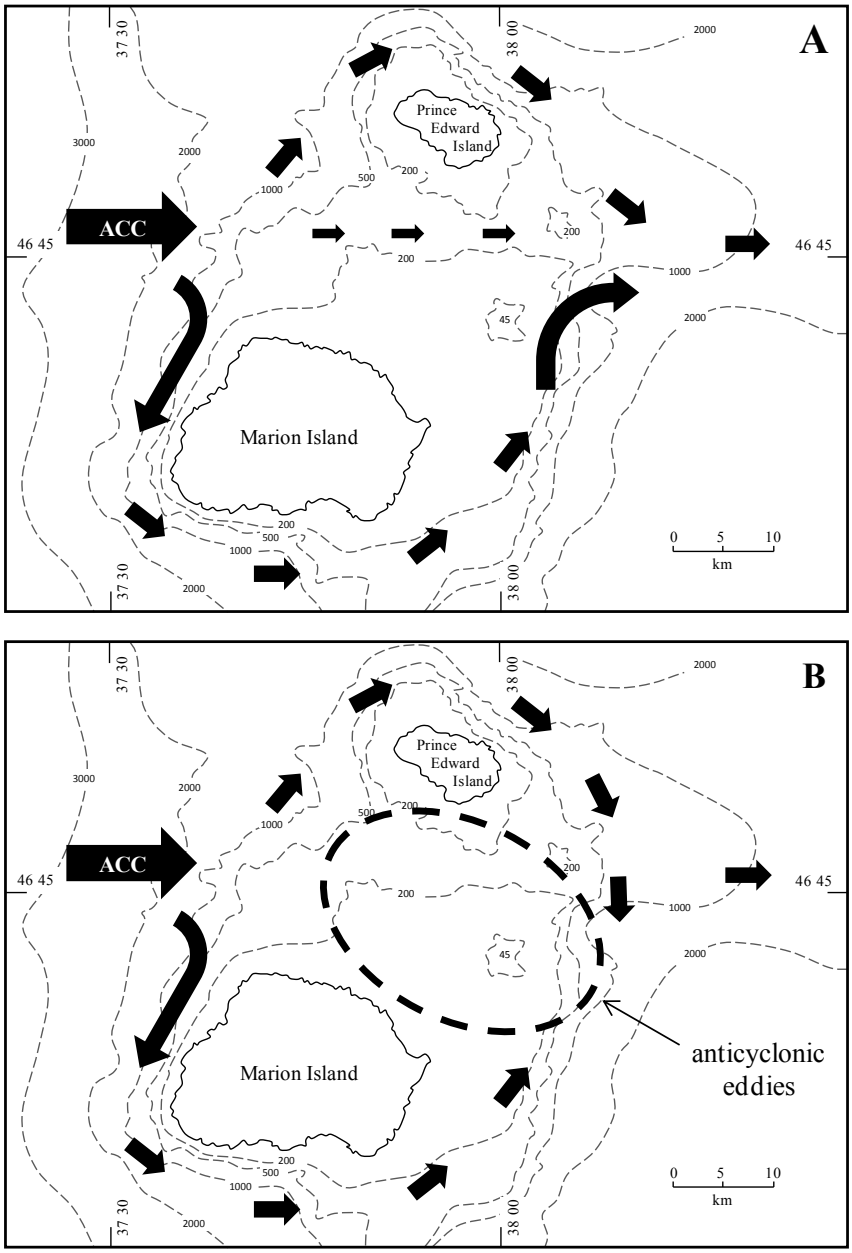

Figure 1.2. Hydrodynamics around the Prince Edward Islands when the sub-Antarctic Front (SAF) lies in closer proximity to the islands, resulting in a flow-through system (A) and when the SAF lies far to the north of the islands, resulting in the formation of anticyclonic eddies between and within the lee of the islands (B). Adapted from Pakhomov and Chown (2003).

Enhanced phytoplankton production between and within the lee of the islands has been attributed to retention of water over the shallow shelf region due to the formation of anticyclonic eddies between the islands (Allanson *et al.*, 1985; Perissinotto and Duncombe Rae, 1990). Freshwater runoff from the islands transports nutrients, particularly reduced forms of nitrogen (ammonia and urea) from guano, into the surrounding surface waters (Ismail, 1990; Perissinotto and Duncombe Rae, 1990). This freshwater runoff is retained in these eddies, resulting in the accumulation of nutrients over the shallow shelf region between the islands (Ismail, 1990; Perissinotto and Duncombe Rae, 1990). The retention of freshwater runoff in the shelf waters also results in increased water column stability, as the depth of the mixed layer becomes shallower than the euphotic zone and promotes the development of periodic phytoplankton blooms if the freshwater is retained between the islands for long enough (minimum 15 days; Allanson *et al.*, 1985; Boden, 1988; Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 1990).

The PEI support a large number of top predators on the islands as well as a high density of benthic organisms (Ryan and Bester, 2008). These populations are supported by either an inshore (autochthonous) component and/or an offshore (allochthonous) component (Pakhomov and Froneman, 1999a; Pakhomov and Chown, 2003; McQuaid and Froneman, 2004). The inshore component, which is important to the rich benthic community as well as a few top predators, is thought to be sustained by the "island mass effect". The offshore component, which supports the majority of top predators, is sustained by the advection of zooplankton/micronekton from the upstream region to the PEI by the easterly flowing ACC (Pakhomov and Froneman, 1999a; Pakhomov and Chown, 2003; McQuaid and Froneman, 2004). These two sources of food supply to the island ecosystem is termed the "life support system" of the PEI.

1.1.3. Ecosystem of the islands

The PEI, together with a small number of other islands and archipelagos, represent the only land masses in the vast Southern Ocean (Fig. 1.1). The nearest landfall to the PEI is the French Crozet Island Group, which lies approximately 950 km to the east, while the nearest landmass is Africa approximately 2000 km away (Fig. 1.1; Chown and Froneman, 2008). Despite their remote positioning, the islands seasonally support up to five million land-based predators, including seals, flying seabirds and penguins (Williams *et al.*, 1979; Condy, 1981;

Pakhomov and Froneman, 1999a; McQuaid and Froneman, 2004). A theoretical food web showing the major carbon flow through the PEI ecosystem is shown in Figure 1.3.

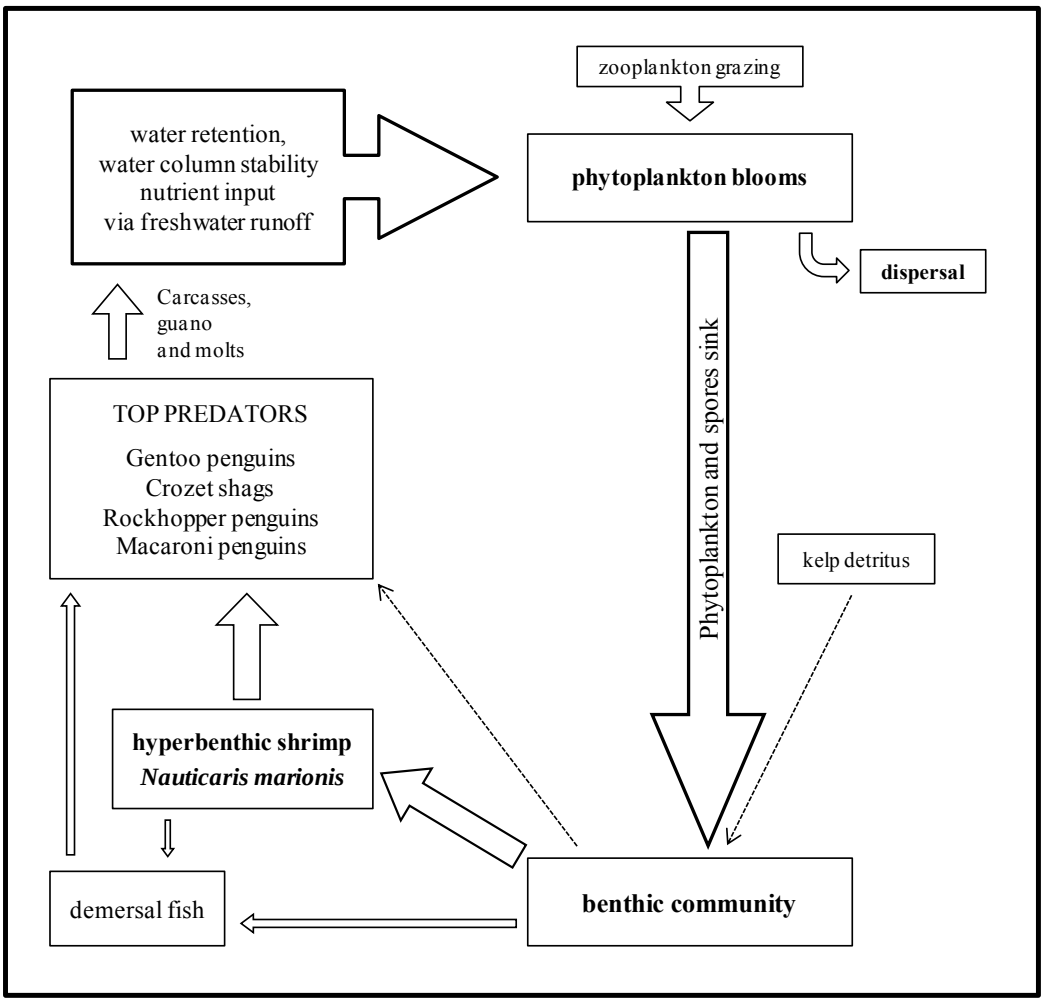

Figure 1.3. Theoretical food web indicating the potential carbon flow in the Prince Edward Islands ecosystem. Adapted from Pakhomov *et al.* (2009).

The shallow inter-island shelf waters of the islands support a diverse (~550 species) and biomass-rich benthic community, which is numerically dominated by suspension-feeders (60%; Branch *et al.*, 1993a). Deposit-feeders and predators/scavengers compose 23 and 12% of the total abundances, respectively (Branch *et al.*, 1993a). Suspension-feeders dominate the benthos in all habitats and depths of the shallow shelf region, but the community composition of the benthos demonstrates some spatial variability reflecting the different habitats (Branch *et al.*, 1993a). Soft substrata are numerically dominated by polychaetes (*Serpula vermicularis* and *Lanice marionensis*), bivalves (*Limatula pygmaea*) and brachiopods (*Magellania kerguelenensis*), while the deep rocky substrata are characterised by the predominance of sponges, bryozoans and octocorals (*Thouarella variabilis*; Branch *et al.*, 1993a). The shallow

shelf region around the islands, particularly between and within the lee of the islands, has a high density of organisms, where ophiuroids, brachiopods and bivalves often exceeded 30 ind m^{-2} (each), and ophiuroids reached an average of 193 ind m^{-2} at one station (Branch *et al.*, 1993a). The hyperbenthic shrimp *Nauticaris marionis* is also abundant often, exceeding 20 ind m^{-2} (Branch *et al.*, 1993a).

The occurrence of a diverse and biomass-rich benthic community on the shelf waters of the PEI suggest a significant and stable food supply. It is now generally accepted that the dominant food source for the benthic community in the vicinity of the PEI is derived from the periodic diatom blooms that occur between and within the lee of the islands (Perissinotto, 1992; Branch *et al.*, 1993a; Pakhomov and Froneman, 1999a; McQuaid and Froneman, 2008). During bloom conditions, when the phytoplankton community is dominated by large diatoms such as *Chaetoceros radicans* and *Rhizosolenia curvata* (Boden, 1988; Perissinotto and Duncombe Rae, 1990), zooplankton grazing utilises only 5 to 10% of chl-*a* standing stock and between 9 and 17% of primary production per day (Perissinotto, 1992). As a result, large quantities of unutilised pelagic material may be horizontally dispersed or sink to depth, therefore providing an important food source for the benthic community in the shallow shelf region (Perisinotto *et al.*, 1990; Perissinotto, 1992; Pakhomov and Froneman, 1999a). During non-bloom conditions the phytoplankton community is dominated by smaller cells (<20 μm), and the zooplankton are able to consume 33 to 48% of the chl-*a* standing stock and 76 to 81% of the new carbon produced by phytoplankton each day (Perissinotto, 1992).

A key component of the benthos of the PEI is the hyperbenthic caridean shrimp *N. marionis* (Perissinotto and McQuaid, 1990). The PEI support a dense population of this shrimp (Branch *et al.*, 1991, 1993a), which represents the second highest areal biomass after bryozoans (Parker, 1984; Beckley and Branch, 1992; Branch *et al.*, 1993a). These shrimp are restricted to the shallow shelf waters within the inter-island region (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999) and are predominantly found at depths between 50 and 100 m (Branch *et al.*, 1991, 1993a). The megalope larvae of shrimp consume mainly phytoplankton, while the subadults/adults predominantly feed on benthic suspension- and deposit-feeders and secondarily on detritus and small plankton (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999; Vumazonke *et al.*, 2003). Adult shrimp represent an important food source for land-based predators such as Gentoo penguins and Crozet shags that primarily feed in the inshore waters (Espitalier-Noël *et al.*, 1988; Adams and Klages, 1989),

and are periodically consumed by Rockhopper and Macaroni penguins (Brown and Klages, 1987). As a result, *N. marionis* is regarded as a key species in the benthic community of the PEI, as it represents a direct food web link between the plankton and land-based predators (Perissinotto and McQuaid, 1990).

In addition to the "island mass effect" another major component of the PEI ecosystem is the extensive kelp beds around the islands. The kelp *Durvillaea antarctica* occurs in the infralittoral fringe within a narrow band around the islands (Haxen and Grindley, 1985; Beckley and Branch, 1992), while the dominant kelp *Macrocystis laevis* forms dense beds at depths from 5 to 20 m, but if rocky substrate exists they can occur at depths of up to 50 m (Attwood *et al.*, 1991; Beckley and Branch, 1992; Perissinotto and McQuaid, 1992). *Macrocystis laevis* generates substantial productivity per unit area, estimated at 2.0 to 3.5 times greater than that of the phytoplankton (Beckley and Branch, 1992). As the majority of kelp production is thought to be washed ashore or transported away from the islands (Beckley and Branch, 1992), it has generally been presumed to be unimportant in the benthic food web of the PEI. Recent studies employing stable isotope techniques, however, revealed that kelp-derived detritus may play a vital role in providing organic matter to benthic communities living within close proximity to the kelp beds (Kaehler *et al.*, 2000, 2006). The kelp beds also modify local hydrology in the region of the inshore waters of the islands as they retain freshwater runoff from the islands and thereby promote water column stability which favours phytoplankton growth (Pakhomov *et al.*, 2002).

1.2. ASSESSING FEEDING RELATIONSHIPS

Trophic and energy pathways in aquatic systems are extremely complex. The most widely used traditional methods for determining animal feeding habits include gut content analysis and gut fluorescence techniques (Peterson *et al.*, 1990; Bautista and Harris, 1992; Pakhomov *et al.*, 1999; Tatián *et al.*, 2002). These methods, however, provide data about very recent feeding activities, and in the case of gut fluorescence only herbivorous feeding (Båmstedt *et al.*, 2000). As these methods provide snap shot views of prey consumption, there is no insight into potential temporal changes in the diets of opportunistic feeders. Furthermore, it is difficult to identify detritus and soft-bodied or partially-digested prey, and it provides information only about ingestion rather than what is assimilated (Boyd *et al.*, 1984; Michener and Schell, 1994). Methods such as fatty acid and stable isotope ratio analysis, however, provide time-integrated information about an organism‟s feeding history, and can help to

determine major carbon sources, even in detritus-driven systems (Michener and Schell, 1994; Parrish *et al.*, 2000; Dalsgaard *et al.*, 2003; Budge *et al.*, 2007).

1.2.1. Stable isotopes

Stable isotope ratios in the body tissues of organisms are used to determine the sources of organic matter in a food web, the dominant trophic pathways through food webs and the trophic level of consumers (Peterson and Fry, 1987). Hydrogen, oxygen, carbon, nitrogen and sulphur are commonly used elements; however, carbon and nitrogen have been widely employed to determine dominant food sources and trophic pathways in aquatic systems (Hobson and Welch, 1992; Kling *et al.*, 1992; Peterson, 1999; Iken *et al.*, 2001; Corbisier *et al.*, 2004; Richoux and Froneman, 2007; Allan *et al.*, 2010). These elements are widely used as the ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ show predictable changes through a food web due to respiration and excretion of lighter isotopes by the consumers (Fry and Sherr, 1984; Peterson and Fry, 1987; Fry, 1988). For example, different species of primary producers fix ^{13}C and ^{12}C isotopes in different ratios, and this resultant „signature" shows little change when assimilated by consumers (enriched by ~1.0‰ per trophic transfer; Fry and Sherr, 1984). In this manner, the original source of organic matter that drives benthic food webs can be determined even after several trophic transfers (Hobson and Welch, 1992; Peterson, 1999; Iken *et al.*, 2001). Ratios of ^{15}N to ^{14}N are typically enriched by ~3.4‰ at each trophic transfer (Peterson and Fry, 1987). This enrichment, or fractionation, is due to the concentration of the lighter ^{14}N isotope in nitrogenous waste, while the heavier ^{15}N isotope is retained in the body tissue (Peterson, 1999). This large fractionation permits the use of nitrogen isotope ratios as indicators of the trophic level of an organism (Peterson, 1999).

Unfortunately, food webs can be difficult to resolve using isotopic ratios, especially in instances where the potential food sources are not isotopically distinct or a wide variety of potential food sources exists (Peterson, 1999; Schmidt *et al.*, 2003; Richoux and Froneman, 2007). In natural environments, nitrogen isotope fractionation is also not constant and many factors, such as the origin (nitrogen-fixation *versus* upwelling or terrigenous nutrient sources), presence of different nutrient forms (nitrates *versus* ammonia), denitrification and nutritional stress, can play vital roles in determining the isotopic composition of the source nitrogen (Hobson, 1993; Gorokhova and Hansson, 1999; Adams and Sterner, 2000; Tyrrell and Lucas, 2002; Needoba *et al.*, 2003). Both carbon and nitrogen isotope fractionation can vary for a single primary producer due to different physiology and metabolic pathways in

different species or with changes in season and geographical region (Michener and Schell, 1994; Montoya and McCarthy, 1995; Needoba *et al.*, 2003). Different turnover rates of distinct tissues, and variations in growth rates among individuals, may all hinder investigations of carbon transfer through a food web (Fry *et al.*, 1983; Tieszen *et al.*, 1983). In addition, different methods for the storage and preservation of samples may alter their $\delta^{13}C$ and $\delta^{15}N$ values (Kaehler and Pakhomov, 2001). Therefore, it has been suggested that stable isotope ratios should be supplemented with additional techniques such as fatty acid analysis (Perga *et al.*, 2006).

1.2.2. Fatty acids

Fatty acid analysis has been successfully used to enhance our understanding of feeding ecology and trophic pathways in a variety of aquatic ecosystems (Graeve *et al.*, 1997; Kharlamenko *et al.*, 2001; Perga *et al.*, 2006; Budge *et al.*, 2007; Richoux and Froneman, 2008). They can be used to determine an organism‟s diet and trophic interactions as well as identify driving processes that may have an impact on ecosystem structure and functioning (Dalsgaard *et al.*, 2003; Budge *et al.*, 2007). Fatty acids are important in maintaining the structure and function of cell membranes and are therefore vital for growth and reproduction (Sargent *et al.*, 1989; Parrish, 1999; Arts *et al.*, 2001). Some fatty acids cannot be effectively synthesised by animals but are vital for the function of organs, therefore these must be obtained from their diet (Olsen, 1999; Parrish, 1999; Arts *et al.*, 2001). These essential fatty acids (EFAs; include 20:4ω6, 20:5ω3 and 22:6ω3) are produced by autotrophs, and they tend to be preferentially conserved in food webs (Arts *et al.*, 2001). This retention and transfer of specific components through a food chain allows for the use of fatty acids as biomarkers. There is evidence, however, that consumers can convert dietary fatty acids such as ω3 and ω6, into longer chain fatty acids with more double bonds (Cook and McMaster, 2002; Tocher, 2003). These conversions can make it difficult to allocate specific fatty acids to specific food sources. As a result, the ideal biomarkers are those synthesised at the base of a food web that persist without major modifications at higher trophic levels (Napolitano *et al.*, 1997; Dalsgaard *et al.*, 2003). Different primary producers and heterotrophs also possess distinct fatty acid profiles which can be utilised as „signatures“ to describe feeding interactions (Graeve *et al.*, 1994; Dalsgaard *et al.*, 2003; Budge *et al.*, 2007). As a result, fatty acids can be used to determine trophic interactions and the sources of lipids assimilated over a period of time (Graeve *et al.*, 1994; Dalsgaard *et al.*, 2003). The use of fatty acids has been particularly successful in aquatic systems with a small number of primary producers

that are highly distinct from one another (Richoux *et al.*, 2005; Allan *et al.*, 2010). Fatty acids can, however, be used to determine the major organic sources in more complex systems such as detrital systems, which cannot be obtained from gut content analysis (Dalsgaard *et al.*, 2003; Richoux and Froneman, 2008). As stable isotopes and fatty acids can provide different information about the feeding ecology of organisms (i.e. an estimate of trophic level *versus* detailed dietary composition, respectively), the use of these two techniques as a complementary approach have been more successful at resolving trophodynamics in complex aquatic systems (Kiyashko *et al.*, 1998; Kharlamenko *et al.*, 2001; Perga *et al.*, 2006; Allan *et al.*, 2010).

1.3. GLOBAL CLIMATE CHANGE IN THE SOUTHERN OCEAN

There is growing evidence from a variety of sources that global climate change is beginning to have an impact on the Southern Ocean ecosystem. Across the sub-Antarctic, there have been gradual increases in the air and sea (surface and sub-surface) temperatures between the 1950‟s and present, but these warming rates have varied both spatially and temporally (Levitus *et al.*, 2000; Gille, 2002; le Roux, 2008). In the vicinity of the PEI, the sea surface temperature has increased by 1.4^{o}C between 1949 and 1999 (Mélice *et al.*, 2003), while the air temperature on Marion Island has increased by 1.2^{o}C over the corresponding period (Smith, 2002; le Roux and McGeoch, 2008). This rapid rate of warming at the PEI is likely due to regional changes in climate, as the Antarctic peninsula and other sub-Antarctic islands have also experienced similar rates of warming over the same period (Frenot *et al.*, 1997; Tweedie and Bergstrom, 2000; Vaughan *et al.*, 2003; Weimerskirch *et al.*, 2003; Thost and Allison, 2005). Marion Island has experienced a concurrent decrease in annual precipitation since the mid 1960‟s, resulting in the island becoming warmer and drier (Smith, 2002). From a biological perspective, the drying and warming of the terrestrial system has resulted in altered patterns of primary productivity, nutrient recycling and habitat structure, and the range expansion of invasive species (Chown and Smith, 1993; Bergstrom and Chown, 1999; Smith *et al.*, 2001; Chown *et al.*, 2002; le Roux and McGeoch, 2008). Evidence for the impact of global climate change on the marine ecosystem is, however, generally lacking.

It has also been suggested that the southern hemisphere westerly winds have intensified in response to global warming, causing shifts in the position and intensity of major frontal systems (Thompson and Solomon, 2002; Oke and England, 2004; Fyfe *et al.*, 2007). The ACC has exhibited a gradual southward shift of up to ~1° of latitude (~111 km) in its average

position over the last 60 years (Gille 2002). The historical data (1959 – 1999) of the sub-Antarctic Front (SAF) in the region of the PEI has also indicated, but not conclusively, a possible southward migration over time (Pakhomov & Chown 2003), likely the result of large scale change in circulation patterns due to the warming of the surface waters (Moore *et al.*, 1999; le Roux, 2008; McQuaid and Froneman, 2008).

1.3.1. Changes in the marine environment around the Prince Edward Islands

The southward shift of the geographic position of the SAF has had a substantial impact on the species composition of the zooplankton assemblages within the region of the PEI. Over the past three decades, the occurrence of Antarctic species in the PFZ has decreased by ~20%, while subtropical species occurrence has increased from 6 to 26% (Pakhomov *et al.*, 2001). The increase in the occurrence of more subtropical species near the PEI suggests an increased frequency of intrusion of warmer sub-Antarctic surface waters into the PFZ (Pakhomov *et al.*, 2001). Since the sub-Antarctic surface waters are generally low in productivity, the increased intrusion of these waters at the PEI could result in a decrease in total zooplankton biomass, which will likely have a substantial effect on marine productivity of the PEI ecosystem (Hunt *et al.*, 2001; Bernard and Froneman, 2003; Chown and Froneman, 2008). Furthermore, the position of SAF relative to the islands also plays a crucial role in the hydrodynamics around the islands (Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 2000; Ansorge and Lutjeharms, 2002). The southward shift in the position of the SAF is likely associated with the predominance of a flow-through system in the region of the islands, with a concomitant decreased frequency of occurrence of the "island mass effect" (McQuaid and Froneman, 2008). The resultant less frequent diatom blooms in the inter-island region may have a direct impact on the benthic community and ultimately the PEI ecosystem as a whole (McQuaid and Froneman, 2008).

A long-term shift in isotope signatures, particularly $\delta^{13}C$ values, have been observed in the hyperbenthic shrimp *Nauticaris marionis* at the PEI over the period 1984 to 2000 (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). Variations in $\delta^{13}C$ signatures of phytoplankton have been linked with changes in isotopic fractionation due to alterations in water temperature, molecular CO_2 concentration and growth conditions (Bidigare *et al.*, 1997; Laws *et al.*, 1997; Rau *et al.*, 1997; Burkhardt *et al.*, 1999a, b). Marine $\delta^{13}C$ was proposed (empirical model) to increase with increasing temperature (Rau *et al.*, 1997), thus warming sea conditions are unlikely to account for the decrease in $\delta^{13}C$ values observed in

N. marionis. An increase in molecular CO_2 concentration can result in a decrease in marine $\delta^{13}C$ (Rau *et al.*, 1997). The increased CO_2 in the atmosphere, due to burning fossil fuel, could decrease the $\delta^{13}C$ value of oceanic dissolved inorganic carbon in subpolar region by -0.15 ‰ per decade (Kroopnick, 1985), resulting in a -0.3 ‰ decrease in $\delta^{13}C$ values at the PEI between 1984 and 2000 (Pakhomov *et al.*, 2004). The shrimp, however, demonstrated a much larger depletion in their $\delta^{13}C$ values over this period (predicted: -0.3 ‰, observed: -1.5 ‰; Pakhomov *et al.*, 2004). The growth rate of phytoplankton has a strong negative relationship with carbon isotope fractionation (Bidigare *et al.*, 1997; Laws *et al.*, 1997; Burkhardt *et al.*, 1999a, b). Thus, fast growing phytoplankton should have a more enriched $\delta^{13}C$ signature than slow growing phytoplankton in the same region. As a result, ^{13}C-depletions in aquatic systems may indicate a decline in pelagic primary productivity in the region (Schell, 2000; Hirons *et al.*, 2001). The apparent depletion in the $\delta^{13}C$ signatures of *N. marionis* at the PEI may result from changes in the carbon signal at the base of the food web caused by decreases in the overall productivity around the islands (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). The apparent decrease in productivity in the vicinity of the islands may reflect global climate change, as a southward shift in the SAF position is thought to promote a decrease in the frequency of occurrence of the "island mass effect" at the PEI (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). The impacts of global climate change on the PEI ecosystem are poorly understood since there are no long-term data available for key components such as the benthos, particularly the suspension- and deposit-feeders.

During the last two decades, there have been increases in the population sizes of offshore feeding land-based predators such as the grey-headed albatross and fur seals, which may be due to decreases in foraging distances from the PEI to frontal systems (Nel *et al.*, 2002; Crawford *et al.*, 2003a; Pakhomov and Chown, 2003; Hofmeyr *et al.*, 2006). Over the corresponding period, there has been concurrent decreases in the populations of inshore pursuit-diving feeders such as Gentoo penguins, Rockhopper penguins and Crozet shags (Pakhomov and Chown, 2003; Ryan and Bester, 2008). Species that feed in both the inshore and offshore regions, such as Macaroni penguins, showed less of a decline over the same period (Ryan and Bester, 2008). The decrease in the populations of inshore feeders likely reflects changes in food availability in the vicinity of the islands (Crawford *et al.*, 2003a, b, c), which may be due to decreased availability of important prey species such as *N. marionis*. Gut content analysis of inshore feeding predators, however, suggests that there is inter-annual

variation in the contribution of *N. marionis* in the diet of these predators, with the shrimp being almost completely replaced by allochthonous zooplankton in certain years (Brown and Klages, 1987; Brown *et al.*, 1990). This shift between the contribution of allochthonous zooplankton and *N. marionis* may result from an increased availability of zooplankton due to a flow-through system and/or fluctuations in the abundance of *N. marionis* due to periods of high predation pressure (Hunt *et al.*, 2001). To date there have been no quantitative studies on the estimates of *N. marionis* in the region of the islands, so long-term trends are not available.

1.4. THESIS OVERVIEW

The benthic community, through the key species *Nauticaris marionis*, plays a vital role in supporting large numbers of top predators at the PEI (McQuaid and Froneman, 2008), thus it is important to understand the dynamics of the benthos around these islands. As a result, the focus of this dissertation is to investigate the spatial changes in the trophic and energy pathways of the benthic and hyperbenthic communities in the shallow shelf waters of the sub-Antarctic PEI using both stable isotope and fatty acid analyses. As the current marine research programme at the PEI is restricted to the autumn months (April/May), no data could be collected to assess seasonal patterns in the benthic trophic ecology and energy pathways in the region of the islands. Historical data were, however, employed in conjunction with data collected during the current investigation to assess the long-term trends in the feeding ecology of the benthos in the region of the islands.

The aims of the study were:

- To provide the first fatty acid compositional data for the benthic community, the hyperbenthic shrimp *N. marionis*, and the major food sources at the PEI (Chapters 3 and 4)
- To assess the importance of phytoplankton (blooms) and kelp as food sources for benthic suspension- and deposit-feeders among different regions around the PEI using stable isotope ratios and target fatty acids (Chapter 3)
- To investigate the ontogenetic and spatial variations in the diet of the shrimp *N. marionis* in the region of the PEI using stable isotope ratios and fatty acid profiles (Chapter 4)
- To assess the potential impact of global climate change on selected components of the benthos and the shrimp *N. marionis* by combining stable isotope data collected during the present study with historical data collected in the region of the PEI over the past 25 years (Chapter 5)

2 MATERIALS AND METHODS

2.1. STUDY AREA AND SAMPLE COLLECTION

The study was conducted in the vicinity of the sub-Antarctic Prince Edward Islands (PEI; 46.77 °S, 37.85 °E) aboard the MV *SA Agulhas* during Voyage 145 in April 2009. The research forms part of the larger project entitled "Variability in the Southern Ocean ecosystems" and is a contribution to the South African National Antarctic Programme (SANAP). To determine regional variations in carbon utilisation by the benthic and hyperbenthic communities in the vicinity of the PEI, 10 stations, occupied over a range of depths from 70 to 295 m, were sampled as follows: seven stations in the inter-island shelf region and three stations in the nearshore regions of both islands (Table 2.1; Fig. 2.1). The inter-island stations were further separated into regions: upstream (east of the islands; Stations 1, 2 and 3), between the islands (Stations 4, 5 and 6) and downstream (west of the islands; Station 7).

2.1.1. Environmental variables and food sources

Surface water samples were collected at the 10 stations to determine total chlorophyll-*a* (chl-*a*) and suspended particulate matter (SPM) concentrations as well as stable isotope and fatty acid signatures of the SPM. These variables were also determined for the surrounding offshore region, in which surface water samples were collected from three stations upstream (east of the islands; Stations i, ii and iii) and five stations downstream (west of the islands; Stations iv, v, vi, vii and viii; Fig. 2.1). Due to logistical constraints, only surface water could be collected during this investigation. Water samples (1 m below the surface) were collected from the nearshore kelps adjacent to Station 8 to determine stable isotope ratios and fatty acid profiles for the SPM generated in the kelp beds. Fresh samples of the abundant kelp *Macrocystis laevis* were obtained from the nearshore kelp beds adjacent to Marion Island using a small motorised boat.

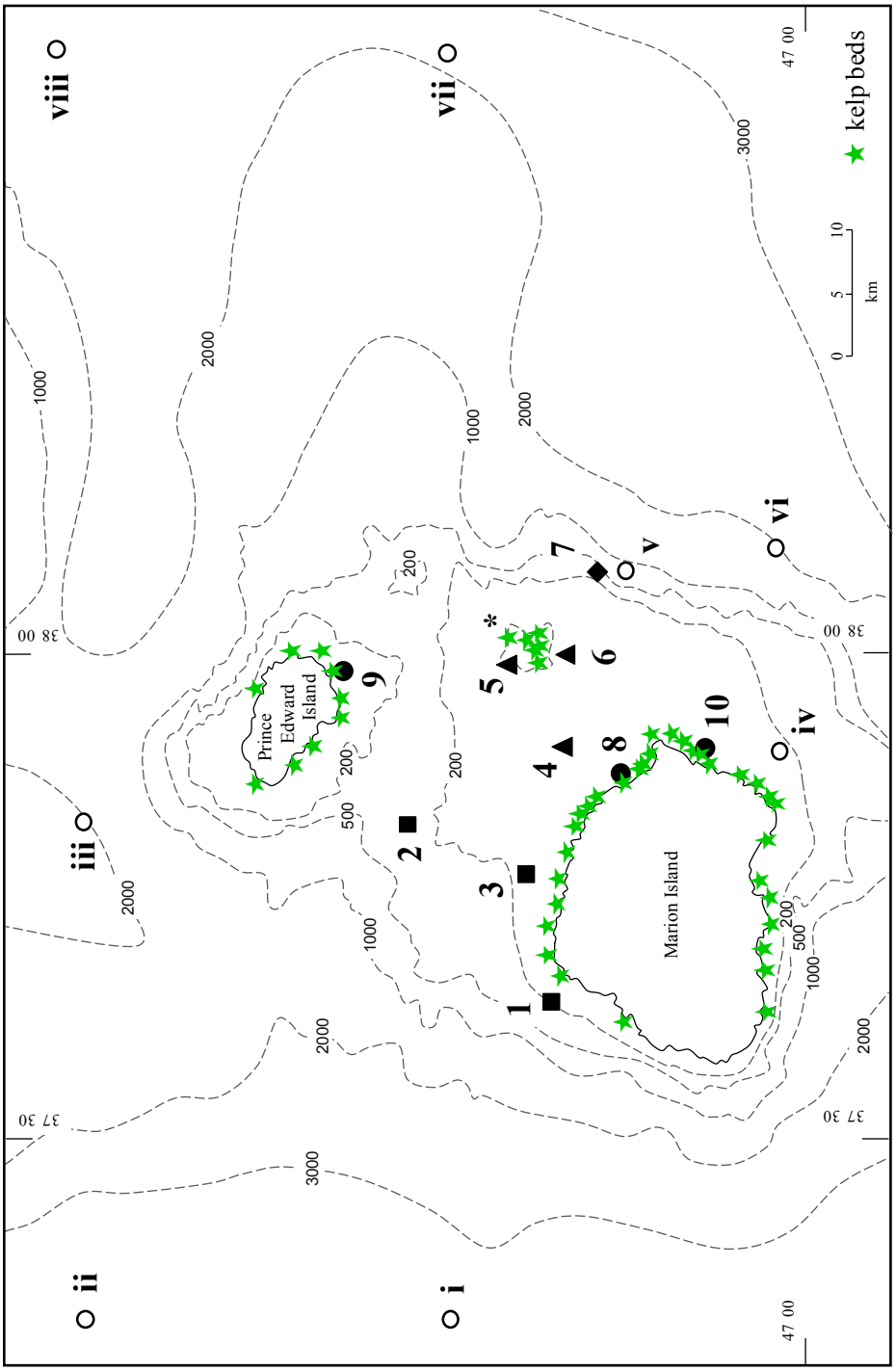

Figure 2.1. Survey area around the Prince Edward Islands indicating position of the 10 benthic stations. The benthic stations were divided into inter-island stations: upstream (1, 2 and 3; ■), between (4, 5 and 6; ▲) and downstream (7; ◆) of the islands, and nearshore (8, 9 and 10; ●). Surface water was collected from the surrounding offshore region (○): upstream (i, ii and iii) and downstream (iv, v, vi, vii). * Natal Bank: shallow bank with kelp beds.

Table 2.1. Position and information about the 10 benthic stations sampled around the Prince Edward Islands during the 2009 investigation.

Station	Position	Depth (m)	Latitude	Longitude	Information
Inter-island					
Upstream					
1	northwest of Marion	130	46°49'55"S	37°38'35"E	little detritus large pieces of sediment large pieces of volcanic rock
2	shelf upstream	295	46°43'14"S	37°49'37"E	little detritus
3	northeast of Marion	100	46°48'54"S	37°46'38"E	detritus large pieces of sediment small pieces of volcanic rock
Between					
4	central	140	46°50'14"S	37°54'08"E	detritus small pieces of sediment
5	Natal Bank	70	46°47'42"S	37°59'52"E	kelp fragments detritus
6	south of Natal Bank	150	46°49'46"S	37°59'31"E	detritus
Downstream					
7	shelf downstream	240	46°51'26"S	38°04'16"E	little detritus small pieces of sediment empty polychaete tubes
Nearshore					
8	east of Marion	70	46°52'16"S	37°52'15"E	kelp fragments detritus
9	southeast of Prince Edward	158	46°40'32"S	37°59'46"E	detritus
10	southeast of Marion	111	46°56'10"S	37°54'11"E	lots of detritus

2.1.2. Benthic community

The benthic community was sampled at each of the 10 stations using a benthic trawl (mouth size: 100 × 30 cm). To assess the relative importance of autochthonous *versus* allochthonous sources of organic matter in supporting the inter-island benthic community, suspension- and deposit-feeding species were selected. A total of 18 species from these two feeding guilds was collected from the 10 stations sampled (Table 2.2).

2.1.3. Hyperbenthic shrimp *Nauticaris marionis*

The hyperbenthic community, which is almost exclusively dominated by the shrimp *Nauticaris marionis*, was sampled at each of the 10 stations using a benthic trawl. Potential benthic food sources for these shrimp, such as detritus and benthic suspension- and deposit-feeding organisms, were also collected with benthic trawls, while pelagic food sources (zooplankton) were collected with plankton tows (Table 2.3). Zooplankton samples were collected using vertical tows during the day and night from three stations over the inter-island shelf region using a WP-2 net (mouth area: 0.25 m^2, mesh size: 200 µm).

Table 2.2. Spatial distribution of benthic suspension- and deposit-feeding organisms collected around the Prince Edward Islands and the analyses conducted (●: isotope ratios; ○: fatty acid profiles; number indicates sample size).

Taxonomic categories or species	Length	Name in plots	Inter-island							Nearshore		
			upstream				between		downstream			
			St 1	St 2	St 3	St 4	St 5	St 6	St 7	St 8	St 9	St 10
Suspension feeders												
Sponge												
sponge sp. 1	-	spon sp. 1	—	—	—	●3○3	—	—	—	—	●3○3	—
sponge sp. 2	-	spon sp. 2	—	—	—	—	—	●3○3	—	—	●3○3	—
sponge sp. 3	-	spon sp. 3	—	—	—	—	—	●3○3	—	—	●3○2	—
sponge sp. 4	-	spon sp. 4	—	—	—	—	—	○3	—	—	—	○3
Bryozoan												
bryozoan sp. 1	-	bryo sp. 1	—	—	●1○1	●1○1	—	●1○2	—	—	●1○3	●3○3
bryozoan sp. 2	-	bryo sp. 2	—	—	—	—	—	○2	●1○3	—	—	—
Brachiopod												
Magellania kerguelenensis (Davidson)	35 – 45 mm	brac	—	—	○1	○2	○1	●1○3	—	—	—	○3
Bivalve												
Limatula pygmaea (Philippi)	11 – 15 mm	biva sp. 1	●3○3	—	○1	—	●2○1	—	○1	—	—	—
Thracia meridionalis Smith	15 mm	biva sp. 2	●1○1	—	—	—	—	—	—	—	—	—
Polychaete												
Serpula vermicularis vermicularis Linnaeus	40 – 45 mm	poly sp. 1	—	—	—	—	—	—	—	—	○1	●1○1
Holothurian												
Pseudocnus laevigatus (Verrill)	33 – 35 mm	holo sp. 1	—	—	—	—	●2○1	—	—	—	—	●1○1
Psolus paradubiosus (Carriol and Feral)	15 – 17 mm	holo sp. 2	—	—	—	—	—	●1○3	—	—	—	—
Hydrozoan												
Plumularia insignis Allman	-	hyd	—	—	—	—	—	—	●1○1	—	—	—
Octocoral												
Thouarella variabilis Wright and Studer	-	gorgo	—	●1○1	—	—	—	—	●1○1	—	—	—
Pennatula inflata Kükenthal	-	sea pen	—	●1○1	—	—	—	—	—	—	—	—
Deposit feeders												
Polychaete												
Lanice marionensis Branch	30 – 40 mm	poly sp. 2	●3○3	—	●3○2	●1○1	○1	●1○1	○1	—	●3○3	—
Thelepus extensus Hutchings and Glasby	55 – 60 mm	poly sp. 3	—	—	—	—	—	—	—	●3○3	—	—
Gastropod												
Margarella expansa Sowerby	8 – 9 mm	gast	○1	—	—	—	—	—	—	○1	—	—

Table 2.3. Spatial distribution of detritus, zooplankton and *Nauticaris marionis* collected around the vicinity of the Prince Edward Islands and the analyses conducted (●: isotope ratios; ○: fatty acid profiles; number indicates sample size).

Taxon	Size class	Inter-island							Nearshore		
		upstream				between		downstream			
		St 1	St 2	St 3	St 4	St 5	St 6	St 7	St 8	St 9	St 10
Food sources											
Benthic											
Detritus		●3○3	—	●3○3	—	●3○3	●3○3	—	—	●3○3	●3○3
Pelagic											
Zooplankton											
< 500 µm [a]	small	—	●1○1	—	—	—	●1○1	●1○1	—	—	—
500 - 1500 µm [b]	medium	—	●1○1	—	—	—	●1○1	●1○1	—	—	—
> 1500 µm [c]	large	—	●1○1	—	—	—	●1○1	●1○1	—	—	—
Consumers											
Shrimp - *Nauticaris marionis* Bate											
4.0 – 5.0 mm	I	—	—	—	—	—	●1○1	—	○1	—	—
5.5 – 6.5 mm	II	—	—	●3○3	●1○3	○2	●3○3	●1○1	●3○3	●3○3	—
7.0 – 8.0 mm	III	●3○3	—	●3○3	●1○3	○3	●3○3	—	—	●3○3	●3○3
8.5 – 9.5 mm	IV	●3○3	—	●3○3	●3○3	●1○3	●3○3	—	●3○3	●1○3	●3○3
10.0 – 11.0 mm	V	●3○3	—	●3○3	●1○3	—	●3○3	●1○2	●1○3	—	●3○3

[a] composed of *Ctenocalanus vanus, Oithona similis* (copepods), *Limacina retroversa* (pteropod), ostracod spp. and unidentified larvae

[b] composed of *Calanus simillimus*, *Clausocalanus brevipes* (copepods), *Limacina retroversa* (pteropod), *Themisto gaudichaudi* (amphipod), *Euphausia vallentini*, *E. longitostris* (euphausiids) and ostracod spp.

[c] composed of *Calanus simillimus*, *Clausocalanus brevipes* (copepods), *Themisto gaudichaudi*, *Primno macropa* (amphipods), *Euphausia vallentini*, *E. longitostris* (euphausiids), *Sagitta gazellae* and *Eukrohnia hamata* (chaetognaths)

2.2. SAMPLE TREATMENT

2.2.1. Environmental variables and food sources

Aboard the MV *SA Agulhas*, total chl-*a* concentration of each water sample was determined using a modified procedure from Parsons *et al.* (1984). For each station, 250 ml aliquots of water were gently filtered (<5 mm Hg vacuum) through GF/F Whatman glass fibre filters (47 mm filters) and the chl-*a* was extracted in 8 ml of 90% acetone for 24 hours at -20°C. Samples were then centrifuged at 5000 rpm, after which the total chl-*a* concentration was measured before and after acidification with 1 M HCl using a Turner Designs 10AU Fluorometer. The total chl-*a* concentration was expressed as $\mu g\ L^{-1}$.

Aliquots of surface water intended for determination of stable isotope signatures (2.0 to 4.5 L), fatty acid composition (4.0 to 6.5 L) and total biomass of SPM (2.0 to 6.5 L) were filtered onto pre-ignited (450^{o}C overnight), pre-weighed GF/F filters. Filters were frozen and stored at -20^{o}C for the duration of the cruise, and transferred to -80^{o}C on return to the laboratory. These freezing procedures were the same for all samples collected during this study. The concentration of SPM (dry mass of the total suspended particulates in the water per unit volume; $mg\ L^{-1}$) was determined by weighing each filter once it had been dried to a constant weight at 60^{o}C.

Fresh fronds of the kelp *Macrocystis laevis* were washed in distilled water and any visible epibionts removed using forceps. Samples intended for fatty acid analysis were placed in boiling distilled water for 2 min to ensure that all lipolytic enzymes were denatured (Budge and Parrish, 1999), after which the samples were frozen at -20^{o}C and stored. A portion of fresh kelp fronds was placed in GF/F (pore size 0.7 μm) filtered seawater (FSW) and left to degrade in a bucket *in situ* for 3 weeks. The degraded fronds were removed and kept, and aliquots of the remaining water (0.4 to 0.6 L) were filtered onto pre-weighed GF/F filters. These samples were collected to obtain isotopic and fatty acid signatures of degraded kelp and kelp particulate organic matter (POM). The filters and kelp fronds were frozen at -20^{o}C and stored.

2.2.2. Benthic community

Following trawling at each site, the benthic organisms were separated according to feeding modes to prevent post-capture feeding and left in FSW for at least 12 hours to facilitate gut evacuation after which all animal samples were frozen at -20^{o}C and stored. In the laboratory,

frozen animal samples were dissected (when possible) and muscle tissue used for subsequent analyses. For some organisms, such as the bivalve *Limatula pygmaea* and the brachiopod *Magellania kerguelenensis*, individuals had to be pooled to obtain an adequate signal. Where possible, individuals of similar size were used (Table 2.2). All animals collected were processed to obtain fatty acid compositional data; however, stable isotope analysis was conducted only when there was ample tissue from an individual animal, or ample individuals sampled (Table 2.2). Where possible, individuals were identified to species level using taxonomic keys (Branch *et al.*, 1991; Branch and Williams, 1993; Branch *et al.*, 1993b; Branch, 1994).

2.2.3. Hyperbenthic shrimp *Nauticaris marionis*

Following collection at each site, the shrimps *Nauticaris marionis* were left in FSW for at least 12 hours to facilitate gut evacuation. Samples were repeatedly checked for dead individuals, and any found were immediately removed to prevent cannibalism. All *N. marionis* samples were then frozen at -20^{o}C and stored. In the laboratory, the frozen shrimp samples were dissected and muscle tissue from the abdomen removed for the analyses. For each individual, carapace length (CL) was measured from the posterior margin of the orbit to the dorsal midline of the posterior margin of the carapace (Pakhomov *et al.*, 1999, 2000a). The shrimps were grouped into the following size classes: 4.0 – 5.0 mm (I), 5.5 – 6.5 mm (II), 7.0 – 8.0 mm (III), 8.5 – 9.5 mm (IV) and 10.0 – 11.0 mm (V). All *N. marionis* collected were processed to obtain fatty acid compositional data; however, stable isotope analysis was conducted only when ample individuals were sampled (Table 2.3). Individual shrimp were analysed at each station.

Following collection, the mixed zooplankton samples were separated into three size fractions <500 µm (small), 500 – 1500 µm (medium) and >1500 µm (large), using a sieve of the corresponding mesh size. Each size fraction was vacuum filtered onto GF/F filters and immediately frozen at -20^{o}C and stored. In the laboratory, the frozen zooplankton size fractions were examined on ice under a dissection microscope to determine the species composition of each sample (Table 2.3) and to remove any contaminant material. Where possible, individuals were identified to species level using taxonomic keys (Bradford-Grieve *et al.*, 1999; Casanova, 1999; Gibbons *et al.*, 1999; van der Spoel and Dadon, 1999; Vinogradov, 1999). All zooplankton samples were processed to obtain fatty acid compositional data and stable isotope ratios (Table 2.3).

2.3. STABLE ISOTOPE ANALYSIS

In the laboratory, the SPM, kelp, detritus, benthic organisms, hyperbenthic *Nauticaris marionis* and zooplankton samples were lyophilized at -60°C for 24 hours. All kelp and benthic samples were individually homogenized using a mortar and pestle. Detritus, bryozoans, brachiopods, gorgonian corals, mixed zooplankton and whole body crustaceans and echinoderms were treated with 1 M HCl to remove carbonates, rinsed in distilled water and re-dried for 24 hours at 60°C (Fry, 1988; Fry and Wainright, 1991). Samples were processed to obtain stable carbon and nitrogen isotope analysis (IsoEnvironmental cc, Department of Botany, Rhodes University) using a Europa Scientific Elemental Analyser coupled to a 20-20 Isotope Ratio Mass Spectrometer (IRMS). In-house standards (Casein and a mixture of beet sugar and ammonium), calibrated against International Atomic Energy Agency (IAEA) standards, were used as internal calibrants. Isotope results were expressed in the δ notation:

$$\delta\ (‰) = (R_{sample} / R_{standard} - 1) \times 1000,$$

where δ (‰) is $\delta^{13}C$ or $\delta^{15}N$ and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively.

As lipids are isotopically lighter than other biochemical components, potential variation in isotope signatures arising from variable lipid content among species was minimized by incorporating a correction model from Post *et al.* (2007):

$$\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99\ (C:N),$$

where C:N is the ratio of carbon-to-nitrogen. In addition, the lipids were removed from a subset of samples from each species using a solution of chloroform:methanol:water (2:1:0.8; *v/v/v*) following Bligh and Dyer (1959). This last procedure was conducted to ensure that the results obtained using the correction model were comparable to the $\delta^{13}C$ signatures obtained when the lipids had been extracted. As no discernable difference was found between the two methods, the correction model was applied to all reported samples.

2.4. FATTY ACID ANALYSIS

In the laboratory, the SPM, kelp, detritus, benthic organisms, shrimp *Nauticaris marionis* and zooplankton samples were lyophilized at -60°C for 24 hours. All kelp and benthic samples were homogenized individually using a mortar and pestle. Each sample, including SPM and

kelp POM filters, was weighed (range 20 to 200 mg of dry mass, depending on availability) and stored at -20°C in 2 ml chloroform with butylated hydroxytoluene (BHT) under nitrogen.

Total lipids were extracted using the methods modified from Folch *et al.* (1957). Samples were homogenised in 2:1 (*v/v*) chloroform:methanol and the lipid layer was separated using aqueous potassium chloride and methanol. A known quantity of an internal standard (23:0) was added to each sample extract to enable fatty acid methyl ester (FAME) quantification. FAMEs were prepared using methods modified from Budge *et al.* (2006). FAME extracts suspended in anhydrous dichloromethane were heated with sulphuric acid (1.5%) at 100°C for 1 hour. Lipid layers were rinsed with hexane and MilliQ-distilled water.

FAME composition of each sample was determined by gas chromatography (GC) analysis in a Hewlett-Packard 5890 Series II GC equipped with a 100% polyethylene glycol capillary column (30 m length, 0.32 mm internal diameter, 0.25 μm film thickness; ZB-Waxplus 320) with helium as the carrier gas. Aliquots (1 μl) of sample were manually injected at 250°C with the oven set at 150°C. After 5 min, the oven temperature was raised to 225°C at 2.5°C min^{-1} and held for 5 min. The temperature of the flame ionization detector was set at 280°C.

Peaks were integrated using Clarity (version 2.6), and identified using gas chromatography-mass-spectrometry (GC-MS; Agilent Technologies 7000 GCMS-QQQ using the NIST 08 MS library) from a subset of samples for each species by comparing retention times with those of known external standards (37 component FAME mix, marine PUFA no. 1 and bacterial acid methyl esters mix, Supelco) and quantified by comparing peak areas with those of the internal standard. Each fatty acid was measured qualitatively as a proportion of the total identified fatty acids (% TFA), and quantitatively as the fatty acid weight per mg dry mass (μg FA mg^{-1} DM). Fatty acids are reported in the shorthand form x:aωb, where x is the number of carbon atoms in the acyl chain, a is the total number of double bonds, and b is the position of the first double bond from the methyl end of the molecule (Dalsgaard *et al.*, 2003).

3 REGIONAL VARIATIONS IN THE DIETS OF BENTHIC SUSPENSION- AND DEPOSIT-FEEDING COMMUNITIES AROUND THE PRINCE EDWARD ISLANDS

3.1. INTRODUCTION

The Prince Edward Islands (PEI), despite being situated in a region of low productivity (Laubscher *et al.*, 1993; Froneman *et al.*, 2001), support a diverse (~550 species) and biomass-rich inter-island benthic community (Branch *et al.*, 1993a; Pakhomov and Froneman, 1999a). The PEI periodically demonstrate localised enhanced phytoplankton production (total chlorophyll-*a* [chl-*a*] concentration: >1.5 μg L^{-1} up to 3.0 μg L^{-1}) within the immediate vicinity of the islands, a phenomenon known as the "island mass effect" (El-Sayed *et al.*, 1979; Allanson *et al.*, 1985; Boden, 1988; Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 1990; Kaehler *et al.*, 2006). This enhanced production is sustained by localised water column stability and increased macronutrient concentrations conferred by freshwater runoff from the islands which is retained on the island shelf due to the presence of anticyclonic eddies (Ismail, 1990; Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 2000). During these blooms, the bulk of the phytoplankton production is not utilised directly, and a large portion sinks to the seafloor, thus providing an important food source for the benthic community in the shallow shelf regions of the islands (Perissinotto, 1992; Pakhomov and Froneman, 1999a). The frequency and intensity of the pelagic blooms vary temporally, as other studies have recorded relatively low total chlorophyll concentrations (<0.3 μg L^{-1}) within the immediate vicinity of the PEI, similar to those typical of the surrounding open ocean (Miller *et al.*, 1984; Allanson *et al.*, 1985; Van Ballegooyen *et al.*, 1989; Balarin, 2000; Pakhomov *et al.*, 2000b; Perissinotto *et al.*, 2000). The periods of relatively low productivity usually occur when the sub-Antarctic Front (SAF) lies in close proximity to the islands, creating the formation of a flow-through system (Pakhomov and Froneman, 1999a; Balarin, 2000; Perissinotto *et al.*, 2000). In addition to the "island mass effect" the extensive kelp beds around the islands are potentially important in providing organic matter to the local benthic communities (Kaehler *et al.*, 2000, 2006).

The benthic community of the shallow inter-island shelf region of the PEI plays an important role in supporting higher trophic levels through benthic-pelagic coupling (Perissinotto and McQuaid, 1990; Pakhomov and Froneman, 1999a; Pakhomov *et al.*, 1999). As a consequence, the benthic community plays a crucial role in the functioning of the entire island ecosystem. As open ocean islands are characterised by variable oceanographic conditions and nutrient inputs, it is important to characterise the diets of this benthic community to determine trophodynamics of the PEI ecosystem. Thus, the aims of this study were to use stable isotope and fatty signatures to determine the role of autochthonous and allochthonous food sources in supporting the benthic community in the vicinity of the PEI, and to determine whether there are spatial variations in carbon utilisation around the islands. It was hypothesized that phytoplankton dominates in the diets of the suspension- and deposit-feeding organisms from the shallow shelf region of the PEI, and that organisms from nearshore stations have higher contributions of kelp in their diets than those from the open shelf region due to their close proximity to kelp beds.

3.2. MATERIALS AND METHODS

3.2.1. Study area, sample collection and treatment

To determine regional variations in the diets of benthic suspension- and deposit-feeding communities in the vicinity of the PEI, 10 stations were sampled as described in Chapter 2, sections 2.1 and 2.1.2. Eighteen species of suspension- or deposit-feeders were collected from the 10 stations (see Table 2.2; Chapter 2). Total chl-*a* and suspended particulate matter (SPM) concentrations were determined in the immediate vicinity of the islands and the larger surrounding region (Chapter 2, sections 2.1.1 and 2.2.1). All suspension- and deposit-feeding organisms (wherever possible), as well as potential food sources (kelp and SPM), were processed for stable isotope and fatty acid analyses (see Table 2.2; Chapter 2, sections 2.2.1 and 2.2.2).

3.2.2. Stable isotope analysis

All isotopic analyses were conducted as described in Chapter 2, section 2.3.

3.2.3. Fatty acid analysis

See Chapter 2, section 2.4 for complete descriptions of the fatty acid protocols used. Essential fatty acids (EFAs) include 20:4ω6, 20:5ω3 and 22:6ω3 (Arts *et al.*, 2001), while bacterial fatty acids (BAFAs) are those with odd-numbered carbon chains and/or *iso*- (*i*-) and

anteiso- (*ai*-) branches (Harvey, 1994; Budge and Parrish, 1998) and higher plant fatty acids (HPFAs) include 18:2ω6 and 18:3ω3 (Dalsgaard *et al.*, 2003). Saturated fatty acids (SFAs) are those without double bonds (e.g. 14:0), monounsaturated fatty acids (MUFAs) contain a single double bond (e.g. 16:1ω7) while polyunsaturated fatty acids (PUFAs) have >1 double bond (e.g. 16:4ω3). All double bonds were assumed to be methylene-interrupted and in *cis* configuration unless otherwise noted.

3.2.3.1. Target fatty acids

The fatty acid 20:5ω3 were used to indicate the presence of diatoms in the diets of the suspension- and deposit-feeders, while 22:6ω3 was used to indicate feeding on dinoflagellates (Parrish *et al.*, 2000; Dalsgaard *et al.*, 2003). To determine the relative importance of the different food sources (i.e. kelp *versus* diatoms and dinoflagellates) in the diets of the benthos among different regions around the islands and among species, specific fatty acids were examined as follows: 18:2ω6, 18:3ω3 and 20:4ω6 for kelp plant (fresh and degraded); 18:1ω7 for degraded kelp-associated bacteria; 20:5ω3 for diatoms; and 22:6ω3 for dinoflagellates. The fatty acids used as kelp indicators were obtained from the profiles obtained from the fresh and degraded kelp fronds, and degraded associated particulate organic matter (POM; see section 3.3.3.1)

3.2.4. Data analysis

Total chl-*a* and SPM concentrations, and $\delta^{13}C$ signatures and total fatty acid (TFA) concentrations of SPM from both offshore and the vicinity of the PEI were plotted using Ocean Data View v. 3.2.2 (Schlitzer, 2010). Coefficient of variation (CV) was calculated from the ratio of the standard deviation to the mean and expressed as a percentage (% CV). Variance is reported as one standard deviation (SD) from the mean.

In kelp systems the majority of photosynthesised carbon likely originates from either kelp or phytoplankton (Dunton and Dayton, 1995; Mann, 2000). To estimate the relative carbon contributions made by these two sources to the suspension- and deposit-feeding communities, a simple mixing model for a two-source system (McConnaughey and McRoy, 1979) was employed. For each animal sample, the percentage contribution of kelp-derived carbon (% $C_{kelp\ derived}$) was calculated as follows:

$$\% C_{kelp\ derived} = (\delta^{13}C_{consumer} - \delta^{13}C_{phytoplankton} - I \times 100) / (\delta^{13}C_{kelp} - \delta^{13}C_{phytoplankton}),$$

where *I* is the average post-photosynthetic fractionation of $\delta^{13}C$ per trophic level (set at 1.00 ‰; DeNiro and Epstein, 1978; Fry and Sherr, 1984; Peterson *et al.*, 1985). The $\delta^{13}C$ value used for kelp was obtained from the degraded kelp detritus (POM). The contributions made by kelp and phytoplankton were determined for a mixed phytoplankton community (likely to be small diatoms, dinoflagellates and coccolithophorids). The $\delta^{13}C$ values used to represent the mixed phytoplankton community were derived from previous studies conducted within the region (Kaehler *et al.*, 2006; Pakhomov *et al.*, 2009). The contribution calculations could potentially be used to determine the sources of assimilated nitrogen, but due to the lack of $\delta^{15}N$ values available for primary producers in the region, this was not feasible (see section 3.3.2.1).

3.3. RESULTS

3.3.1. Environmental variables and food sources

Total chl-*a* concentrations in the vicinity of the islands showed no distinctive spatial patterns (Fig. 3.1A) and were similar to those in the surrounding offshore region (vicinity of the islands: 0.13 to 0.29 µg L^{-1}; offshore: 0.16 to 0.33 µg L^{-1}; Figs. 3.1A and C), with the exception of Station viii (0.66 µg L^{-1}). Moderately enhanced SPM concentrations were recorded at Stations 3 and 8 (7.33 and 8.04 mg L^{-1}, respectively; Fig. 3.1B). The SPM concentrations in the vicinity of the islands were still relatively low and similar to those in the offshore region (3.04 to 8.04 mg L^{-1} and 3.64 to 6.72 mg L^{-1}, respectively; Figs. 3.1B and D).

3.3.2. Stable isotopes

3.3.2.1. Food sources

As only small volumes of particulate matter could be obtained by filtration, $\delta^{15}N$ values could not be accurately determined in surface water SPM and the degraded kelp POM samples. Therefore, only $\delta^{13}C$ signatures were used to estimate the importance of different primary producers to the diets of the selected consumers. The surface water SPM in the vicinity of the islands showed similar $\delta^{13}C$ signatures to that of the offshore region and ranged from -25.00 to -23.54 ‰ (Figs. 3.2A and B).

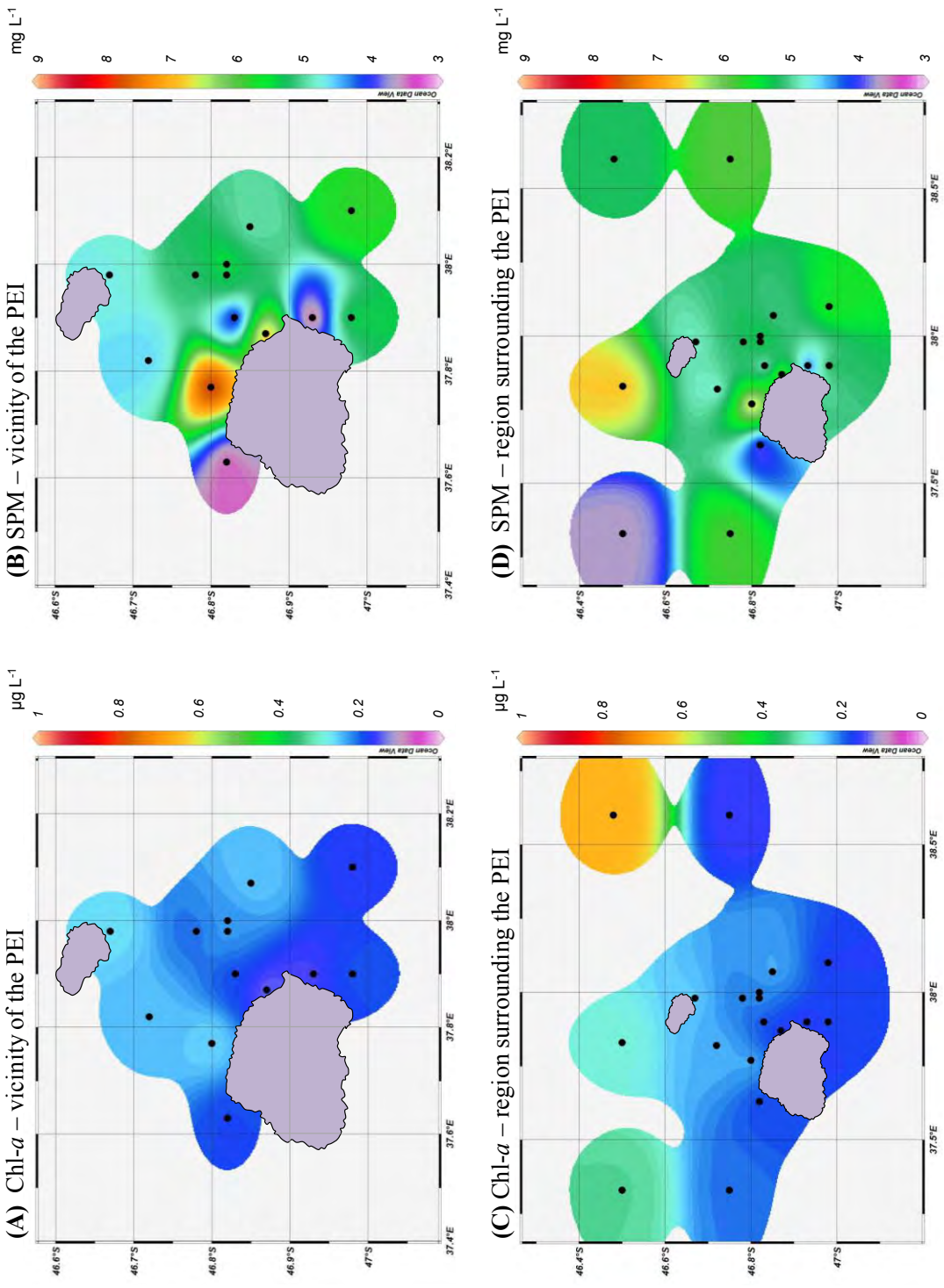

Figure 3.1. Surface water total chlorophyll-*a* (chl-*a*; µg L^{-1}) and suspended particulate matter (SPM; mg L^{-1}) concentrations in the vicinity (A and B, respectively) and in the offshore region (C and D, respectively) of the Prince Edward Islands.

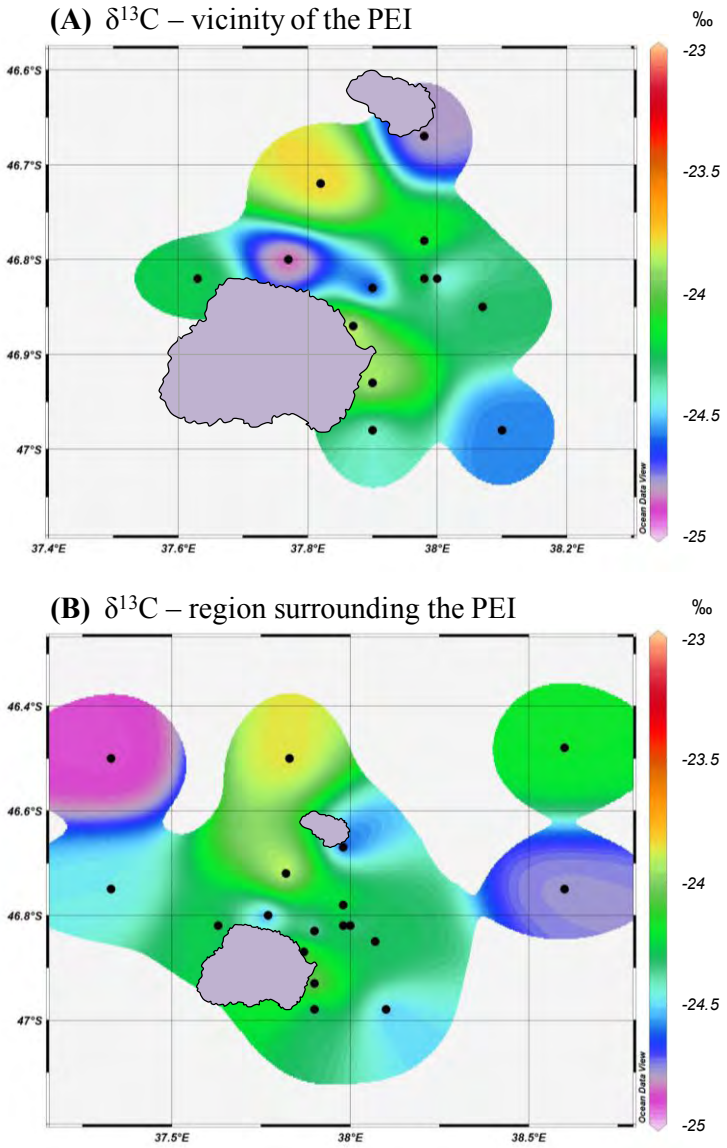

Figure 3.2. $\delta^{13}C$ signatures (‰) of the surface water suspended particulate matter in the vicinity (A) and in the offshore region (B) of the Prince Edward Islands.

The two dominant types of primary producers found in the vicinity of the PEI had distinct $\delta^{13}C$ signatures (SPM [mixed phytoplankton and detritus]: -25.00 to -23.54 ‰ and kelp: -19.31 to -15.34 ‰; Tables A1 and A2). The kelp *Macrocystis laevis* had $\delta^{13}C$ and $\delta^{15}N$ signatures that varied between degraded and fresh fronds, whereby degraded fronds were more depleted (-19.01 ± 0.29 ‰ and 3.67 ± 0.31 ‰, respectively) than the fresh fronds (-15.57 ± 0.20 ‰ and 4.27 ± 0.52 ‰, respectively). Interestingly, the $\delta^{13}C$ signature of the degraded kelp POM fell between those of the fresh and degraded fronds (-17.50 ‰).

3.3.2.2. Suspension- and deposit-feeders

The suspension-feeding organisms showed a wide range of $\delta^{15}N$ signatures (0.41 to 8.81 ‰; Fig. 3.3) compared to the deposit-feeders (3.82 to 5.91 ‰; Fig. 3.4). Some species such as

bryozoan sp. 1, had a wide range of $\delta^{15}N$ signatures among stations, while others such as sponge sp. 1, sponge sp. 2 and bivalve sp. 1 had similar $\delta^{15}N$ signatures among stations (Fig. 3.5). The $\delta^{13}C$ signatures of the suspension- and deposit-feeding organisms also showed a wide range of values among species (Figs. 3.3 and 3.4). The signatures, however, were similar in both feeding guilds (-23.15 to -19.02 ‰ and -23.74 to -20.52 ‰ in suspension- and deposit-feeders, respectively), and all organisms were enriched by ≥1.00 ‰ relative to surface water SPM (-24.25 ± 0.47 ‰; Figs. 3.3 and 3.4).

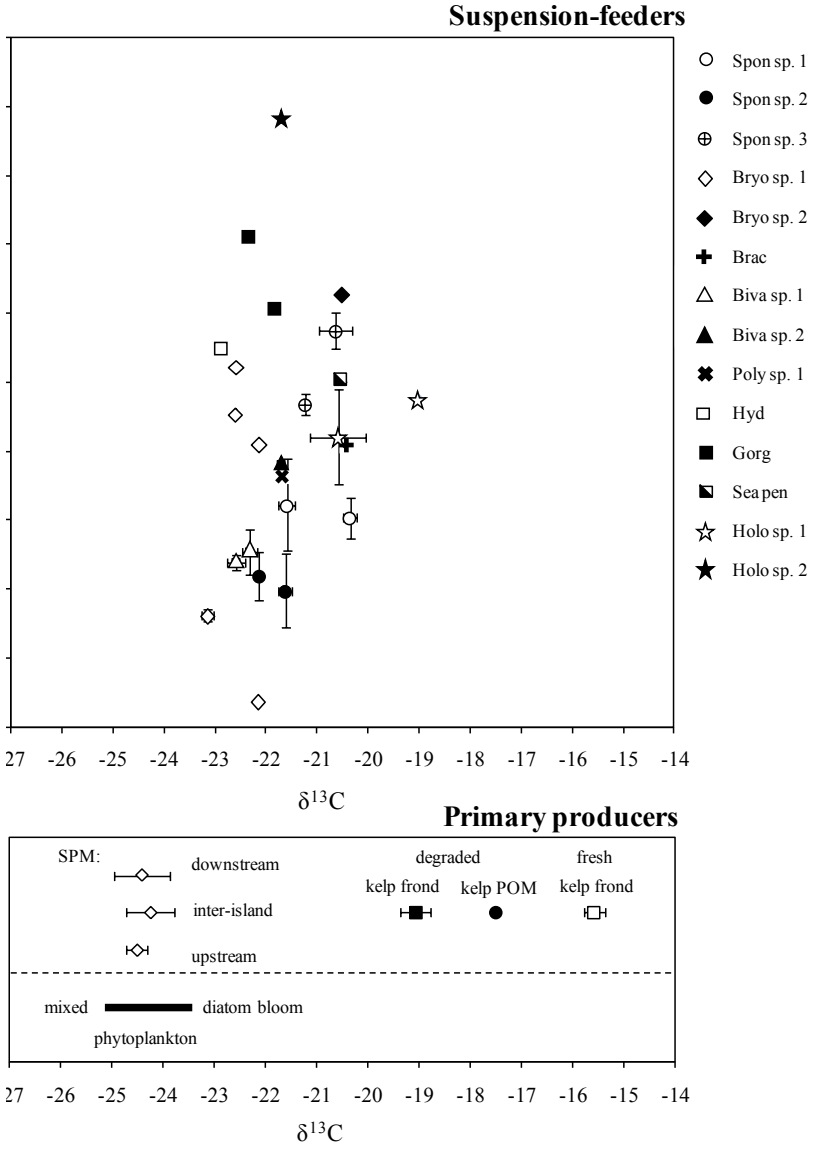

Figure 3.3. $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of the benthic suspension-feeding organisms collected at all regions around the Prince Edward Islands and $\delta^{13}C$ signatures (‰) of the potential primary producers contributing to their diets. Phytoplankton signatures were obtained from previous studies in the region (Kaehler *et al.*, 2006; Pakhomov *et al.*, 2009); range of $\delta^{13}C$ values for various phytoplankton communities is indicated by the black line with community composition indicated at each end (mixed: mixture of small diatoms, dinoflagellates and coccolithophorids; diatom bloom: a phytoplankton community dominated by large chain-forming diatoms); error bars represent standard deviations.

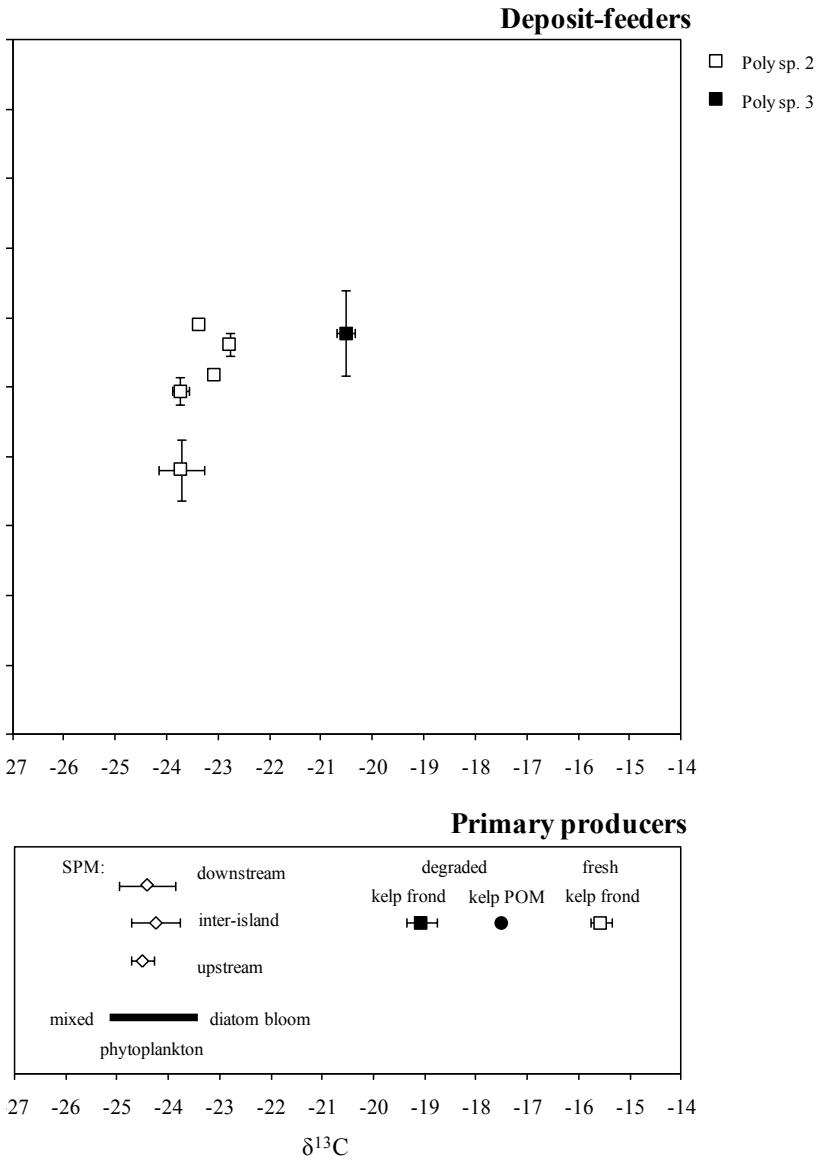

Figure 3.4. $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of the benthic deposit-feeding organisms collected at all regions around the Prince Edward Islands and $\delta^{13}C$ signatures (‰) of the potential primary producers contributing to their diets. Phytoplankton signatures were obtained from previous studies in the region (Kaehler *et al.*, 2006; Pakhomov *et al.*, 2009); range of $\delta^{13}C$ values for various phytoplankton communities is indicated by the black line with community composition indicated at each end (mixed: mixture of small diatoms, dinoflagellates and coccolithophorids; diatom bloom: a phytoplankton community dominated by large chain-forming diatoms); error bars represent standard deviations.

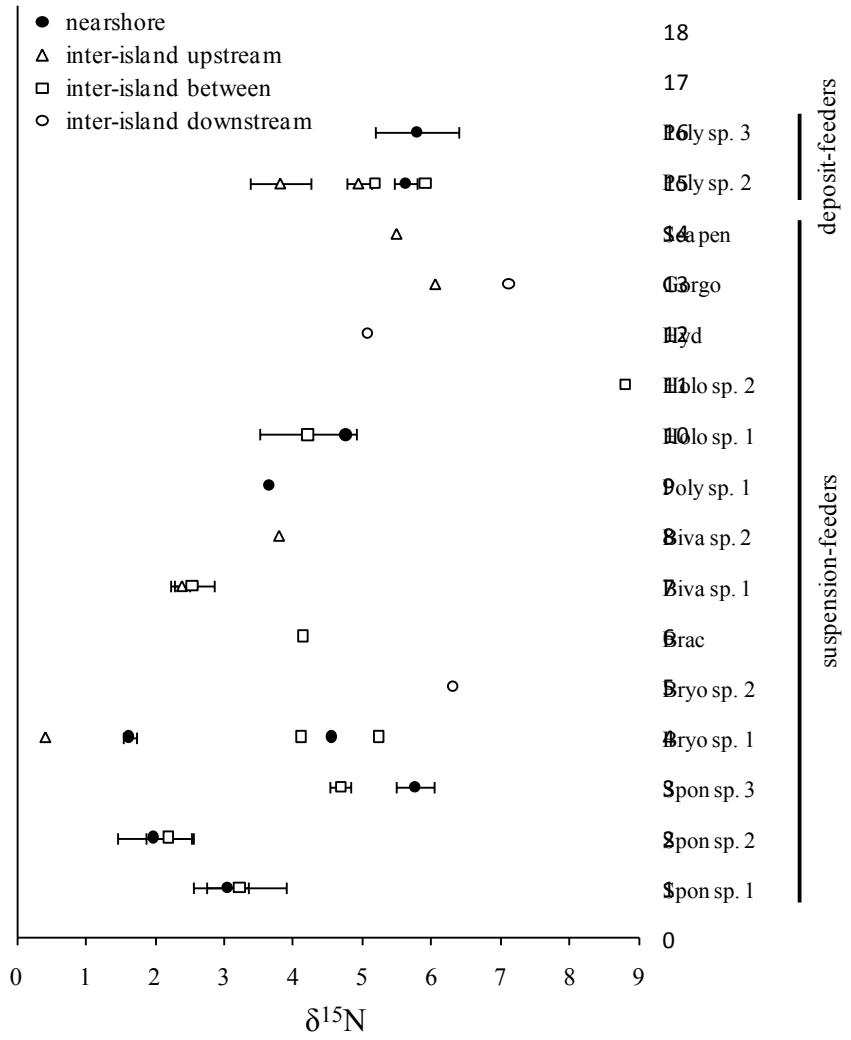

Figure 3.5. $\delta^{15}N$ signatures (‰) of the benthic suspension- and deposit-feeding organisms in the different regions around the Prince Edward Islands. Error bars indicate standard deviations.

The contributions of phytoplankton and kelp to the diets of the benthic suspension- and deposit-feeders among the different regions are depicted in Figure 3.6. As kelp enters the food web through the detrital food chain (Mann, 1988; Duggins *et al.*, 1989; Kaehler *et al.*, 2000; Fredriksen, 2003), the $\delta^{13}C$ signature for kelp detritus (i.e. degraded kelp POM) was used to denote kelp that could be ingested by benthic organisms. For all the suspension- and deposit-feeding organisms, except nearshore holothurian sp. 1, their diet constitution was between a 50% kelp/phytoplankton and a 100% mixed phytoplankton diet. Of the 17 species in Figure 3.6, nine showed a diet almost completely composed of phytoplankton (either from 100% mixed phytoplankton or 100% diatom origin). In general, there was a depletion in $\delta^{13}C$ signatures from upstream individuals to those from between the islands and the nearshore individuals, suggesting an increase in the contribution of kelp detritus in their diets at stations closer to the islands.

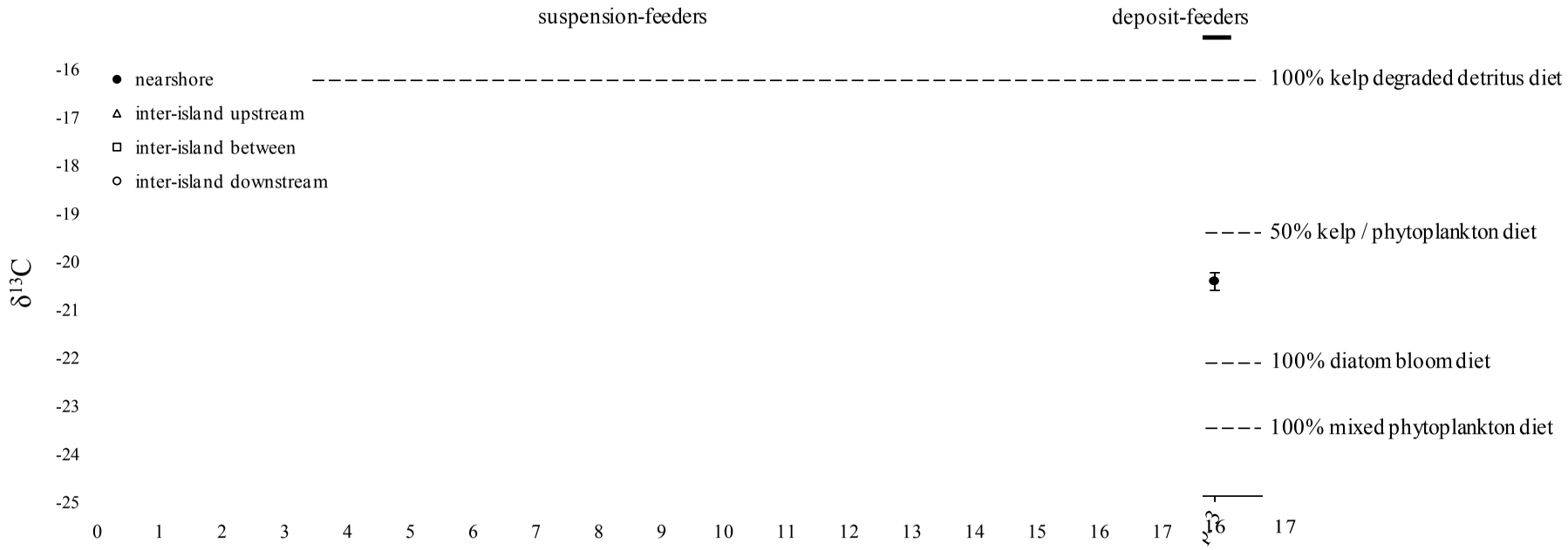

Figure 3.6. $\delta^{13}C$ signatures (‰) of the benthic suspension- and deposit-feeding organisms in the different regions around the Prince Edward Islands. Estimated 100% diet lines were calculated using an average trophic enrichment of 1.00 ‰ for carbon (Fry and Sherr, 1984; Peterson *et al.*, 1985); signatures for diatom blooms from a similar region were obtained from Pakhomov *et al.* (2009); error bars represent standard deviations.

Using a simple linear mixing model for a two-source system (mixed phytoplankton community and kelp; McConnaughey and McRoy, 1979) the kelp was estimated to contribute between 8.8 and 65.5% to the diet of the suspension-feeders and between 0.8 and 44.9% to the deposit-feeders.

3.3.3. Fatty acids

3.3.3.1. Food sources

The fatty acid profiles of the fresh and degraded kelp fronds (*M. laevis*) both contained large proportions of 16:0, 18:1ω9 and 20:4ω6; however, the degraded kelp contained proportionally less of these three fatty acids than the fresh kelp (Table A2). The fresh and degraded kelp both had large proportions of PUFAs (47.0 ± 10.6% TFA and 51.4 ± 7.0% TFA; respectively) and EFAs (25.6 ± 3.5% TFA and 27.1 ± 4.6% TFA, respectively), and moderate proportions of HPFAs (12.5 ± 3.2% TFA and 11.6 ± 2.9% TFA, respectively). The degraded kelp had proportionally more BAFAs and contained >3 times the quantity of TFAs than the fresh kelp (BAFAs: 3.6 ± 0.4% TFA and 0.7 ± 1.0% TFA, respectively; TFAs: 43.9 ± 5.2 µg FA mg^{-1} DM and 13.2 ± 1.3 µg FA mg^{-1} DM, respectively). The POM from the degraded kelp contained smaller TFA concentrations, and PUFA and EFA proportions but greater MUFA proportions than the actual degraded kelp (TFA: 20.4 µg FA mg^{-1} DM *versus* 43.9 ± 5.2 µg FA mg^{-1} DM; PUFAs: 14.5% TFA *versus* 51.4 ± 7.0% TFA; EFAs: 6.2% TFA *versus* 27.1 ± 4.6% TFA; MUFAs: 56.1% TFA *versus* 18.6 ± 2.5% TFA). The fatty acids 18:2ω6, 18:3ω3 and 20:4ω6 were prevalent in both fresh and degraded kelp fronds (Table A2). These fatty acids (18:2ω6, 18:3ω3 and particularly 20:4ω6) can also be found in other plant and macroalgae species (Arts *et al.*, 2001; Dalsgaard *et al.*, 2003), but as there is a high density of *M. laevis* kelp around Marion and Prince Edward Islands (~12 kg m^{-2}; Attwood *et al.*, 1991; Beckley and Branch, 1992), which generates substantial productivity (estimated 2.0 to 3.5 times greater than that of phytoplankton; Beckley and Branch, 1992), it was estimated that the majority of these fatty acids originated from the kelp. Therefore, these three fatty acids (18:2ω6, 18:3ω3 and 20:4ω6) were used as target identifiers for kelp plant material (fresh and degraded). The fatty acids 16:1ω7 and 18:1ω7 were found in large proportions in the degraded kelp POM (34.4 and 17.7% TFA, respectively; Table A2). As 16:1ω7 can also be associated with diatoms (Parrish *et al.*, 2000; Dalsgaard *et al.*, 2003), only 18:1ω7 was used to indicate the prevalence of bacteria associated with degraded kelp POM.

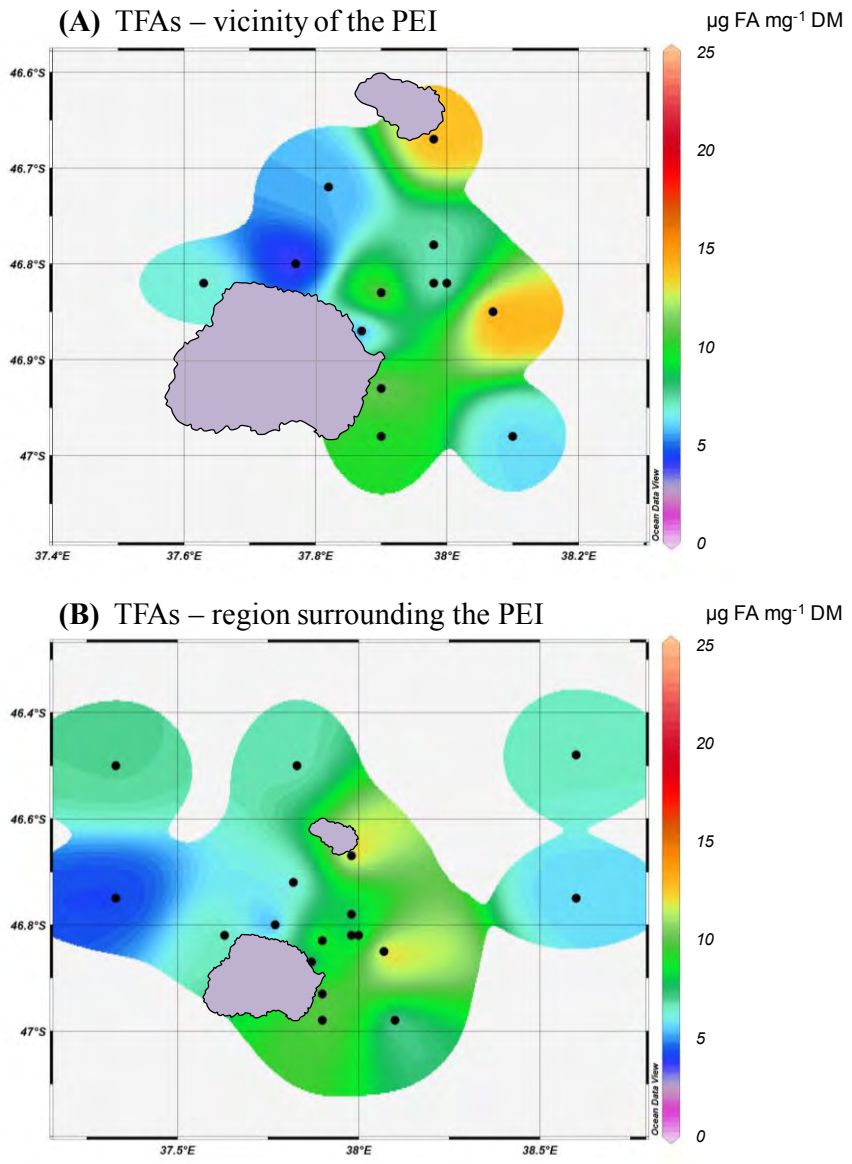

Figure 3.7. Concentration (µg FA mg^{-1} DM) of total fatty acids (TFAs) in the surface water suspended particulate matter in the vicinity (A) and in the offshore region (B) of the Prince Edward Islands.

The concentration of TFAs in the surface SPM in the vicinity of the islands showed a high degree of spatial variation (2.6 to 13.8 µg FA mg^{-1} DM; Table A1; Fig. 3.7A), but were generally greater between and within the lee of the islands than the surrounding open ocean area (4.1 to 6.9 µg FA mg^{-1} DM; Table A1; Fig. 3.7B). The SPM from offshore and around the islands contained large proportions of SFAs (57.6 to 91.1% TFA) and moderate MUFA proportions (6.4 to 25.5% TFA). The SPM from all the stations, except Station 8 (nearshore east of Marion), contained very small proportions of EFAs (all stations: 0.0 to 4.8% TFA and Station 8: 13.3% TFA; Table A1). In the vicinity of the islands, the SPM generally contained small proportions of the diatom (20:5ω3: 0.0 to 2.6% TFA), dinoflagellate (22:6ω3: 0.0 to

1.9% TFA) and degraded kelp bacterial fatty acids (18:1ω7: 0.0 to 1.2% TFA). The nearshore station adjacent to the Marion Island kelp beds (Station 8) appeared to act independently of the island system, as the SPM from this station contained greater proportions of 22:1ω9, 22:6ω3 and 20:5ω3 (diatom fatty acid) than SPM from the other stations (Table A1). The SPM from offshore stations contained small proportions of the diatom fatty acid (20:5ω3: 0.0 to 1.3% TFA), but SPM at stations downstream of the islands (i.e. Stations vii and viii) had slightly enhanced proportions of this fatty acid relative to the upstream stations (i.e. Stations i, ii and iii; Table A1). For all offshore stations, the SPM contained very small proportions of the degraded kelp bacterial and dinoflagellate fatty acids (18:1ω7: 0.0 to 0.5% TFA and 22:6ω3: 0.0 to 0.5% TFA, respectively).

3.3.3.2. Suspension- and deposit-feeders

Forty seven fatty acids were detected at concentrations >1.0% TFA in at least one of the consumers (Tables A3 to A12). The four species of sponge contained the greatest number of fatty acids. Sponge sp. 1 contained large proportions of 16:0, 18:0, 20:5ω3, 22:6ω3 and SFAs, while the major fatty acids in sponge sp. 2 were 16:0, 24:0 and SFAs, and those in sponge sp. 3 were 16:0, 16:1ω3, 20:4ω6, 22:6ω3 and PUFAs, and those in sponge sp. 4 were *ai*-15:0, 16:0, 18:0, 18:1ω7 and SFAs (Table A3). Sponge sp. 1 and 3 were EFA-rich (24.0 to 25.2% TFA and 20.9 to 25.0% TFA, respectively) while sponge sp. 2 and 4 were less so (5.9 to 6.9% TFA and 7.5 to 10.1% TFA, respectively). The BAFAs were abundant in sponge sp. 1 (only in specimens from Station 4), sp. 2 and sp. 4. The two bryozoan species were dominated by 16:0, 22:6ω3, EFAs and PUFAs, with moderate proportions of 20:5ω3 and 20:2 nonmethylene interrupted (NMI), except for bryozoan sp. 2 (Table A4).

The brachiopod *Magellania kerguelenensis* was dominated by 16:0, 18:0, SFAs and PUFAs, but also had relatively high proportions of 20:5ω3, 22:6ω3 and EFAs, except for those from Station 3 (northeast of Marion; Table A5). There were no detectable (>1.0% TFA) HPFAs in any of the brachiopods. The individuals from Station 3, however, had relatively high proportions of the degraded kelp bacterial fatty acid (18:1ω7; 7.7% TFA *versus* 1.2 to 2.8% TFA). The bivalves *Limatula pygmaea* (sp. 1) and *Thracia meridionalis* (sp. 2) contained similar proportions of fatty acids among regions with elevated proportions of 22:6ω3, SFAs, PUFAs and EFAs as well as relatively large proportions of 16:0, 18:0 and 20:5ω3 (Table A6). The suspension-feeding polychaete *Serpula vermicularis vermicularis* (sp. 1) contained large proportions of 16:0, 20:1ω11, 20:5ω3, 22:6ω3, PUFAs and EFAs; however,

they contained no detectable HPFAs (Table A7). The holothurians *Pseudocnus laevigatus* (sp. 1) and *Psolus paradubiosus* (sp. 2) both contained moderate proportions of 18:1ω7, 20:1ω9, 20:2 NMI, 22:6ω3 and BAFAs, but *P. paradubiosus* contained greater proportions of these fatty acids than *Pseudocnus laevigatus* as well as relatively large proportion of 16:1ω7, 18:1ω9, PUFAs and EFAs (Table A8). The diatom fatty acid 20:5ω3, however, was predominant in both holothurians (20.0 to 29.2% TFA *versus* the next dominant at 6.6 to 10.7% TFA). The hydrozoan *Plumularia insignis* contained large proportions of 16:0, 18:1ω9, 20:5ω3, 22:6ω3, SFAs, PUFAs and EFAs, while the sea pen *Pennatula inflata* and the gorgonian coral *Thouarella variabilis* contained large proportions of 16:0, 18:1ω9, 24:6ω3, PUFAs and EFAs as well as elevated proportions of 20:5ω3 (Table A9).

For the deposit-feeding organisms, the polychaete *Thelepus extensus* (sp. 3) was dominated by 16:0, 18:1ω7 and 20:5ω3 and had large proportions of PUFAs and EFAs and no detectable HPFAs (Table A10). The other deposit-feeding polychaete, *Lanice marionensis* (sp. 2), which is likely to be a selective deposit-feeder (Buhr and Winter, 1977; Fauchald and Jumars, 1979), contained moderate proportions of 22:5ω3 and 22:6ω3 and large proportions of 14:0, 16:0, 20:5ω3, SFAs, PUFAs and EFAs, except for those from Station 3 (Table A11). There were also no detectable HPFAs in any of the *L. marionensis*. The gastropod *Margarella expansa* contained moderate to large proportions of 16:0, 18:1ω7, 20:4ω6 (kelp plant), 20:5ω3, 22:6ω3, PUFAs, EFAs and BAFAs (Table A12).

3.3.4. Diets of suspension- and deposit-feeders using target fatty acids

To determine the importance of the main food sources, i.e. kelp and phytoplankton, in the suspension- and deposit-feeders from different regions around the PEI, the target fatty acids for these three food sources were examined in detail. As different species tend to have different amounts of total lipids (Richoux and Froneman, 2008; Richoux, in press) quantitative differences between lipid-rich and lipid-poor organisms will overwhelm any potential differences due to dietary fatty acids. Therefore, proportional data (% TFA) were used for among-species comparisons (section 3.3.4.1), while quantitative data (µg FA mg^{-1} DM) were used to investigate intra-specific variations among regions (section 3.3.4.2).

3.3.4.1. Inter-specific variation

There were no distinct patterns in the diets of the suspension- and deposit-feeders among the different regions, but there were differences among species at each station (Figs. 3.8 and 3.9).

In the suspension-feeders, the target fatty acids present in the greatest proportions in the majority of the species were those of diatoms (20:5ω3) and/or dinoflagellates (22:6ω3; Fig. 3.8). The exceptions were the sponges and bryozoans, in which the kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; bacterial: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids occurred in similar proportions. There were no distinct differences in the proportions of target fatty acids among the suspension-feeding communities of the inter-island and nearshore regions. A notable exception was the brachiopod from the inter-island upstream Station 3, in which the degraded kelp bacterial, diatom and dinoflagellate fatty acids occurred in similar proportions.

For the deposit-feeders, the diatom fatty acid 20:5ω3 occurred in substantially greater proportions than the other fatty acids in most regions (Fig. 3.9). The polychaete *L. marionensis* (sp. 2) at the inter-island downstream Station 7 also had substantial proportions of the dinoflagellate fatty acid, while the polychaete *T. extensus* (sp. 3; which only occurred at the nearshore Station 8) had large proportions of degraded kelp bacterial fatty acid (18:1ω7). All the gastropods (*M. expansa*) contained substantial kelp (plant and bacterial) fatty acids, but the individuals from the nearshore Station 8 had more kelp bacterial fatty acid, while those from the upstream Station 1 had enhanced kelp plant fatty acids, in particular the EFA 20:4ω6.

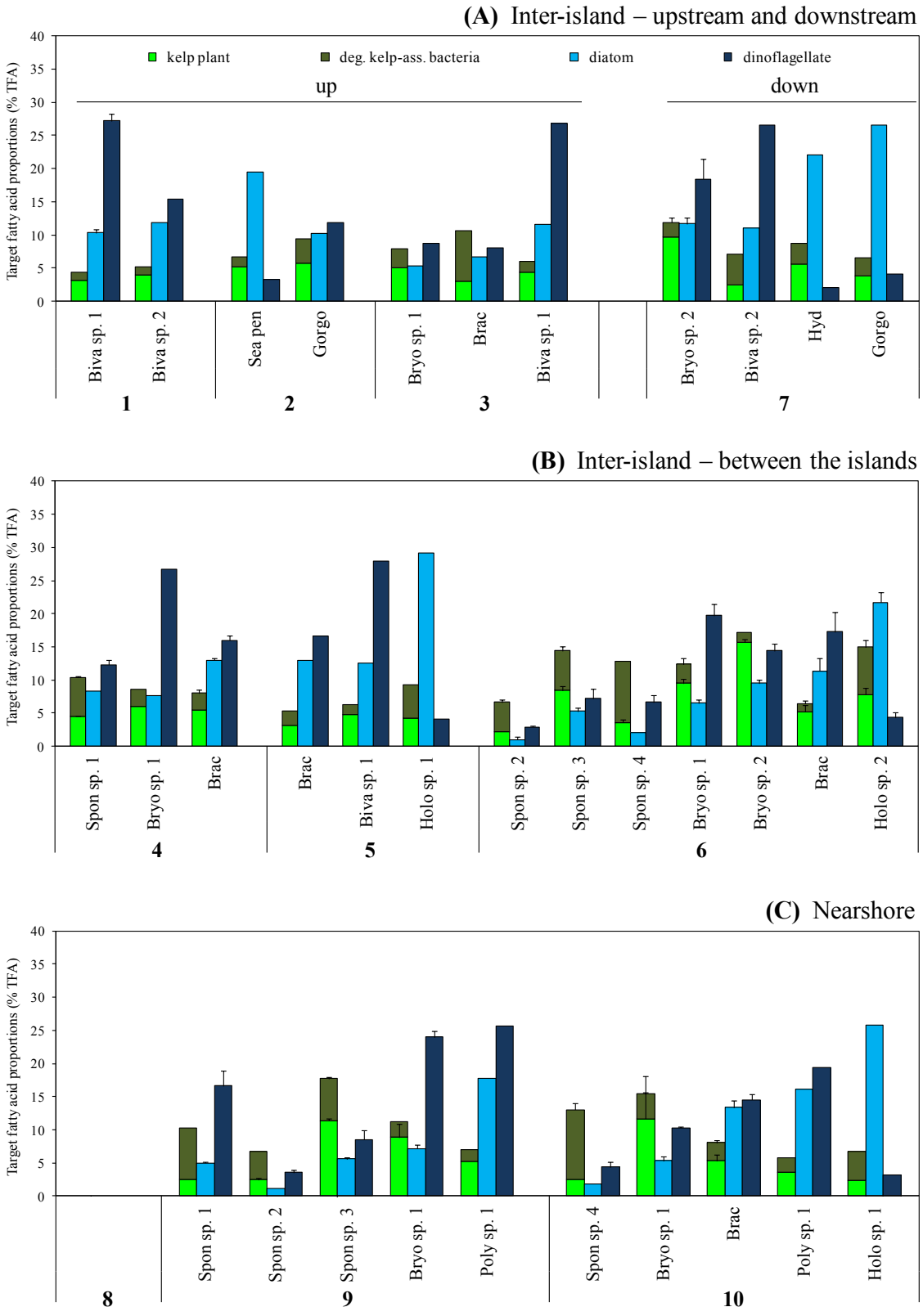

Figure 3.8. Proportions (% TFA) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the benthic suspension-feeding organisms among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island - upstream and downstream of the islands (A), inter-island - between the islands (B) and nearshore (C). Error bars indicate standard deviations.

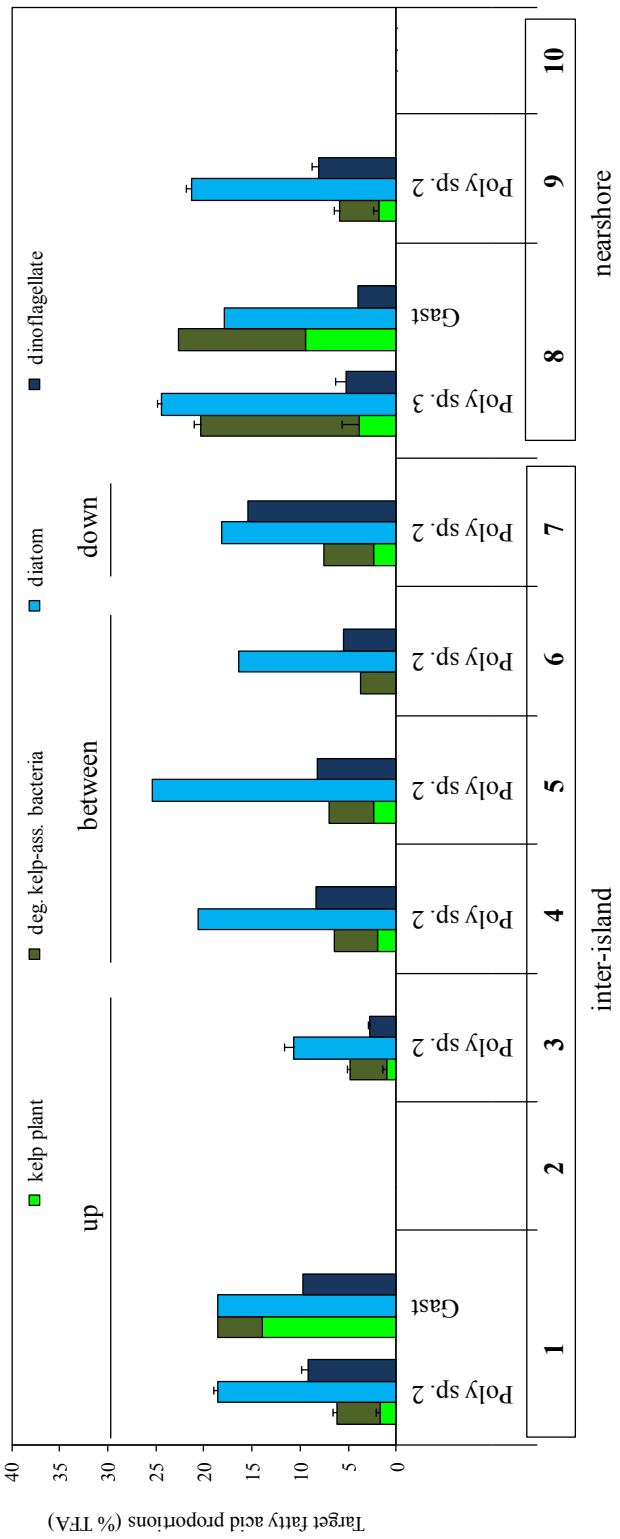

Figure 3.9. Proportions (% TFA) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the benthic deposit-feeding organisms among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations.

3.3.4.2. Regional variation

Spatial changes in the importance of each food source were investigated using species that occurred at four or more stations and/or covered a variety of regions around the PEI. Bryozoan sp. 1 showed similar quantities of each target fatty acid among the different regions, with the exceptions of those from Stations 4 (inter-island between) and 9 (nearshore), in which the dinoflagellate fatty acid occurred in higher quantities than the others (Fig. 3.10A). The brachiopod *Magellania kerguelenensis* from each region contained more diatom and dinoflagellate fatty acids, with the exception of those individuals from Station 3 (inter-island upstream), in which the quantities of the various food source fatty acids were similar (Fig. 3.10B). The bivalve *Limatula pygmaea* showed no differences among specimens from different stations and contained relatively large quantities of the dinoflagellate fatty acid compared to the other benthic organisms (Fig. 3.10C). The polychaete *Lanice marionensis* contained higher quantities of the diatom fatty acids, with the exception of Station 7 (inter-island downstream), in which there were also higher quantities of the dinoflagellate fatty acid (Fig. 3.10D). Of the four species selected for the regional investigation, the polychaete *L. marionensis* contained the greatest quantities of TFAs (39.30 to 147.83 µg FA mg^{-1} DM; Fig. 3.11D), followed by the bivalve *Limatula pygmaea* at approximately a third of the quantity (32.23 to 40.47 µg FA mg^{-1} DM; Fig. 3.11C), then the brachiopod *M. kerguelenensis* (10.83 to 26.10 µg FA mg^{-1} DM; Fig. 3.11B), and finally the bryozoan sp. 1 (0.31 to 2.42 µg FA mg^{-1} DM; Fig. 3.11A). *Lanice marionensis* contained approximately 100 times the concentration of TFAs compared to that of bryozoan sp. 1.

The deposit-feeding polychaete *L. marionensis* from upstream Station 1 had substantially less TFAs compared to those from the other regions (39.3 µg FA mg^{-1} DM *versus* 73.0 to 147.8 µg FA mg^{-1} DM; Table A11), with the greatest quantities occurring in individuals from Station 3. The gastropod *Margarella expansa* from upstream Station 1 also contained substantially less TFAs compared to the individuals collected from the nearshore Station 8 (Table A12). The proportion of PUFAs and EFAs in *L. marionensis* were relatively similar among stations (42.9 to 48.9% TFA and 28.4 to 35.0% TFA, respectively), with the exception of Station 3, and to a lesser extent Station 6, which had smaller proportions (PUFAs: 19.4 and 30.6% TFA, EFAs: 13.7 and 21.9% TFA, respectively; Fig. 3.12).

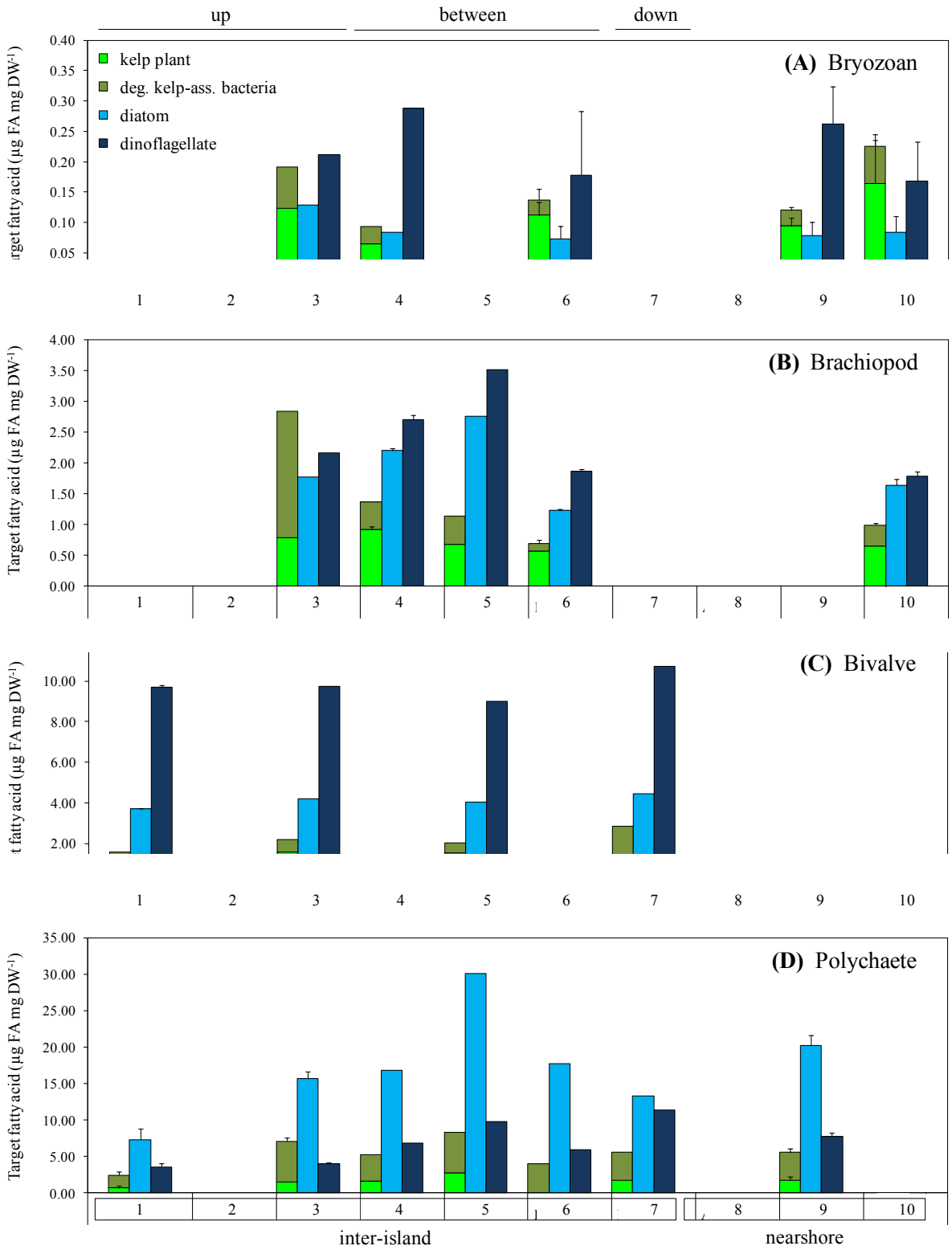

Figure 3.10. Quantities (µg FA mg DW^{-1}) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the suspension-feeding bryozoan sp. 1 (A), brachiopod *Magellania kerguelenensis* (B), bivalve *Limatula pygmaea* (C) and the deposit-feeding polychaete *Lanice marionensis* (D) among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations; note y-axis consists of different scales starting from smallest (A) to largest (D) quantities.

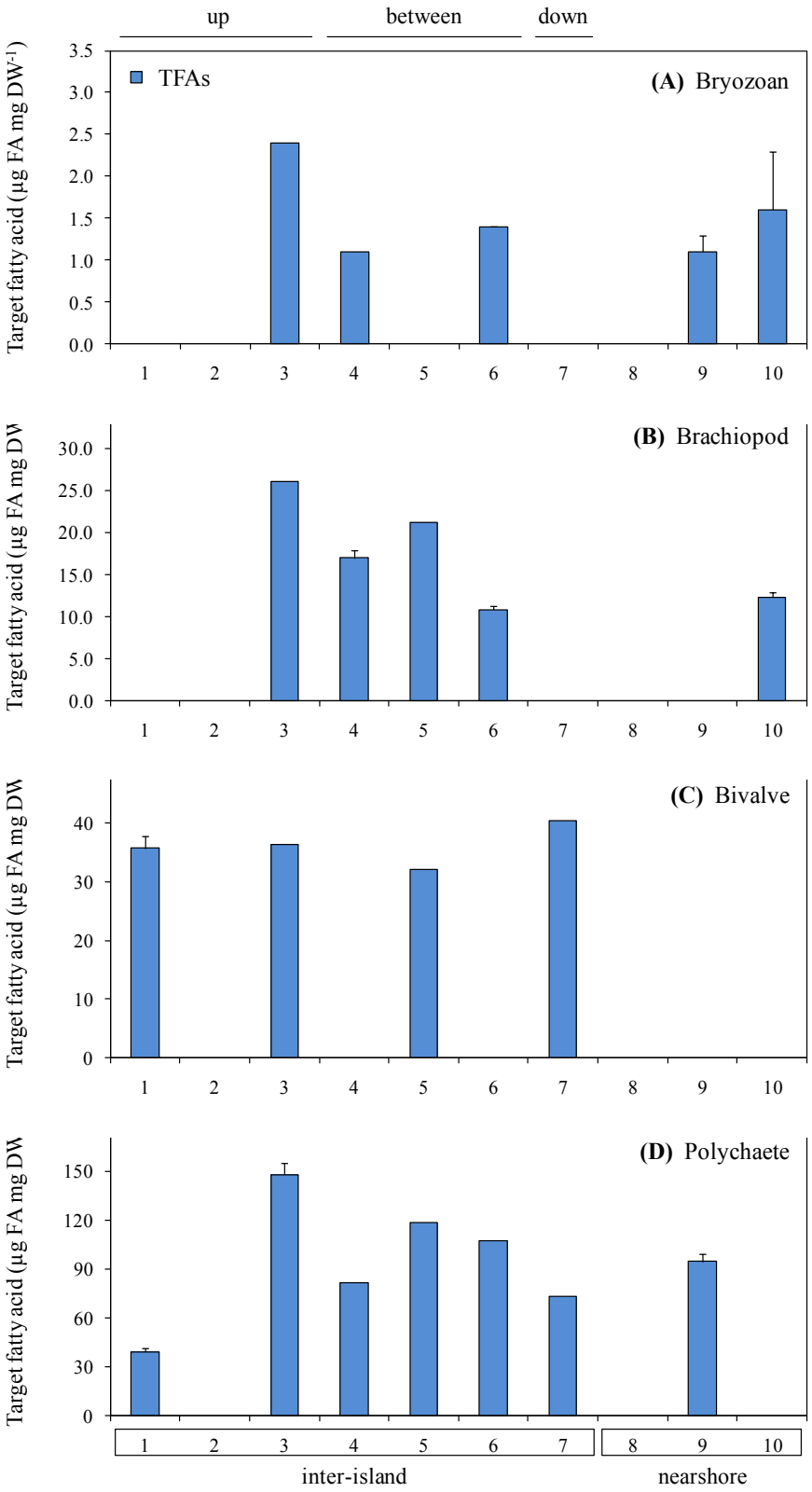

Figure 3.11. Quantities (µg FA mg DW^{-1}) of total fatty acids (TFAs) in the suspension-feeding bryozoan sp. 1 (A), brachiopod *Magellania kerguelenensis* (B), bivalve *Limatula pygmaea* (C) and the deposit-feeding polychaete *Lanice marionensis* (D) among the 10 stations around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations; note y-axis consists of different scales starting from smallest (A) to largest (D) quantities.

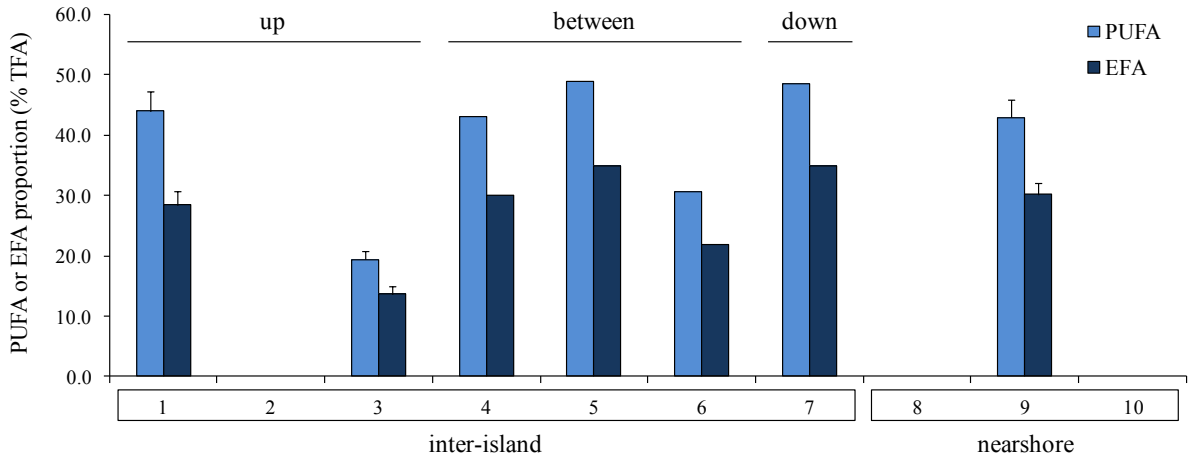

Figure 3.12. Proportions (% TFA) of polyunsaturated fatty acids (PUFAs) and essential fatty acids (EFAs) in the deposit-feeding polychaete *Lanice marionensis* at the seven stations from where it was collected around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations.

The gorgonian coral *Thouarella variabilis* showed an accumulation of fatty acids in the specimen from the inter-island downstream Station 7 compared to the specimen from the inter-island upstream Station 2, in which the kelp, diatom and dinoflagellate fatty acids were 1.7, 2.5 and 4.6 times higher, respectively (Fig. 3.13). The concentration of TFAs was also 2.9 times higher in the specimen collected from the downstream station compared to the specimen from the upstream station (upstream: 4.9 µg FA mg^{-1} DM and downstream: 14.2 µg FA mg^{-1} DM; Table A9). The quantity of PUFAs and EFAs were also higher in the specimen collected from the downstream station (2.8 and 2.4 times higher, respectively).

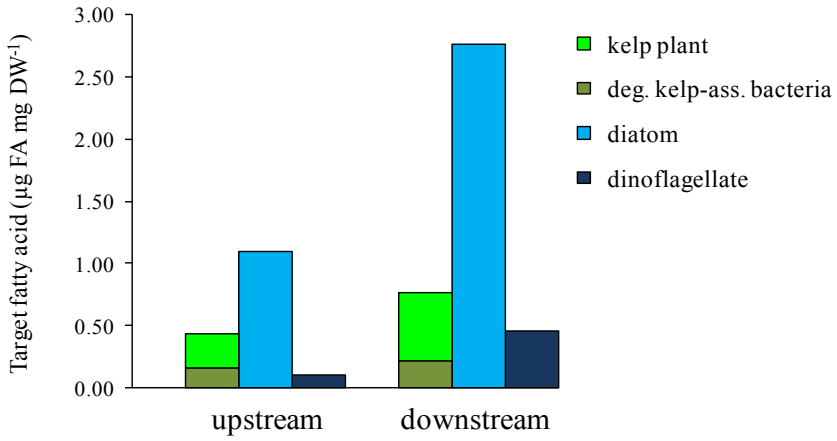

Figure 3.13. Changes in the quantities (µg FA mg DW^{-1}) of kelp (plant: 18:2ω6, 18:3ω3 and 20:4ω6; associated bacteria: 18:1ω7), diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the gorgonian coral *Thouarella variabilis* between upstream (inter-island Station 2) and downstream (inter-island Station 7) areas of the Prince Edward Islands. Error bars indicate standard deviations.

3.4. DISCUSSION

The two dominant primary producers in the vicinity of the PEI are the extensive beds of *Macrocystis laevis* and phytoplankton (Pakhomov and Froneman, 1999a). These two sources have distinctly different isotopic signatures and target fatty acids, thus enabling the assessment of their dietary contributions to benthic suspension- and deposit-feeders in different regions around the PEI.

3.4.1. Environmental conditions

As the total chl-*a* and SPM concentrations and $\delta^{13}C$ values of SPM in the vicinity of the PEI were low ($\leq$0.29 µg L^{-1}, $\leq$8.04 mg L^{-1}, $\leq$-23.54 ‰, respectively), and in the range reported for the offshore region (Figs. 3.1A and C; Figs. 3.1B and D and Figs. 3.2A and B, respectively), there were no apparent phytoplankton blooms in the vicinity of the islands during the 2009 investigation (PEI bloom chl-*a* concentration: 1.5 to 3.0 µg L^{-1}, and $\delta^{13}C$ signature: ~-23.3 ‰; Kaehler *et al.*, 2000, 2006; Pakhomov *et al.*, 2009). During bloom periods in Trinity Bay (Newfoundland), the mean TFA content of the SPM reached 41.0 µg FA mg^{-1} DM (Budge and Parrish, 1998). The comparatively low quantity of TFAs obtained in the vicinity of the PEI (2.6 to 13.8 µg FA mg^{-1} DM) further corroborates the absence of blooms prior to or during this investigation. Interestingly, a study conducted in the vicinity of the PEI during March/April 2003 documented elevated concentrations of total chl-*a* (up to 2.0 µg L^{-1}) and SPM in the lee of the islands (~18000 particles L^{-1} but frequently >30000 particles L^{-1}; Kaehler *et al.*, 2006). The lack of distinct spatial variation in the biological variables in the surface water during the 2009 investigation suggests little to no retention of water around the islands, and hence a flow-through system was evident during this period.

It is important to note, however, that there were slightly enhanced SPM concentrations at the inter-island upstream Station 3 (northeast of Marion) and the nearshore Station 8 (adjacent to kelp beds east of Marion; 7.33 and 8.04 mg L^{-1}, respectively; Fig. 3.1B). These enhanced SPM concentrations suggest possible microscale oceanographic processes were responsible for retaining water in some isolated areas. For example, the kelp beds around Marion Island retain freshwater, which in turn promotes water column stability that may lead to elevated productivity (Pakhomov *et al.*, 2002). The elevated SPM concentrations and proportions of diatom and dinoflagellate fatty acids in the SPM at Station 8 are likely due to the close proximity of the kelp beds (see Fig. 2.1; Chapter 2). As there are no seasonal data available,

it is not clear whether this microscale water retention at Stations 3 and 8 varies temporally; however, there is evidence to suggest that during periods of water retention between the islands, this microscale retention is less evident (see Figure 2 in Kaehler *et al.*, 2006).

3.4.2. Food sources

The $\delta^{13}C$ signatures of the degraded kelp and its detrital POM (-19.07 ± 0.29 ‰ and -17.50 ‰, respectively) were more depleted than those of the fresh kelp (-15.57 ± 0.20 ‰). The difference in $\delta^{13}C$ signatures between fresh and degraded kelp was likely due to the decomposition of the kelp by microbes, thus the degraded kelp had a combined signature of the plant and the microbial communities (Newell *et al.*, 1982; Mann, 1988; Levinton *et al.*, 2002). The fatty acid profiles also showed differences between fresh and degraded kelp, such as greater proportions of BAFAs and 18:1ω7 in the degraded kelp (Table A2), also related to decomposition and presence of microbes.

The $\delta^{13}C$ signatures for the SPM in the vicinity of the islands were similar to those in the offshore region (Fig. 3.2B) and within the range reported for a mixed phytoplankton community (present study mean: -24.25 ± 0.47 ‰, mixed phytoplankton range: -24.84 to -23.51 ‰; Kaehler *et al.*, 2000, 2006). As SPM is composed of a mixture of phytoplankton, detritus and bacteria, the values obtained in 2009 suggested that the SPM around the islands was dominated by phytoplankton. Furthermore, SPM from the lee of the islands contained enhanced quantities of TFAs (Fig. 3.7B) suggesting that the islands could play a role in enhancing the quality of available food sources in the water column.

3.4.3. Diets of benthic suspension- and deposit-feeders

3.4.3.1. Stable isotopes

The suspension- and to a lesser extent deposit-feeding community had a wide range of $\delta^{13}C$ and $\delta^{15}N$ signatures among species and regions (Figs. 3.3, 3.4, 3.5 and 3.6). This is in agreement with the findings of Kaehler *et al.* (2000), which revealed no apparent distinct trophic levels in the benthic community of the PEI, suggesting that it exhibits a trophic continuum. A wide range of $\delta^{13}C$ and $\delta^{15}N$ values have also been observed in the benthic suspension- and deposit-feeders at the sub-Antarctic Bouvet Island (east of the PEI; Jacob *et al.*, 2006). Benthic suspension-feeding invertebrates in the temperate Kariega Estuary (South Africa) had a large range of $\delta^{13}C$ values most likely owing to the wide range of $\delta^{13}C$ values present in their food sources (seston and/or SPM; Richoux and Froneman, 2007). Selective

feeding on different size fractions of SPM, as well as among-location variations in food sources, usually contribute to differences in $\delta^{13}C$ values among consumers (Dittel *et al.*, 2000; Doi *et al.*, 2005). The wide range of $\delta^{13}C$ and $\delta^{15}N$ signatures among the suspension- and deposit-feeders suggests a degree of feeding plasticity most likely resulting from a variety of feeding modes.

The $\delta^{13}C$ signatures in all the suspension- and deposit-feeders suggested that both these communities were incorporating phytoplankton and kelp (detritus) in their diets (Fig. 3.6), although the contribution by kelp was highly variable (kelp contribution range: 0.8 to 65.5%; 58.3% CV). For all the suspension- and deposit-feeding organisms, regardless of region and proximity to kelp beds, kelp detritus did not exceed 50% of the diet, except for the holothurian *Pseudocnus laevigatus* (sp. 1) at Station 10. In the deposit-feeding community, there were substantial differences in $\delta^{13}C$ signatures between the polychaete *Lanice marionensis* (sp. 2) and the polychaete *Thelepus extensus* (sp. 3), in which *L. marionensis* appeared to consume very little kelp detritus (kelp contribution range: 0.8 to 13.9%; Fig. 3.6). Benthic organisms collected from stations in the nearshore region tended to have ^{13}C-enriched signatures compared to those from the inter-island shelf region (Fig. 3.6). This enrichment could be due to increased incorporation of kelp-derived detritus in their diets due to their close proximity to the fringing kelp beds. This is a tentative pattern that requires further exploration, as few species were collected from both inter-island and nearshore regions, and the opposite pattern was observed in bryozoan sp. 1. A similar pattern, however, has previous been observed in the benthos at the PEI, whereby organisms near the kelp beds derived high proportions of their diet from the kelp, and this dietary contribution decreased with increased distance from the kelp beds (Kaehler *et al.*, 2006).

3.4.3.2. Fatty acids

The proportions of target fatty acids (% TFA) in both the suspension- and deposit-feeders indicated no distinct spatial differences in the utilisation of kelp *versus* phytoplankton among the different regions (Figs. 3.8 and 3.9). The suspension-feeders in general had large proportions of either diatoms and/or dinoflagellate fatty acids, even in the nearshore organisms (Fig. 3.8). All sponges, however, contained similar proportions of kelp, diatom and dinoflagellate fatty acids. Although sponges have a non-selective mode of feeding, they can consume only those particles between 0.1 and 50.0 μm, i.e. small enough to be engulfed by a single cell (Reiswig, 1971; Pearse *et al.*, 1987; Reiswig, 1990; Pile *et al.*, 1996). Most

sponges feed primarily on small plankton <20 µm (Reiswig, 1971, 1990; van de Vyver *et al.*, 1990; Pile *et al.*, 1996). Thus, it would appear that the sponges would be unable to utilise the large diatoms that predominate during the "island mass effect" (Boden, 1988; Perissinotto and Duncombe Rae, 1990). However, as the total chl-*a* concentrations in the Polar Frontal Zone (PFZ) within the region of the islands are dominated by small pico- and nanophytoplankton (<20 µm; Laubscher *et al.*, 1993; Froneman *et al.*, 2001; Froneman and Bernard, 2004), sponges would be able to utilise this offshore productivity in the absence of blooms and/or during flow-through scenarios. Therefore, the similar proportions of target fatty acids of the three food sources found in all sponges (Fig. 3.8) are likely to result from size-limited non-selective feeding rather than changes in available food sources. Interestingly, the two species of bryozoan also contained similar proportions of kelp and diatom fatty acids, but slightly higher proportions of the dinoflagellate fatty acid (Fig. 3.8). Bryozoans, like sponges, can consume particles within a limited size range, but unlike sponges they can selectively feed upon phytoplankton (McKinney, 1990). This may explain why the bryozoans showed spatial variations in the proportions of these target fatty acids, in particular those of dinoflagellates, as they could actively select phytoplankton.

Few species and individuals of deposit-feeding organisms were collected, which was not unexpected as the benthic community around the PEI is generally dominated (≥60%) by suspension-feeders (Branch *et al.*, 1993a). Like the suspension-feeders, deposit-feeders utilise phytoplankton as their main food source, but unlike the suspension-feeders, the diet of the deposit-feeders was dominated by diatoms (Fig. 3.9). The large proportions of diatom and dinoflagellate fatty acids present in the benthic suspension- and deposit-feeders, most pronounced in the deposit-feeding polychaete *L. marionensis*, supports the suggestion that large quantities of unutilised pelagic material, predominantly from blooms, regularly sinks to depth where it is utilised by the benthic organisms. It is interesting to note that the holothurians *P. laevigatus* and *Psolus paradubiosus*, which typically feed on suspended detritus (Jarre-Teichmann *et al.*, 1997; O'Loughlin *et al.*, in press), contained elevated proportions of diatom fatty acids further indicating the presence of large amounts of bloom material settling to the benthos.

The suspension- and deposit-feeders were collected at depths ranging from 100 to 295 m (except for two stations at 70 m; see Table 2.1; Chapter 2). The depth of the euphotic zone in the Southern Ocean is highly variable and ranges from 20 to 100 m (Walsh, 1971; Glibert *et*

al., 1982; Arrigo, 1994; Pakhomov *et al.*, 1997). In the region of the PEI, the euphotic zone depth ranges from 78 to 85 m (Perissinotto and McQuaid, 1992). As the majority of the samples were collected from depths well below the euphotic depth it is unlikely that the diatom fatty acids recorded in the benthic organisms originated from benthic diatoms. Microphytobenthos (predominantly composed of benthic diatoms; MacIntyre *et al.*, 1996; de Bower *et al.*, 2003) have substantially more enriched $\delta^{13}C$ signatures (~-16.70 ‰; Corbisier *et al.*, 2004) than pelagic diatoms (~-23.34 ‰; Kaehler *et al.*, 2000; Pakhomov *et al.*, 2009). These two sources of diatoms are thus isotopically distinct from one another. The mean $\delta^{13}C$ value recorded for sediment from in the inter-island region between the PEI during 1999 was -23.82 ‰ (Kaehler *et al.*, 2000), close to that recorded for diatom blooms in the region. These data provide further evidence to support that the bulk of the production associated with the "island mass effect" sinks to depth where it accumulates in the shelf sediments of the islands.

3.4.4. Regional variations in food availability and utilisation by benthic organisms

There were no distinct patterns in the utilisation of the various food sources by suspension- and deposit-feeding organisms among the different regions (Figs. 3.8 and 3.9). Phytoplankton (diatom and/or dinoflagellate) generally dominated in the diets of these organisms. There were, however, site-specific enhanced contributions of kelp (upstream Station 3 and nearshore Station 8), likely due to the position of these stations and their local environment. For example, despite the upstream position of Station 3 (northeast of Marion), the brachiopod *Magellania kerguelenensis* and bryozoan sp.1 collected at this station contained elevated proportions of kelp fatty acids compared to individuals of the same species from other stations between or downstream of the islands (Figs. 3.10A and B, respectively). Station 3 also had elevated SPM concentrations, possibly an effect of water retention within the region of this station arising from microscale oceanographic hydrodynamics around the PEI. The elevated proportions of kelp fatty acids, coupled with substantially higher quantities of TFAs in the polychaete *L. marionensis* (sp. 2) from Station 3 compared to those from Station 1 (northwest of Marion), i.e. another upstream station (Fig. 3.10D), further suggest the retention of water and primary production (phytoplankton and kelp) within this region.

Site-specific enhanced contributions of kelp also occurred at Station 8, in which the deposit-feeding polychaete *T. extensus* (sp. 3) and gastropod *Margarella expansa* collected at this

station both contained large proportions of diatom (20:5ω3) and degraded kelp bacterial fatty acids (18:1ω7; Fig. 3.9). As Station 8 was situated close to the kelp beds off the east coast of Marion Island, the large proportions of 18:1ω7 were not unexpected. The *M. expansa* at Station 1 also contained elevated proportions of kelp fatty acids, but these were dominated by kelp plant fatty acids (in particular the EFA 20:4ω6) and only contained a small proportion of the degraded kelp bacterial fatty acid. The benthic trawl at Station 1 consisted of large quantities of volcanic rock and sediment with very little detritus, unlike Station 8 (see Table 2.1; Chapter 2). As protozoans and microeukaryotes in sediment have been proposed as important sources of 20:4ω6 (Bell and Sargent, 1985; Fullarton *et al.*, 1995), this apparent enhanced kelp contribution may not in fact originate from kelp but from the sediment.

On a broad scale, the $\delta^{13}C$ signatures of the suspension- and deposit-feeders collected from nearshore stations generally had ^{13}C-enriched signatures compared with those from the inter-island shelf region (Fig. 3.6), possibly due to an increased incorporation of enriched kelp. Previous studies also observed a similar pattern at the PEI (Kaehler *et al.*, 2000, 2006). The fatty acid analysis, however, indicated that organisms collected from nearshore Station 8 contained higher proportions of kelp fatty acids than organisms from inter-island stations, while organisms from Stations 9 and 10 had similar proportions to those from inter-island stations (Figs. 3.8 and 3.9). As Stations 9 and 10 are not situated adjacent to kelp beds, unlike Station 8, kelp likely contributes more to the diets of benthic communities situated close to kelp beds.

Another example of site-specific enhanced contribution of a food source was apparent in the organisms collected at the inter-island downstream Station 7, particularly the polychaete *L. marionensis*. Despite this species' presence at seven of the ten stations, it exhibited an enhanced contribution (quantity) of the dinoflagellate fatty acid only in individuals from Station 7 (Fig. 3.10D). As dinoflagellates tend to replace diatom populations once a bloom region has become silicon depleted (Conley *et al.*, 1993; Pitcher *et al.*, 1993; Martin-Jézéquel *et al.*, 2000; Bruland *et al.*, 2001), the elevated quantity of the dinoflagellate fatty acid in *L. marionensis* at Station 7 could result if water is retained over the shallow shelf region for sufficiently long periods for silicon to become depleted. Evidence for enhanced phytoplankton biomass in the vicinity of the islands was also reflected in the gorgonian coral *Thouarella variabilis*. This organism was collected only at the two deepest stations, the inter-island upstream Station 2 (295 m) and the downstream Station 7 (255 m). The gorgonian

corals from the downstream Station 7 contained 2.9 times more TFAs, and 2.8 and 2.4 times more PUFAs and EFAs than those from the upstream station (Table A9), potentially reflecting an increased quality of food in the downstream region of the islands. The quantity of kelp, diatom and dinoflagellate fatty acids were also more concentrated in the downstream gorgonians relative to upstream (1.7, 2.5 and 4.6 times higher, respectively; Fig. 3.13). This downstream enhancement may indicate increased food quality downstream of the islands compared to upstream. Of particular importance, however, are the substantially higher quantities of diatom and dinoflagellate fatty acids in the downstream gorgonians, which supports the suggestion that the "island mass effect" has a measurable impact on the benthos within the immediate vicinity of the islands. Although many species of gorgonian corals contain zooxanthellae, the deep and/or cold water species do not (Cairns *et al.*, 2009; De Mol *et al.*, 2009). As *T. variabilis* at the PEI has only been recorded at depths >150 m (majority < 350 m; Branch *et al.*, 1993a), and as average sea temperatures range between 3 and 7°C around the PEI (Pakhomov and Froneman, 1999a; Perissinotto *et al.*, 2000), it is highly unlikely to contain zooxanthellae. The diatom and dinoflagellate fatty acids in *T. variabilis* thus likely originate from its diet sources rather than zooxanthellae.

The quantities (μg FA mg^{-1} DM) of TFAs in the abundant species also showed some variation among the different regions, in particular those from the upstream stations (Fig. 3.11). The polychaete *L. marionensis*, which was collected at the majority of stations, had a wide range of TFA concentrations among stations, the most pertinent of which was the substantially lower quantities in individuals from the upstream Station 1 (northwest of Marion; Table A11; Fig. 3.11D). Similar patterns were also observed in the gastropod *M. expansa* and the gorgonian coral *T. variabilis*, in which individuals from upstream stations (Stations 1 and 2, respectively) had substantially lower quantities of TFAs than those from nearshore or downstream stations (Stations 8 and 7, respectively; Tables A12 and A9, respectively). The lower TFA concentrations in individuals from Stations 1 and 2 potentially reflect a decreased food quality upstream of the islands. The open waters of the PFZ upstream of the islands are generally characterised by low levels of productivity (Laubscher *et al.*, 1993; Froneman *et al.*, 2001; Hunt *et al.*, 2001; Bernard and Froneman, 2002). Thus, the decreased food quality in organisms in upstream stations suggest that these organisms may rely more on the advection of productivity from the surrounding PFZ than on the enhanced productivity associated with the islands ("island mass effect"). During the 2009 investigation, the TFA concentrations in the surface water SPM were in general greater

between and within the lee of the islands than the upstream island region (Stations 1, 2 and 3) and surrounding open ocean (Figs. 3.7A and B), suggesting an increased food quality between and immediately downstream of the islands. The benthic trawls at both Station 1 and 2 consisted of large quantities of volcanic rock and sediment with very little detritus, unlike the benthic trawls at the other stations (see Table 2.1; Chapter 2), further supporting the lack of accumulation of island-generated detrital productivity at these stations.

Some species had a substantially higher variation in the quantities of TFAs among the different regions (e.g. polychaete *L. marionensis*; 36.8% CV; Fig. 3.11D) than other species (e.g. bivalve *Limatula pygmaea*; 9.3% CV; Fig. 3.11C). The low among-station variation in TFA concentrations in *L. pygmaea* (9.3% CV) suggests that these organisms had a similar diet quality at all stations. In contrast, bryozoan sp. 1, *M. expansa* (brachiopod), *Lanice marionensis* and *T. variabilis* (gorgonian coral) all showed different nutritional conditions depending on the region inhabited (TFAs: 57.2, 36.2, 36.8 and 68.4% CV, respectively; Figs. 3.11A, B, D and 3.13, respectively). The polychaete *L. marionensis* does not actively feed and either consumes SPM deposited behind the anterior projections of its tube (deposit-feeding mode) or by trapping SPM on mucus on its tentacles (suspension-feeding mode; Fish and Fish, 1996). Bivalves, however, are active suspension-feeders, and some species (scallop and mussel) appear to be able to sustain relatively high filtration rates at very low food concentrations (Winter, 1978; Cahalan *et al.*, 1989), which may account for the apparent similarity in food quality among specimens from different stations. Interestingly, despite the different food quality consumed by *L. marionensis* at different stations, the proportions of PUFAs and EFAs were high (30.6 to 50.0% TFA and 21.9 to 34.9% TFA, respectively) and relatively similar (16.0 and 16.1% CV, respectively) among all stations, with the exception of Station 3. As the amphipod *Acanthostepheia malmgreni* (Conception Bay, Newfoundland) maintained high (38.2% TFA) and similar (11.4% CV) proportions of ω3 fatty acids during and after the spring blooms, unlike various other suprabenthic and benthic invertebrates, it was suggested to be effective at sequestering ω3 fatty acids from its food (Parrish *et al.*, 2009). Therefore, the similar proportions of EFAs, and to a lesser extent PUFAs among regions (particularly Station 1), could suggest that these organisms are relatively well adapted at sequestering these essential components from their habitats despite the apparent differences in food quality, particularly upstream.

3.5. CONCLUSIONS

The target fatty acids for kelp, diatoms and dinoflagellates were found in all suspension- and deposit-feeders, indicating that phytoplankton and kelp both play roles in the diets of the benthic organisms in the shallow shelf waters around the PEI. The $\delta^{13}C$ signatures of the benthic consumers ranged from -23.74 to -19.02 ‰ and indicated that phytoplankton (mixed community) contributed between 52.8 and 92.2% to the diets of suspension-feeders, and between 34.5 and 99.2% to the diets of deposit-feeders. The elevated proportions of the diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids in the profiles of the suspension- and deposit-feeding organisms further supported the notion that pelagic primary production contributed substantially to their diets. Even those species with increased proportions of kelp fatty acids in their diets were still highly reliant on phytoplankton as a food source. This investigation revealed no distinct spatial patterns in the contributions of the different food sources between the inter-island (upstream, between and downstream) and nearshore regions of the islands in the suspension- and deposit-feeders. There was, however, strong evidence for increased food quality between and within the lee of the islands. As this investigation was conducted during April 2009, it is important to note that there may be temporal changes in the contribution of kelp *versus* phytoplankton, as well as the quantity and/or quality of the food sources available to the benthic community.

4 ONTOGENETIC AND SPATIAL VARIATIONS IN THE DIET OF THE HYPERBENTHIC SHRIMP *NAUTICARIS MARIONIS* AROUND THE PRINCE EDWARD ISLANDS

4.1. INTRODUCTION

Nauticaris marionis is a sub-Antarctic hyperbenthic shrimp with a wide distribution from southern New Zealand to the Prince Edward Islands (PEI; Perissinotto and McQuaid, 1990). Although it inhabits depths of 5 to 697 m at the PEI, this shrimp is most abundant between 50 and 100 m (Branch *et al.*, 1991, 1993a). *Nauticaris marionis* is a major component of the benthic community at the PEI, comprising the second highest biomass after bryozoans (Parker, 1984; Perissinotto and McQuaid, 1990; Beckley and Branch, 1992; Branch *et al.*, 1993a). Despite spatial and temporal variations in the diet of *N. marionis*, the megalope larvae (carapace length [CL] <4.0 mm) tend to consume phytoplankton, while subadults (and juveniles) and adults (CL >4.0 mm) predominantly feed on benthic suspension- and/or deposit-feeders (mainly bryozoans, hydrozoans, polychaetes and foraminifera) and at times on detritus and pelagic organisms (mainly euphausiids and copepods; Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999; Vumazonke *et al.*, 2003).

Despite their remote position in the Southern Ocean, the PEI seasonally support up to five million land-based predators, including seals and seabirds (penguins in particular), during the summer breeding season (Williams *et al.*, 1979; Condy, 1981; Pakhomov and Froneman, 1999a). *Nauticaris marionis* represents a very important food source for Gentoo penguins and Crozet shags (Espitalier-Noël *et al.*, 1988; Adams and Klages, 1989), and at times contributes substantially to the diets of both Macaroni and Rockhopper penguins (Brown and Klages, 1987). The shrimp has also been recorded in the stomach contents of the inshore fish *Paranotothenia magellanica* (Blankley, 1982) and King penguins (Adams and Klages, 1989). The PEI periodically demonstrates enhanced phytoplankton biomass compared to the surrounding open waters of the Polar Frontal Zone (PFZ; total chlorophyll-*a* [chl-*a*] concentration: >1.5 μg L^{-1} *versus* <0.3 μg L^{-1}, respectively; Boden, 1988; Perissinotto and Duncombe Rae, 1990). The majority of this biomass is not utilised directly by the local zooplankton assemblages and sinks to depth where it provides an important food source for

the benthic community (Perissinotto, 1992; Pakhomov and Froneman, 1999a; Chapter 3). As *N. marionis* contributes substantially to the diets of seabirds that feed close to the islands, they enable pelagic production to become available to large numbers of land-based predators (Perissinotto and McQuaid, 1990). As a result, *N. marionis* is regarded as a key species within the inter-island ecosystem of the PEI.

At the PEI, subadult and adult *N. marionis* consume benthic suspension- and deposit-feeders (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999). Kelp appeared to have an increased contribution in the diets of benthic species situated close to the kelp beds as well as those with size-restricted feeding modes (Chapter 3). Overall, however, the suspension- and deposit-feeders showed no distinct spatial patterns in the food sources utilised, with phytoplankton contributing substantially in the diets of all organisms (Chapter 3). There is evidence, however, that there may be differences in quantity (concentrations of chl-*a* and suspended particulate matter [SPM]; Kaehler *et al.*, 2006) and quality (concentration of total fatty acids [TFAs]; Chapter 3) of food sources available between the PEI *versus* upstream, reflecting the importance of the "island mass effect" (enhanced pelagic productivity) between and within the lee of the islands. As a result, potential regional differences in food quality consumed by the benthos (upstream *versus* downstream and/or inter-island *versus* nearshore) may have an impact on the hyperbenthic shrimp. In turn, any changes in the nutritional condition of these shrimp may have a subsequent impact on top predators, particularly those that predominantly feed inshore.

Long-term changes in the isotope signatures, particularly $\delta^{13}C$, of *N. marionis* at the PEI have been observed over the period of 1984 to 2000, likely reflecting changes in the overall productivity of the PEI ecosystem (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). The suggested decrease in productivity in the vicinity of the islands is thought to result from global climate change culminating in the decreased frequency of occurrence of the "island mass effect" (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). A decrease in productivity around the islands may result in changes in the abundance of *N. marionis*. To date there have been no quantitative studies on the biomass and abundance of *N. marionis* in the region of the PEI since the initial photographic assessments of the benthos conducted between 1984 and 1989 (Branch *et al.*, 1993a). As a consequence, long-term trends in the population dynamics or status of *N. marionis* at the PEI are unknown. As *N. marionis* forms a crucial link between phytoplankton and selected top predators, it is important to ascertain

the spatial, temporal and ontogenetic variations in its diet to enable predictive modelling of climate change effects on the greater food web. The aim of this study was to determine spatial and ontogenetic changes in the diet of *N. marionis* around the PEI. It was hypothesized that there are differences in the diets of large and small shrimp, but that there are no spatial differences in diet due to their motility. The phytoplankton were also hypothesized to provide an important carbon source (indirectly) to these shrimp, reflecting the predominant dietary intake of the suspension- and deposit-feeding organisms at the PEI.

4.2. MATERIALS AND METHODS

4.2.1. Study area, sample collection and treatment

To determine ontogenetic and spatial variations in the diet of *Nauticaris marionis*, 10 stations were sampled as described in Chapter 2, sections 2.1 and 2.1.3. The shrimps were divided into five size classes according to their CL (Chapter 2, section 2.2.3). All *N. marionis* (wherever possible), in addition to potential benthic (detritus, suspension- and deposit-feeding organisms) and pelagic (zooplankton) food sources (obtained from gut content analyses; Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999), were processed for stable isotope and fatty acid analyses (see Table 2.3; Chapter 2, section 2.2.3).

4.2.2. Stable isotope analysis

All isotopic analyses were conducted as described in Chapter 2, section 2.3.

4.2.3. Fatty acid analysis

See Chapter 2, section 2.4 for complete descriptions of the fatty acid protocols used. Essential fatty acids (EFAs) include 20:4ω6, 20:5ω3 and 22:6ω3 (Arts *et al.*, 2001), while bacterial fatty acids (BAFAs) are those with odd-numbered carbon chains and/or *iso*- (*i*-) and *anteiso*- (*ai*-) branches (Harvey, 1994; Budge and Parrish, 1998) and higher plant fatty acids (HPFAs) include 18:2ω6 and 18:3ω3 (Dalsgaard *et al.*, 2003). Saturated fatty acids (SFA) are those without double bonds (e.g. 14:0), monounsaturated fatty acids (MUFAs) contain a single double bond (e.g. 16:1ω7) while polyunsaturated fatty acids (PUFAs) have >1 double bond (e.g. 16:4ω3). All double bonds were assumed to be methylene-interrupted and in *cis* configuration unless otherwise noted.

4.2.3.1. Target fatty acids

The fatty acid 20:5ω3 were used to indicate the presence of diatoms in the diet of the shrimp, while 22:6ω3 was used to indicate dinoflagellates (Parrish *et al.*, 2000; Dalsgaard *et al.*, 2003). The fatty acids 18:1ω7, 18:2ω6, 18:3ω3 and 20:4ω6 were used to indicate consumer uptake of kelp-derived material (plant and associated bacteria; Chapter 3). The ratio 18:1ω9/18:1ω7 was used to determine the relative contribution of animal prey, i.e. carnivory index (Cripps and Atkinson, 2000; Dalsgaard *et al.*, 2003), and the sum of 22:1ω11 and 20:1ω9 was employed to indicate the consumption of copepods particularly calanoids (Sargent and Falk-Petersen, 1988; Saito and Kotani, 2000; Scott *et al.*, 2001).

4.2.4. Data analysis

Principal component analysis (PCA) was used to examine associations of the fatty acid profiles among the different size classes of *N. marionis* in the different regions around the PEI. All fatty acids >1.0% of the total fatty acids (% TFA) were included, and the proportional data were arcsine square root transformed for standardisation and to improve normality. Statistical analyses were completed using PAST 1.42 (Hammer *et al.*, 2001). Coefficient of variation (CV) were calculated from the ratio of the standard deviation to the mean and expressed as percentages (% CV). Variance is reported as one standard deviation (SD) from the mean.

4.3. RESULTS

The shrimp *Nauticaris marionis* was collected at all stations except for the upstream Station 2 (deep shelf). All five size classes were recorded only at Station 6 (inter-island south of Natal Bank; see Table 2.3; Chapter 2). No shrimp were collected in the vertical WP-2 net tows. The greatest abundances of *N. marionis* were found at Station 3 (nearshore northeast of Marion), Station 6 (inter-island south of Natal Bank) and Station 8 (nearshore east of Marion), while Station 5 (shallow mount Natal Bank) and Station 7 (deep shelf downstream) had the fewest. Shrimps ranged in size from 4.0 to 11.0 mm (CL), but the majority were 7.0 to 9.5 mm (size class III and IV) with very few large (10.0 – 11.0 mm) or small (4.0 – 5.0 mm) individuals. As megalope larvae generally have a CL <4.0 mm (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 2000a), it is likely that only subadults and adults (and the occasional juvenile) were collected during this investigation.

4.3.1. Ontogenetic and spatial variation

4.3.1.1. Stable isotopes

Nauticaris marionis demonstrated an enrichment in $\delta^{13}C$ and $\delta^{15}N$ signatures with an increase in size at all stations (Fig. 4.1). A notable exception was recorded in the individuals collected at the downstream Station 7. There were distinct separations in the isotopic signatures among size classes, except at Stations 3 (upstream) and 6 (between the islands) where there was some overlapping of size classes (II + III and III + IV). At each station, there were substantial differences between the isotope signatures of shrimps in the smallest and largest size classes, whereby the largest size class was always more ^{13}C- and ^{15}N-enriched, except at Stations 5 (Natal Bank) and 7 (downstream; Fig. 4.1). Overall the shrimp collected from the nearshore stations, particularly those from Station 8 (east of Marion), had enriched $\delta^{13}C$ signatures compared to those from the inter-island regions (Fig. 4.2).

The spatial variation in isotope signatures among the different size classes of *N. marionis* is shown in Figure 4.2, excluding size class I (4.0 – 5.0 mm) as there were data only from one station. All the size classes of *N. marionis* showed relatively similar ranges in $\delta^{15}N$ values. Individuals from Station 6 (inter-island shelf) were the most ^{15}N-enriched in every size class. Individuals from the second smallest size class (II: 5.5 – 6.5 mm) had the narrowest range of $\delta^{13}C$ values, even when including individuals from Station 8 (-21.89 to -21.03 ‰). Individuals in the next size class (III: 7.0 – 8.0 mm) showed a wider range of $\delta^{13}C$ values (-22.28 to -21.04 ‰), followed by those in the second largest size class (IV: 8.5 – 9.5 mm), which had the widest range (-22.04 to -20.97 ‰, excluding Station 5). Shrimps from the largest size class (V: 10.0 – 11.0 mm), however, showed a relatively narrow range in $\delta^{13}C$ values (-21.20 to -20.67 ‰, excluding downstream Station 7), as well as a narrower (but isotopically heavier compared with other size classes) range in $\delta^{15}N$ values (7.94 to 9.84 ‰). In general, the smallest *N. marionis* (size classes I and II), had the most ^{13}C-depleted signatures (-22.13 to -21.60 ‰), while the largest (size class V) had the most ^{13}C-enriched signatures (-21.20 to -20.67 ‰).

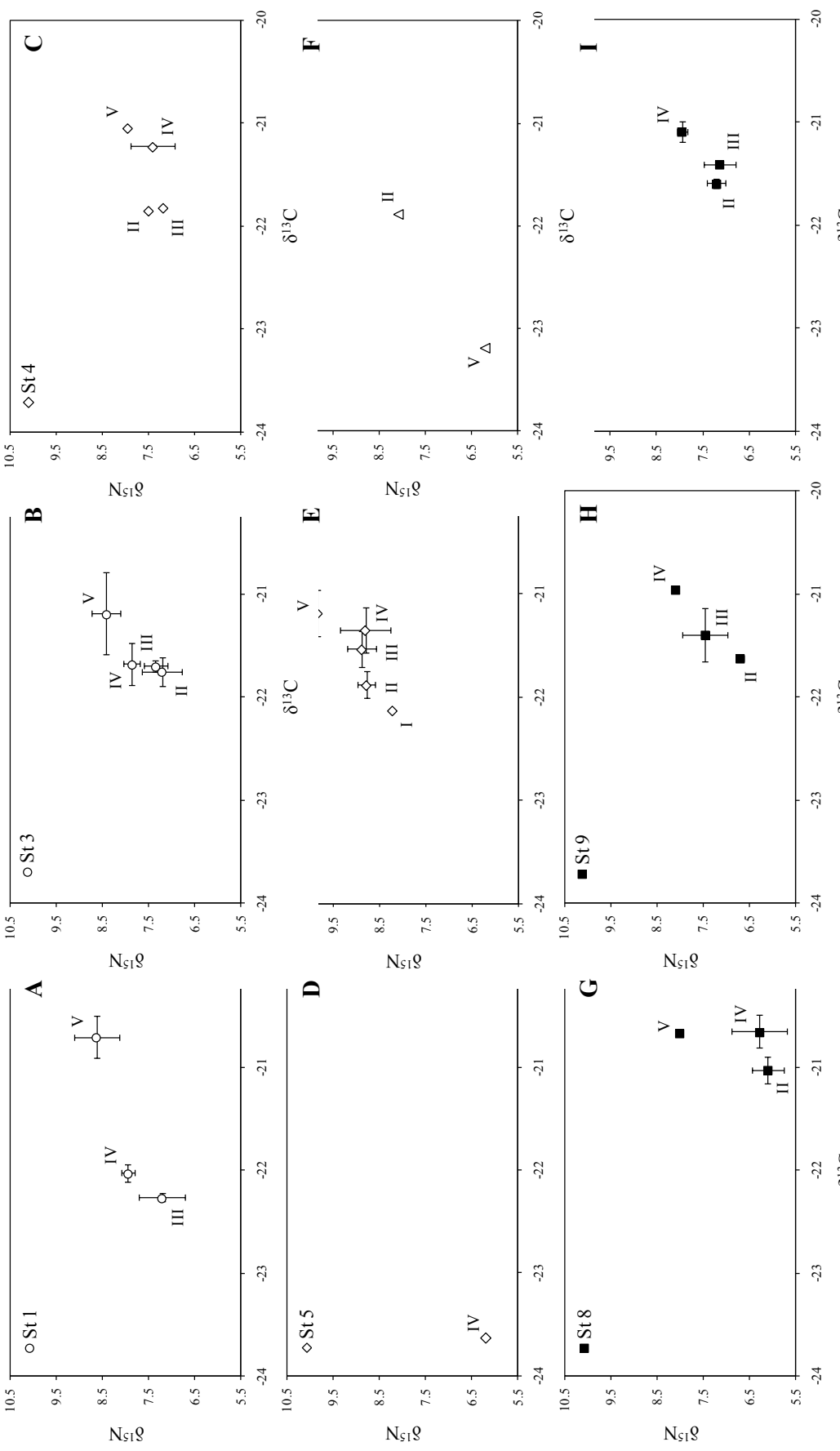

Figure 4.1. $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of *Nauticaris marionis* collected at each station (A to I) around the Prince Edward Islands. Size classes: 4.0 – 5.0 mm (I), 5.5 – 6.5 mm (II), 7.0 – 8.0 mm (III), 8.5 – 9.5 mm (IV) and 10.0 – 11.0 mm (V); regions: inter-island upstream (○), between (◇) and downstream (△) of the islands, and nearshore (■); error bars represent standard deviations.

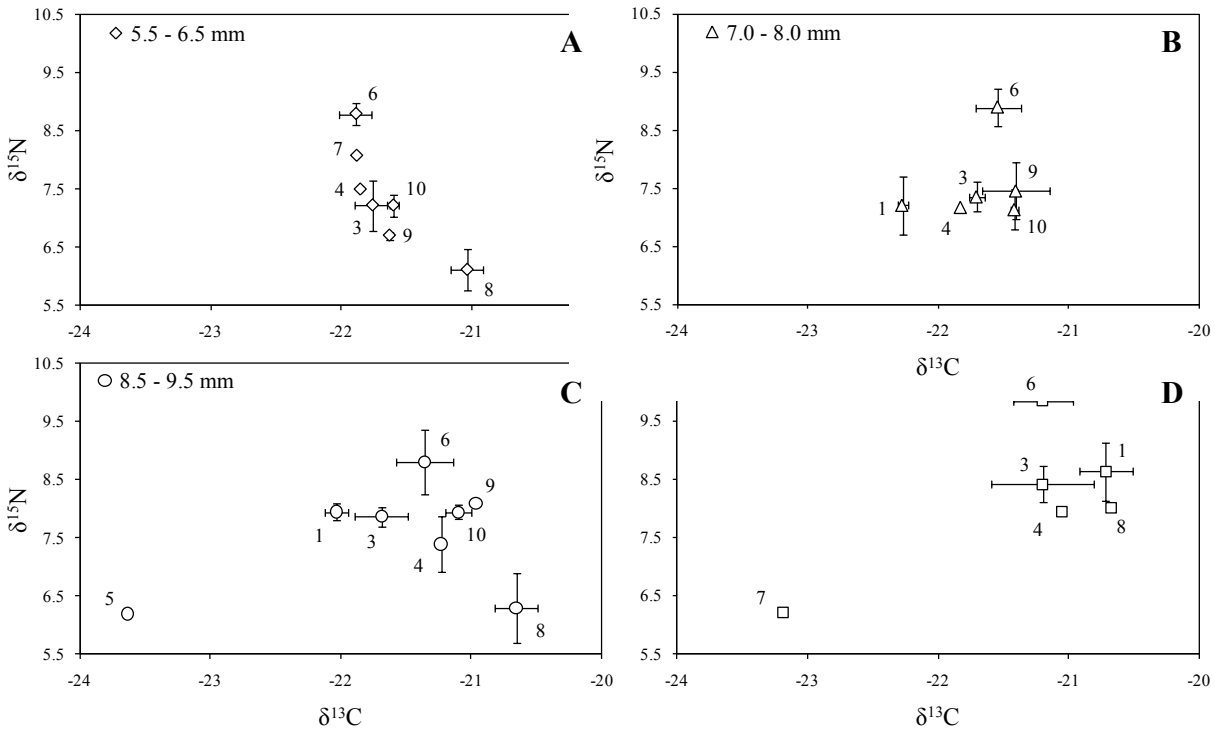

Figure 4.2. $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) for each size class of *Nauticaris marionis* (A to D) collected around the Prince Edward Islands. Regions: inter-island upstream (1 and 3), between (4, 5 and 6) and downstream (7) of the islands, and nearshore (8, 9 and 10); error bars represent standard deviations.

4.3.1.2. Fatty acids

Eighteen fatty acids were detected in *N. marionis* at concentrations >1.0% TFA (Table A13). The predominant fatty acids in all size classes and sampling locations were 16:0, 20:5ω3 and 22:6ω3. The principal fatty acids showed a range of values but no distinct spatial patterns were evident (ranges 16:0: 14.7 to 25.7% TFA, 20:5ω3: 17.4 to 24.7% TFA and 22:6ω3: 13.6 to 23.7% TFA). The principal fatty acids were also consistently found in substantially greater proportions than all other fatty acids (next most abundant were 18:1ω7: 5.2 to 8.0% TFA and 18:1ω9: 5.6 to 10.9% TFA). There were also moderate proportions of BAFAs (1.5 to 5.5% TFA) and very small proportions of the copepod fatty acids 22:1ω11 and 20:1ω9 (0.0 to 1.1% TFA) in all *N. marionis* samples. The ratios of 18:1ω9/18:1ω7 ranged from 0.8 to 1.8 (carnivory index). All fatty acids and indices showed no distinct ontogenetic or spatial patterns. The results from the PCA scores plot were first examined by size class (Fig. 4.3A) and then by sample location (Fig. 4.3B). Fatty acid profiles in shrimps of different size classes were highly variable and overlapped within the PCA scores plot. Fatty acid profiles of *N. marionis* from different locations were also highly variable and overlapped in several cases; however, Stations 5 and 8 (inter-island Natal Bank and nearshore east of Marion, respectively) and Stations 6 and 9 (inter-island south of Natal Bank and nearshore

southeast of Prince Edward, respectively) were all distinct. Principal components (PCs) 1 and 2 explained 30 and 15%, respectively, of the variance. The fatty acids with influential loadings (>0.2) for PC-1 included 16:0, 16:1ω7, 18:1ω7, 18:1ω9, 18:2ω6, 22:0, 22:5ω3 and 22:6ω3, whereas those for PC-2 were 14:0, 16:0, 18:0, 22:5ω3, 18:2ω6, 20:4ω6 and 22:6ω3.

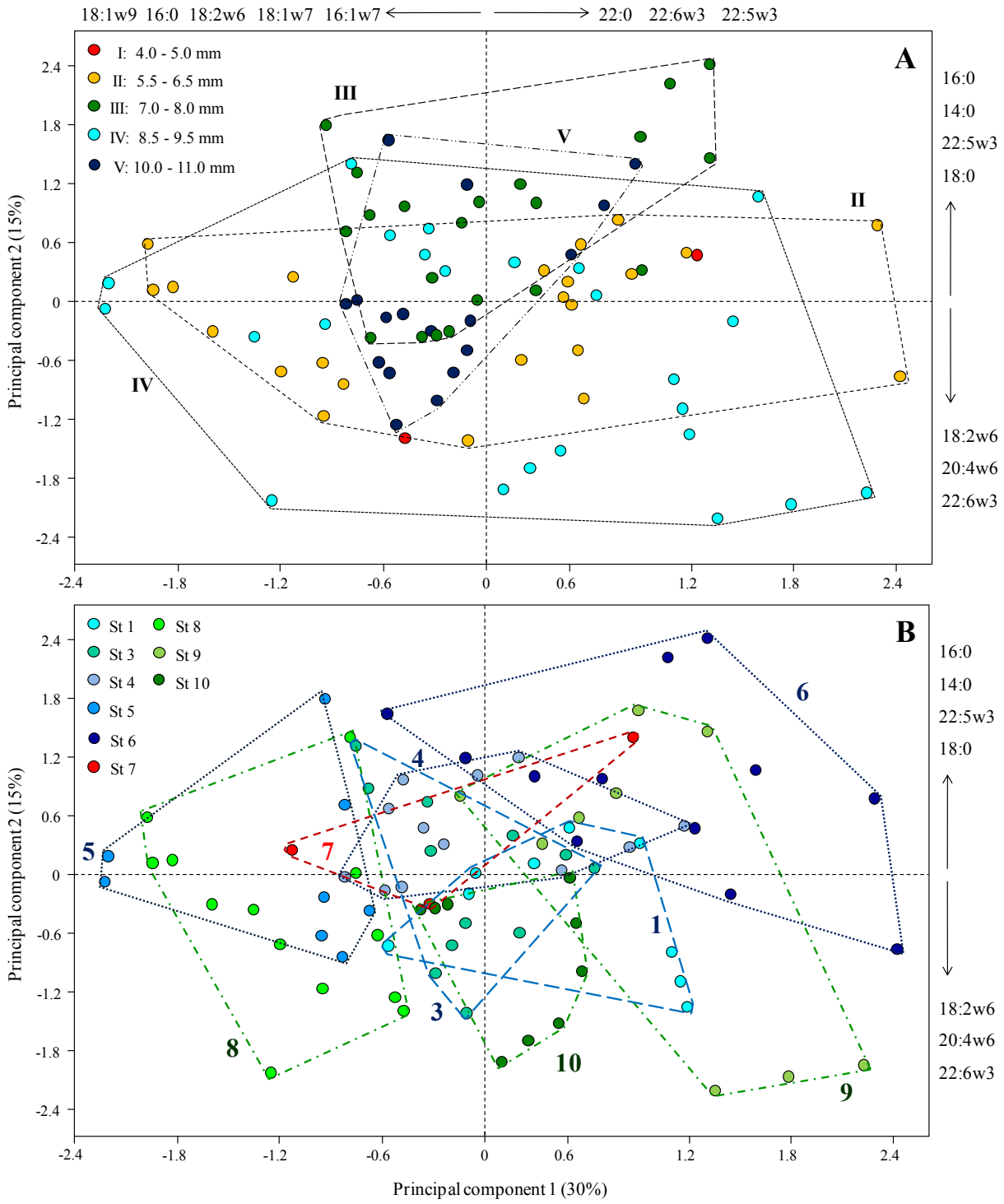

Figure 4.3. Principal component analysis (PCA) of transformed proportional data of *Nauticaris marionis* collected around the Prince Edward Islands. Convex hulls indicate size classes (A) and stations (B). Arrows running parallel to each axis denote the influence of the specified fatty acids that have loading values >0.2.

The proportions of EFAs in *N. marionis* were substantial (ranged from 35.5 to 49.4% TFA) and similar among size classes and regions (Fig. 4.4A). The concentrations of TFAs in *N. marionis* showed more variability with ontogeny and region than the proportion of EFAs (TFAs: 30.5% CV *versus* EFAs: 8.0% CV; Fig. 4.4B). The largest shrimps (V: 10.0 – 11.0 mm) contained the lowest concentrations of TFAs (33.0 to 37.7 µg FA mg^{-1} DM) and had the least variability among regions relative to the other size classes (I: 24.3% CV, II: 26.9% CV, III: 16.8% CV, IV: 35.3% CV and V: 6.5% CV). Overall, the *N. marionis* at Station 8 had the highest concentration of TFAs in each size class.

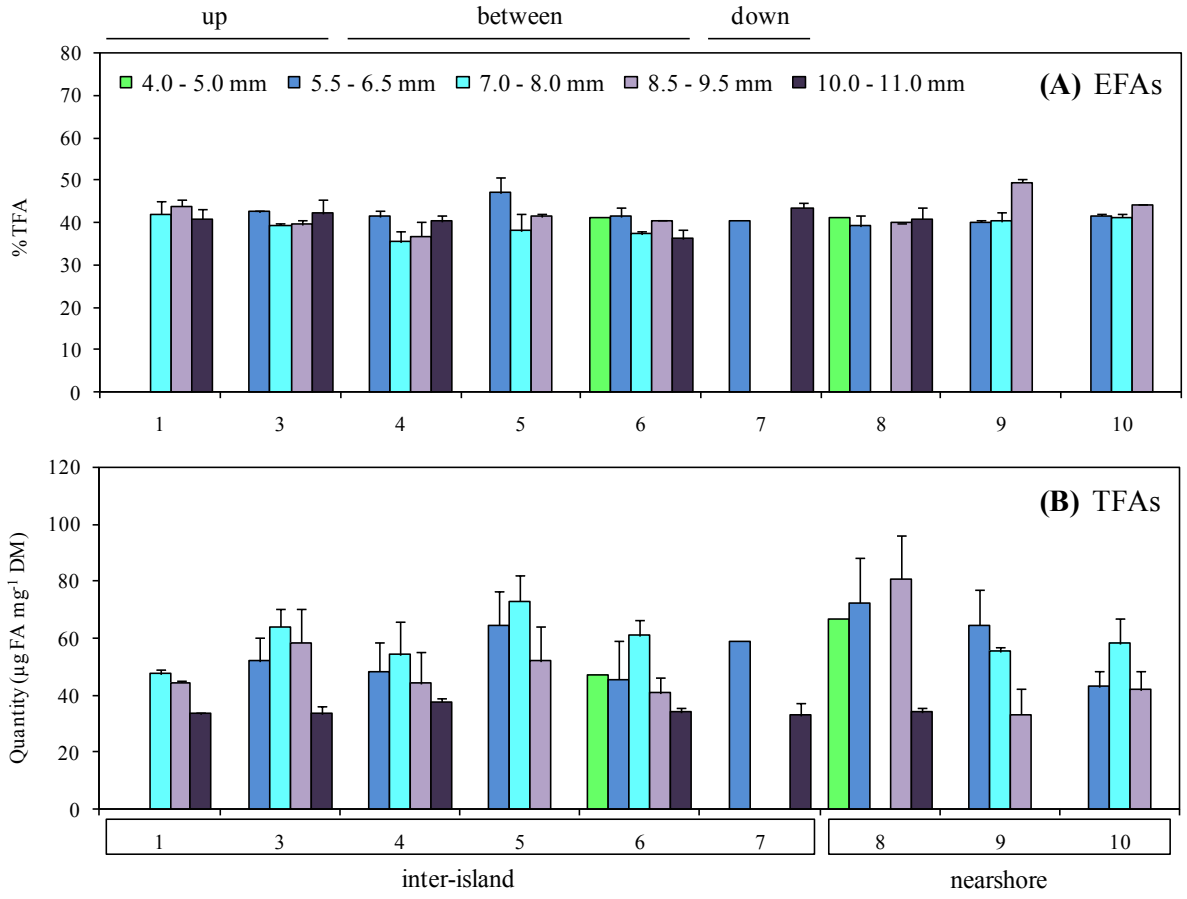

Figure 4.4. Proportion (% TFA) of essential fatty acids (EFAs; A) and quantity (µg FA mg^{-1} DM) of total fatty acids (TFAs; B) in the various size class of *Nauticaris marionis* at the nine stations it was collected from around the Prince Edward Islands. Stations are divided into regions: inter-island (upstream, between and downstream of the islands) and nearshore. Error bars indicate standard deviations.

4.3.2. Food sources

The detritus had a wide range in $\delta^{13}C$ values (from -31.79 to -23.01 ‰) and a narrower range in $\delta^{15}N$ values (from 0.64 to 2.79 ‰; Table 4.1). The detritus collected at Station 6 (south of Natal Bank), Station 9 (southeast of Prince Edward) and Station 10 (southeast of Marion) had

similar $\delta^{13}C$ values (-23.88 to -23.01 ‰), while the detritus samples from Station 1 (upstream northwest of Marion) and Station 5 (Natal Bank) were more ^{13}C-depleted (-25.32 ± 0.40 ‰ and -27.17 ± 0.99 ‰, respectively). The detritus from Station 3 (upstream northeast of Marion) was the most depleted (-31.79 ± 1.79 ‰). The zooplankton fractions had relatively narrow ranges in $\delta^{13}C$ and $\delta^{15}N$ signatures (-23.67 to -22.97 ‰ and -0.02 to 1.87 ‰, respectively; Table 4.1). The benthic suspension- and deposit-feeders, however, had wide ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures (-23.74 to -20.36 ‰ and 0.41 to 7.12 ‰, respectively, Table 4.1), and were generally more enriched than those of the zooplankton and detritus. In general, the shrimp were more ^{13}C-enriched than the detritus and zooplankton (Table 4.1). For the benthic community, the shrimp were consistently more ^{13}C-enriched than sponge sp. 2, bryozoan sp. 1, *Lanice marionensis* (tube-dwelling polychaete), *Thouarella variabilis* (gorgonian coral), *Plumularia insignis* (hydrozoan) and both bivalve species (Table 4.1).

Even though the fatty acid profiles of the detritus were highly variable among stations (Table A14), all detrital samples had relatively large proportions of EFAs (27.8 to 65.0% TFA), dominated by 20:4ω6 and 22:6ω3 (6.6 to 41.3% TFA and 12.2 to 22.0% TFA, respectively). The detritus contained moderate proportions of BAFAs (3.3 to 7.9% TFA) and large proportions of PUFAs (51.5 to 77.4% TFA). The concentrations of TFAs in the detritus, however, were relatively small (1.3 to 6.0 µg FA mg^{-1} DM). The fatty acid profiles of the zooplankton showed distinct changes among size fractions (Table A15). The small fraction (<500 µm) was almost completely dominated by SFAs (95.6 ± 1.4% TFA), while the medium (500 – 1500 µm) and large fractions (>1500 µm) contained relatively large proportions of PUFAs (44.5 ± 3.8% TFA and 48.3 ± 8.3% TFA, respectively). The small size fraction contained the most BAFAs of the three categories (10.1 ± 2.2% TFA *versus* 2.1 ± 0.3% TFA and 2.6 ± 1.8% TFA, respectively) but had no EFAs, unlike the medium and large fractions with relatively large proportions (39.6 ± 3.6% TFA and 40.2 ± 10.6% TFA, respectively). Only the medium and large zooplankton fractions contained fatty acids generally associated with calanoid copepods (Σ22:1ω11+20:1ω9). The small zooplankton had the lowest concentrations of TFAs (8.6 ± 1.5 µg FA mg^{-1} DM), followed by the medium fraction (20.6 ± 0.7 µg FA mg^{-1} DM), while the large zooplankton fraction had the greatest concentrations (51.0 ± 8.8 µg FA mg^{-1} DM). Fatty acid profiles of the benthic suspension- and deposit-feeding organisms (for individual species and collection locations) are described in Chapter 3 (section 3.3.3.2). Overall, these organisms contained moderate to

large proportions of 16:0, 18:0, 20:5ω3, 22:6ω3 and EFAs, but moderate proportions of 18:1ω7 (Tables A3 to A12).

Table 4.1. $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SD; ‰) of all potential pelagic and/or benthic food sources (zooplankton, detritus and benthic suspension-/deposit-feeders) and *Nauticaris marionis* (consumer) at each station around the Prince Edward Islands.

Taxonomic category or species		Station	$\delta^{13}C$	$\delta^{15}N$
Food sources				
Pelagic				
Zooplankton	< 500 µm	shelf	-22.97 ± 0.24	-0.02 ± 0.21
	500 – 1500 µm	shelf	-23.51 ± 0.32	0.84 ± 0.57
	> 1500 µm	shelf	-23.67 ± 0.16	1.87 ± 0.66
Benthic				
Detritus		1	-25.32 ± 0.40	1.33 ± 0.27
		3	-31.79 ± 1.79	1.73 ± 0.12
		5	-27.17 ± 0.99	0.64 ± 0.40
		6	-23.01 ± 0.38	2.79 ± 0.33
		9	-23.32 ± 0.61	2.16 ± 0.88
		10	-23.88 ± 0.41	1.44 ± 0.37
Sponge	sponge sp. 1	4	-21.59 ± 0.17	3.22 ± 0.67
		9	-20.36 ± 0.12	3.03 ± 0.30
	sponge sp. 2	6	-22.15 ± 0.04	2.20 ± 0.35
		9	-21.62 ± 0.13	1.98 ± 0.54
	sponge sp. 3	6	-21.23 ± 0.07	4.68 ± 0.16
		9	-20.63 ± 0.32	5.76 ± 0.26
Bryozoan	bryozoan sp. 1	3	-22.15	0.41
		4	-22.13	4.12
		6	-22.58	5.24
		9	-22.60	4.56
		10	-23.15 ± 0.12	1.62 ± 0.09
	bryozoan sp. 2	7	-20.50	6.31
Bivalve	*Limatula pygmaea*	1	-22.60 ± 0.18	2.39 ± 0.11
		5	-22.32 ± 0.14	2.53 ± 0.33
	Thracia meridionalis	1	-21.71	3.80
Polychaete	*Serpula vermicularis vermicularis*	10	-21.64	3.65
	Lanice marionensis	1	-23.74 ± 0.16	4.95 ± 0.19
		3	-23.72 ± 0.45	3.82 ± 0.44
		4	-23.38	5.91
		6	-23.08	5.17
		9	-22.79 ± 0.08	5.62 ± 0.17
	Thelepus extensus	8	-20.52 ± 0.17	5.78 ± 0.61
Hydrozoan	*Plumularia insignis*	7	-22.83	5.50
Gorgonian coral	*Thouarella variabilis*	7	-22.31	7.12

Table 4.1. (cont.)

Taxonomic category or species	Station	$\delta^{13}C$	$\delta^{15}N$
Consumer			
Nauticaris marionis			
7.0 – 8.0 mm	1	-22.28 ± 0.04	7.21 ± 0.50
8.5 – 9.5 mm		-22.04 ± 0.09	7.95 ± 0.15
10.0 – 11.0 mm		-20.71 ± 0.21	8.63 ± 0.49
5.5 – 6.5 mm	3	-21.76 ± 0.14	7.21 ± 0.44
7.0 – 8.0 mm		-21.71 ± 0.06	7.35 ± 0.26
8.5 – 9.5 mm		-21.69 ± 0.20	7.87 ± 0.17
10.0 – 11.0 mm		-21.20 ± 0.40	8.42 ± 0.31
5.5 – 6.5 mm	4	-21.86	7.49
7.0 – 8.0 mm		-21.83	7.17
8.5 – 9.5 mm		-21.23 ± 0.01	7.40 ± 0.48
10.0 – 11.0 mm		-21.05	7.94
8.5 – 9.5 mm	5	-23.63 ± 0.06	6.19 ± 0.24
4.0 – 5.0 mm	6	-22.13	8.22
5.5 – 6.5 mm		-21.89 ± 0.13	8.79 ± 0.19
7.0 – 8.0 mm		-21.54 ± 0.17	8.89 ± 0.31
8.5 – 9.5 mm		-21.36 ± 0.22	8.81 ± 0.55
10.0 – 11.0 mm		-21.19 ± 0.22	9.84 ± 0.02
5.5 – 6.5 mm	7	-21.88	8.07
10.0 – 11.0 mm		-23.19 ± 0.08	6.20 ± 0.67
5.5 – 6.5 mm	8	-21.03 ± 0.13	6.10 ± 0.35
8.5 – 9.5 mm		-20.66 ± 0.16	6.29 ± 0.60
10.0 – 11.0 mm		-20.67	8.01
5.5 – 6.5 mm	9	-21.63 ± 0.01	6.69 ± 0.07
7.0 – 8.0 mm		-21.40 ± 0.26	7.45 ± 0.49
8.5 – 9.5 mm		-20.97	8.09
5.5 – 6.5 mm	10	-21.60 ± 0.05	7.21 ± 0.20
7.0 – 8.0 mm		-21.42 ± 0.03	7.13 ± 0.34
8.5 – 9.5 mm		-21.10 ± 0.10	7.95 ± 0.12

4.4. DISCUSSION

4.4.1. Ontogenetic variation

The general pattern of enrichment in $\delta^{13}C$ signatures with increasing body size of *Nauticaris marionis* (Fig. 4.1), resulting in relatively distinct separation of size classes, suggests that these shrimp feed on different food sources throughout their development. This ontogenetic variation in the diet results in resource partitioning through niche separation. The observed pattern was relatively consistent among stations, suggesting that this niche separation with ontogeny is similar among shrimp inhabiting different regions in the shallow shelf of the PEI. The pattern of enrichment in $\delta^{13}C$ and $\delta^{15}N$ values with increased size has previously been documented between megalope larvae (CL <4.5 mm) and subadult/adult (CL >4.5 mm) shrimp at the PEI ($\delta^{13}C$: -20.11 ‰ and -19.54 ‰, respectively; $\delta^{15}N$: 4.85 ‰ and 8.34 ‰; Pakhomov *et al.*, 2004). The isotopic shift is thought to reflect changes in the diet as megalope larvae feed predominantly on phytoplankton, while subadult/adult shrimp consume mainly benthic organisms and detritus, and at times, zooplankton (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999). The deep-water prawn *Pandalus borealis* from the marginal ice zone of the Southern Scotia Sea also exhibits ontogenetic changes in diet composition, whereby younger prawns mostly consume calanoid copepods, while the older prawns also consumed euphausiids (Hopkins *et al.*, 1993). Niche separation between subadult and adult *N. marionis* is thus not unexpected.

It is particularly interesting, however, that this separation is also evident in later developmental stages i.e. that different adult size classes were isotopically different. This apparent niche separation may lead to reduced cannibalistic interactions among the different size classes of the shrimp (Pakhomov *et al.*, 1999). The $\delta^{15}N$ values of the shrimp also showed an enrichment with an increase in size where the largest shrimp (CL:10.0 – 11.0 mm) were generally more ^{15}N-enriched than the smaller shrimp (CL: 4.0 – 5.0 mm; mean $\delta^{15}N$ value: 8.17 and 7.37 ‰, respectively). This ontogenetic enrichment could result from the consumption of different food sources, however, body size related differences in tissue turnover rates (Gorokhova & Hansson 1999, Sweeting et al. 2007) and/or impact of moulting on $\delta^{15}N$ signatures (Doi et al. 2007) could also result in the ontogenetic differences observed in the $\delta^{15}N$ values of the shrimp. It is important to note, however, that all individuals contained large proportions of PUFAs and EFAs (39.8 to 55.1% TFA and 35.5 to 49.4% TFA, respectively) with no differences among size classes (Fig. 4.4). These similarities may

suggest that the different developmental stages are well adapted at sequestering these vital components from their habitats despite the apparent niche separation (Parrish *et al.*, 2009).

In contrast, the fatty acid profiles of *N. marionis* exhibited no apparent pattern among the different size classes of shrimp and were similar regardless of size or location (Table A13; Fig. 4.3A). The fatty acids 16:0, 20:5ω3 and 22:6ω3 were always present in high proportions. Similar patterns have been observed among the later developmental stages of copepod species in various high latitude regions (Kattner and Krause, 1987; Kattner and Hagen, 1995). It is interesting to note that, unlike some deposit-feeders at the PEI (Station 1; Chapter 3), each size class of *N. marionis* had relatively similar TFA concentrations among regions (Fig. 4.4), indicating that the same size classes in each region were maintaining a similar nutritional condition regardless of region. Out of all the size classes, however, the largest shrimp had the smallest TFA concentrations, which was consistent among regions (Fig. 4.4). Low quantities of TFAs have been observed in spent females of *Mysis mixta* (Mysidacea) in a cold temperate bay (Richoux *et al.*, 2005). At the PEI, large numbers of gravid female *N. marionis* have been recorded during March, with only a few gravid females recorded in April and May (Pakhomov *et al.*, 2000a). Furthermore, as *N. marionis* exhibits sexual dimorphism, only females have a CL >9 mm (Pakhomov *et al.*, 2000a), thus the largest size class are unlikely to contain males. Therefore, the lowest quantities of TFAs in the largest size class of shrimp may be reflect the reproductive state of these shrimp.

Although there was a clear trend of ^{13}C- and ^{15}N-enrichment in *N. marionis* with increasing size at each station (Fig. 4.1), there were large ranges of $\delta^{13}C$ and $\delta^{15}N$ values in each size class among stations (Fig. 4.2). Small *N. marionis* (size class II) had the narrowest range of $\delta^{13}C$ signatures among stations (-21.98 to -21.03 ‰, excluding nearshore Station 8). As the shrimps increased in size, so did their range of $\delta^{13}C$ signatures (-23.63 to -20.66 ‰; Fig. 4.2). The increase in $\delta^{13}C$ values with size suggests that the smaller size classes of *N. marionis* may have a more restricted diet than larger individuals. Generally, pelagic prey and detritus contribute more to the diet of smaller shrimps (CL: <7.0 mm), while benthic prey is more prevalent in larger individuals (CL: >8.5 mm; Pakhomov *et al.*, 1999; Vumazonke *et al.*, 2003). Zooplankton and detritus had depleted $\delta^{13}C$ signatures (-23.67 to -22.97 ‰ and -31.79 to -23.01 ‰, respectively), while the benthic suspension- and deposit-feeders were generally more enriched (-23.74 to -20.36 ‰). As individuals in the smallest size classes (I and II) generally had the most ^{13}C-depleted values (-21.77 ± 0.17 ‰, excluding Station 8), the

isotope data provide support that zooplankton and detritus may form a large component in the diet of these smaller shrimp. The fatty acids often associated with calanoid copepods (22:1ω11 and 20:1ω9) were, however, not particularly abundant in the shrimps (0.0 to 1.1% TFA; Table A13). Euphausiids (in particular *Thysanoessa* spp.) and harpacticoid copepods, together with calanoid copepods, can also contribute substantially to the pelagic prey recorded in the stomach contents of *N. marionis* (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999). As a result, the observed pattern in the stable isotopes may not be reflected in the fatty acid profiles as euphausiids and non-calanoid copepods generally do not have specific target fatty acids associated with them.

4.4.2. Food sources

Nauticaris marionis were generally more ^{13}C-enriched than the detritus, zooplankton and a select group of benthic suspension-/deposit-feeding organisms including bryozoans, bivalves, octocorals, hydrozoans and the tube-dwelling polychaete *Lanice marionensis* (Table 4.1). As there is an enrichment of ~1.00 ‰ in δ^{13}C per trophic level (DeNiro and Epstein, 1978; Fry and Sherr, 1984; Peterson *et al.*, 1985), it is likely that the detritus, zooplankton and various benthic invertebrates represent potential carbon sources for these shrimp. The detritus, particularly at Stations 1, 3 and 5, were very ^{13}C-depleted compared to the shrimp, while the δ^{13}C signatures of the various benthic invertebrates, and at times the zooplankton, were generally closer to that of the shrimp (Table 4.1). Therefore, *N. marionis* probably consume a combination of food sources, a conclusion supported by previous gut content analysis of juvenile, subadult and adult shrimp (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999; Vumazonke *et al.*, 2003). The contributions of detritus *versus* benthic organisms vary spatially and temporally, but overall detritus tends to contributed proportionally more to the diets of smaller individuals than benthic organisms (Pakhomov *et al.*, 1999). The fatty acid data indicated that the ratios of 18:1ω9/18:1ω7 in *N. marionis* ranged from 0.8 to 1.8 (Table A13). As suspension-feeders at the PEI such as sponges and brachiopods, had ratios between 0.0 and 0.7 (Table A3 and A5), and cnidarians (predominantly carnivorous; Cairns *et al.*, 2009) had ratios between 3.3 and 9.9 (Table A9), the mid-range values obtained in *N. marionis* suggest an omnivorous diet. The shrimps also contained moderate proportions of BAFAs, indicating a microbial component in their diet. As the BAFAs likely originated from the detritus (Levinton *et al.*, 2002), an omnivorous diet is further supported. The carnivory index of the shrimp had a wide range of values among size class and region (from 0.1 to 2.1), which, like the proportion of BAFAs, showed no distinct spatial or ontogenetic patterns,

suggesting that the dietary contributions of animal prey and detritus were highly variable and location-specific. As *N. marionis* is an omnivorous opportunistic feeder (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999), these findings were not unexpected.

Despite the apparent variation in food source contribution among individuals, all *N. marionis* specimens were dominated by the fatty acids 16:0, 20:5ω3 and 22:6ω3 (Table A13). As 20:5ω3 and 22:6ω3 are important component of membranes (Olsen, 1999; Arts *et al.*, 2001) and help maintain membrane fluidity at lower temperatures (22:6ω3 to a lesser extent than 20:5ω3; Buda *et al.*, 1994; Hall *et al.*, 2002; Copeman and Parrish, 2003), the conservation of these fatty acids by shrimps in all size classes is not surprising. As 20:5ω3 and 22:6ω3 are EFAs, they cannot be synthesised by most heterotrophs and must therefore be obtained in consumer diets (Olsen, 1999; Parrish, 1999; Arts *et al.*, 2001). As a consequence, these EFAs are highly conserved in aquatic systems (Arts *et al.*, 2001). Both these fatty acids were found in large proportions in the majority of benthic suspension- and deposit-feeding organisms at the PEI, likely obtained through consumption of phytoplankton (20:5ω3: diatom, and 22:6ω3: dinoflagellate; Chapter 3). These EFAs were also prevalent in the medium (500 – 1500 μm) and large (>1500 μm) zooplankton fractions (20:5ω3: 15.0 to 15.2% TFA, and 22:6ω3: 23.8 to 24.1% TFA). As a result, pelagic primary production was accessible by *N. marionis* through the consumption of benthic or pelagic prey. The next most abundant fatty acid in *N. marionis* was 18:1ω9 (Table A13). As 18:1ω9 is generally abundant in animal prey (Stevens *et al.*, 2004), the dominance of this fatty acid supports an omnivorous feeding mode. The fatty acid 18:1ω7 was also present in relatively significant proportions in *N. marionis*. This component occurs in abundance when a food source contains a large amount of bacteria (Kharlamenko *et al.*, 1995; Dalsgaard *et al.*, 2003), and was present in kelp detrital particulate organic matter (POM) and most benthic suspension- and deposit-feeders at the PEI (Chapter 3). These data suggest that the shrimp may consume kelp detritus either directly or indirectly. Thus, kelp and phytoplankton may contribute (directly or indirectly) to the diet of *N. marionis* in the vicinity of the PEI. Chain elongation of 16:1ω7 (has been associated with diatoms; Parrish *et al.*, 2000; Dalsgaard *et al.*, 2003) to 18:1ω7 can also occur (Sargent and Henderson, 1986), so the 18:1ω7 in *N. marionis* could also have originated from diatoms. The deep water prawn *P. borealis* (shelf off northeast Greenland) contained the same dominant fatty acids (20:5ω3, 22:6ω3, 16:0, 18:1ω9, 18:1ω7 and 16:1ω7) as *N. marionis* and in similar relative proportions (Graeve *et al.*, 1997), suggesting the importance of these fatty acids in cold aquatic food webs. As *P. borealis* contributes to the

diet of several species of fish, in particular cod, and marine mammals (Pedersen and Riget, 1993; Berenboim *et al.*, 2000; Nilssen *et al.*, 2000), and as the phytoplankton fatty acids occurred in highest proportions, this prawn also forms a key species linking primary production to higher trophic levels.

4.4.3. Spatial variation

Despite *N. marionis* exhibiting a high degree of variation in isotopic signatures among stations, shrimp collected from the inter-island Station 6 as well as the nearshore stations (particularly Station 8) showed an overall increase in $\delta^{15}N$ and $\delta^{13}C$ signatures (respectively) among size classes (Fig. 4.2). All *N. marionis* collected at Station 6 had the highest $\delta^{15}N$ values in each size class; however, their $\delta^{13}C$ values were similar to individuals from other stations. Pakhomov *et al.* (2004) also observed differences in $\delta^{15}N$ values in *N. marionis* between regions, possibly a result of the consumption of difference food sources by shrimps in different regions (nearshore regions: more deposit-feeding polychaetes, crustaceans and detritus, inter-island regions: more suspension-feeding hydrozoans). *Nauticaris marionis* from the nearshore stations, particularly those from Station 8, were the most ^{13}C-enriched shrimp in size classes II, III and IV (Fig. 4.2). This ^{13}C-enrichment was particularly pronounced in the smaller shrimp (size class II), as the other specimens from different stations had very similar $\delta^{13}C$ values (-21.98 to -21.55 ‰), while those from Station 8 were more enriched (-20.91 ± 0.23 ‰). As Station 8 was situated close to the kelp beds, and as kelp detritus had an enriched $\delta^{13}C$ value (-17.50 ‰; Chapter 3), it is likely that the ^{13}C-enrichment in *N. marionis* at Station 8 resulted from kelp entering the food web. Kaehler *et al.* (2000) found that benthic organisms near the kelp beds (similar position to Station 8) exhibited more enriched $\delta^{13}C$ signatures than those in the inter-island region. A similar but less prominent trend was also observed in the benthic organisms during the current study (see Fig. 3.6; Chapter 3). Therefore, the substantial ^{13}C-enrichment of *N. marionis* at Station 8, compared to individuals from other stations, suggested that Station 8 shrimp were feeding primarily on benthic organisms from within the kelp beds rather than on benthic organisms from the open shelf region.

Interestingly, the shrimp collected at Stations 8 (east of Marion) and 5 (Natal Bank), both situated near kelp beds, clustered together in the fatty acid PCA plot and showed little overlap with other stations (Fig. 4.3B). As the fatty acids 18:2ω6 and 18:1ω7, of which elevated proportions were associated with kelp (plant and degraded kelp-associated bacteria,

respectively; Chapter 3), contributed to the separation of *N. marionis* from these two stations, it is likely that enhanced input of kelp into the food web in these regions was responsible for these spatial patterns. The fatty acid data, therefore, suggest some broad spatial differences in diet between *N. marionis* that live in shallow regions, possibly feeding within the kelp beds, and those that live in the deeper open shelf region. Off the northeast coast of Greenland, the proportion of fatty acids in the copepod *Calanus hyperboreus* changed according to the hydrographic system from which they were collected, and were strongly linked to changes in their food sources, i.e. a shift between diatom- and dinoflagellate-dominated phytoplankton communities (Kattner and Hagen, 1995). As a result, individuals in the marginal ice zone had similar proportions of dietary target fatty acids among sampling sites since the phytoplankton community was dominated by dinoflagellates (Kattner and Hagen, 1995).

4.5. CONCLUSION

Stable isotope and fatty acid signatures of *Nauticaris marionis* both showed some degree of variation among size class and region, indicative of an opportunistic omnivore. The $\delta^{13}C$ and $\delta^{15}N$ signatures of the shrimp showed an enrichment from small to large individuals, indicating niche separation among the size classes. The data further suggested that smaller individuals may have had more restricted diets than larger individuals. Despite the niche separation and variation in carbon sources utilised, all shrimp had similar fatty acid profiles, with large proportions of PUFAs and EFAs that indicated that all of the shrimp were well adapted at sequestering these vital components from their habitats. The nearshore shrimp, particularly those from Station 8, were more ^{13}C-enriched than those from the inter-island region, suggesting a increased consumption of kelp (directly or indirectly). The diatom and dinoflagellate fatty acids (20:5ω3 and 22:6ω3, respectively), however, dominated the fatty acid profiles of all the shrimps, suggesting that indirectly phytoplankton was an important component in the diet of *N. marionis* in all regions around the PEI. These shrimp demonstrate a high degree of plasticity in their diet, most likely in response to the variable supply of food within the region.

5 TEMPORAL VARIATION IN STABLE ISOTOPE SIGNATURES OF THE BENTHIC AND HYPERBENTHIC COMMUNITY IN THE VICINITY OF THE PRINCE EDWARD ISLANDS AND POTENTIAL LONG-TERM CHANGES

5.1. INTRODUCTION

Global climate change has been associated with changes oceanic circulation in the Southern Ocean resulting from strengthening and shifting of southern hemisphere westerly winds, thus causing shifts in the position and intensity of major frontal systems (Oke and England, 2004; Fyfe *et al.*, 2007). The Antarctic Circumpolar Current (ACC) has exhibited a gradual southward shift of up to ~1° of latitude in its average position over the last 60 years (Gille, 2002), while historical data (1959 – 1999) of the sub-Antarctic Front (SAF) in the region of the PEI has also indicated, but not conclusively, a possible southward migration over time (Pakhomov and Chown, 2003). The Prince Edward Islands (PEI) are situated in the direct path of the easterly flowing ACC between two of the major oceanic frontal systems of the Southern Ocean, the SAF to the north and the Antarctic Polar Front (APF) to the south. The position of the SAF relative to the islands plays a crucial role in the oceanographic conditions around the islands (Perissinotto *et al.*, 2000). When the SAF is far to the north, the flow rate of the ACC is slow enough that frictional forces between it and the islands result in the formation of trapped anticyclonic eddies within the inter-island region and lee of the islands (Perissinotto and Duncombe Rae, 1990; Ansorge and Lutjeharms, 2002). However, when the SAF lies close to the islands, the flow rate of the ACC near the islands is much faster, resulting in a flow-through system occurring and the absence of eddies between the islands (Perissinotto *et al.*, 2000). Decreased water retention between the islands results in less frequent diatom blooms within the inter-island region, which may have an impact on the benthic community due to changes in food availability (McQuaid and Froneman, 2008).

There is growing evidence that global climate change is impacting the terrestrial ecosystem of the PEI through increased air temperatures, decreased precipitation and the melting of Marion Island's ice plateau (Smith, 2002; Sumner *et al.*, 2004; le Roux and McGeoch, 2008). From a biological perspective, these changes have been associated with a decrease in the primary productivity of terrestrial plants and the range expansion of invasive species (Chown

and Smith, 1993; Bergstrom and Chown, 1999; Chown *et al.*, 2002). Evidence for the impact on the marine ecosystem is, however, generally lacking. Pakhomov *et al.* (2004) observed an overall depletion in the $\delta^{13}C$ signatures of the hyperbenthic shrimp *Nauticaris marionis* at the PEI over the period of 1984 to 2000. As carbon isotope fractionation has a strong negative relationship with phytoplankton growth rates (Bidigare *et al.*, 1997; Laws *et al.*, 1997; Burkhardt *et al.*, 1999a, b), fast growing phytoplankton should have more enriched $\delta^{13}C$ signatures than slow growing phytoplankton in the same region. Thus, phytoplankton in less productive oceanic waters are likely to have more depleted $\delta^{13}C$ values compared to those in productive coastal waters at the same latitude (Michener and Schell, 1994; Rau *et al.*, 1997). As a result, ^{13}C-depletions in aquatic systems can indicate an overall decline in pelagic primary productivity (Schell, 2000; Hirons *et al.*, 2001). The overall depletion in the $\delta^{13}C$ signatures of the shrimp, independent of changes in the $\delta^{15}N$ signatures, may have resulted from shifts in the carbon signal at the base of the food web due to the long-term decrease in productivity within the PEI ecosystem (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). It is therefore important to determine whether concurrent changes in isotope signatures are occurring in the shrimp and other key components of the benthic community in the vicinity of the islands.

This chapter represents an analysis of the temporal trends in the isotopic signatures of selected components of the benthic community of the PEI towards an attempt to determine the impact of global climate change on this productive ecosystem. It was hypothesized that there is a temporal depletion in $\delta^{13}C$ values of the benthic organisms, reflecting an increased frequency of flow-through system conditions between the islands as a direct result of long periods of less productive small cell-dominated phytoplankton communities (i.e. more ^{13}C-depleted than diatom-dominated communities). Organisms such as sponges and hydrozoans, however, may not reflect the decreased frequency in bloom events due to their size restricted and/or selective feeding modes. It was also hypothesized that if the frequency of blooms between the islands has further decreased since 2000, the shrimp will reflect a subsequent depletion in $\delta^{13}C$ values.

5.2. MATERIALS AND METHODS

5.2.1. $\delta^{13}C$ and $\delta^{15}N$ signatures in the hyperbenthic shrimp *Nauticaris marionis*

Stable carbon and nitrogen signatures in *Nauticaris marionis* (defatted samples) for the period April/May 1984 to 2000 were obtained from Pakhomov *et al.* (2004). The 2009

investigation (Chapter 4) demonstrated that *N. marionis* from the nearshore and inter-island regions and different size classes had different isotope signatures (see Figs. 4.1 and 4.2). For comparative purposes, only *N. marionis* within the same size ranges (carapace length [CL]: 5.0 – 7.5 mm) and collection locations (Station 8: nearshore east of Marion, Station 4: inter-island central shelf, Station 6: inter-island south of Natal Bank and Station 7: inter-island downstream) were employed for this comparison. Furthermore, as shrimps collected from Station 8 had substantially different isotope signatures from those collected from the open shelf region between the islands, the shrimp were separated according to their region, i.e. nearshore or inter-island shelf. The $\delta^{13}C$ and $\delta^{15}N$ signatures of *N. marionis* from 1984, 1985 and 1997 were corrected for preservation according to Pakhomov *et al.* (2004). By combining isotope data from Pakhomov *et al.* (2004) with data generated from this current study, the dataset was expanded from 16 to 25 years, providing a long-term data set to assess temporal variations in the shrimp in the vicinity of the PEI.

5.2.2. $\delta^{13}C$ and $\delta^{15}N$ signatures in the benthic community: nearshore and inter-island

Stable carbon and nitrogen signatures for selected components of the benthos in the nearshore and inter-island benthic communities (defatted samples) from April 1999 were obtained from Kaehler *et al.* (2000). The 2009 data (Chapter 3) demonstrated that benthic organisms from different locations within the nearshore and inter-island regions (see Figs. 3.5 and 3.6) tended to have different isotope signatures. As a result, the comparisons of the 2009 data (Chapter 3) with Kaehler *et al.* (2000) were made on the benthos collected from the same locations: nearshore, which included individuals from Station 8 (east of Marion) and inter-island central shelf which included individuals from Station 4 (central shelf) and Station 6 (south of Natal Bank). The same species from the two studies were compared within each region. Sponges were not identified to species level in either study and were thus regarded as a single taxonomic group. Hydrozoans collected in 1999 (Kaehler *et al.*, 2000) were not identified to species but are likely the same species (*Plumularia insignis*) collected in 2009 (Kaehler pers. comm.). Two species of zooplankton (the chaetognath *Sagitta gazellae* and the euphausiid *Euphausia vallentini*) collected from the vicinity of the islands during both studies were also compared. Isotopic analyses of the asteroids and ophiuroids in 2009 were conducted as described in Chapter 2, section 2.3. By combining isotope data from Kaehler *et al.* (2000) with data generated from the 2009 study, the first evaluation of long-term changes in stable isotope ratios of select components of the benthic

community at the PEI, including suspension- and deposit-feeders as well as scavengers/ predators, could be performed.

5.2.3. $\delta^{13}C$ signatures of suspended particulate matter at the Prince Edward Islands

Stable carbon signatures for suspended particulate matter (SPM) around the PEI during March/April 2003 were obtained from Kaehler *et al.* (2006) and compared to those obtained in April 2009 (Chapter 3). Sea-surface temperature data for the region surrounding the PEI during both study periods (March/April 2003 and April 2009) were obtained from monthly averages (11 micron day, MODIS-Terra.R1.1) using NASA's Giovanni product (available at http://disc.sci.gsfc.nasa.gov/giovanni), hereafter NASA Giovanni. The position of the SAF was determined by the 8.0 to 8.5°C isotherms, as described by Uddstrom and Oien (1999).

5.3. RESULTS

Compared to the historical data (1984 to 2000), *Nauticaris marionis* collected in 2009 were more ^{13}C-depleted in both the nearshore and inter-island individuals (Figs. 5.1A and B).

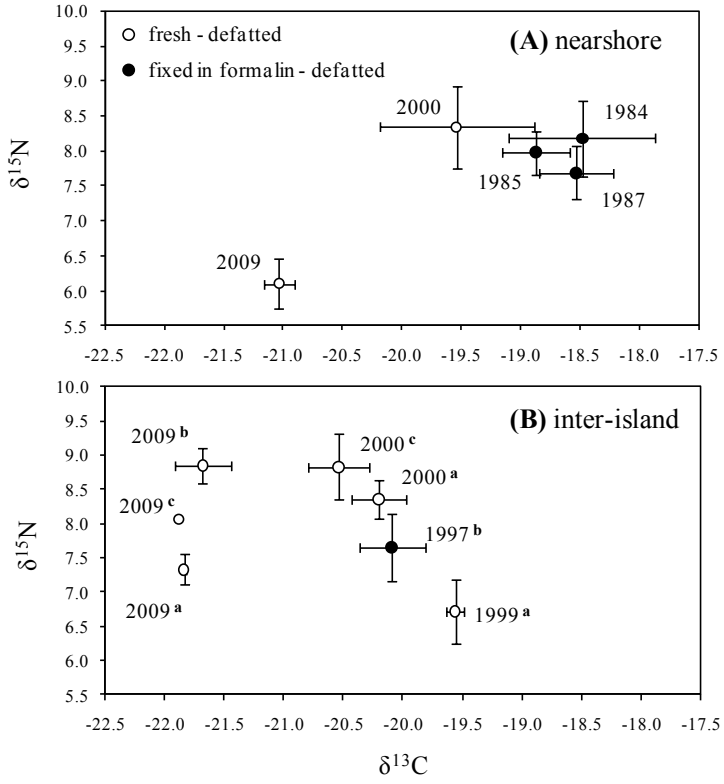

Figure 5.1. Temporal shifts in $\delta^{13}C$ and $\delta^{15}N$ signatures (‰) of *Nauticaris marionis* collected from nearshore (A) and inter-island (B) regions around the Prince Edward Islands during April/May between 1984 and 2009. Data (mean ± SD) for *N. marionis* from 1984, 1985, 1987, 1999 and 2000 were obtained from Pakhomov *et al.* (2004). Nearshore: near kelp beds (Station 8); inter-island: [a] central shelf (Station 4), [b] south of Natal Bank (Station 6) and [c] downstream (Station 7). Note that the $\delta^{13}C$ and $\delta^{15}N$ signatures of *N. marionis* from 1984, 1985, 1987 and 1997 were corrected for preservation according to Pakhomov *et al.* (2004).

There was some inter-annual variation in the $\delta^{13}C$ signatures of *N. marionis* among years, but the overall trend was a substantial depletion in $\delta^{13}C$ values over time in both the nearshore and inter-island individuals ($\delta^{13}C$ change: -2.55 ‰ and -2.32 ‰, respectively). The $\delta^{13}C$ signatures of the benthic organisms obtained in 2009 were more depleted than those from 1999 ($\delta^{13}C$ change: from -1.96 to -4.70 ‰), with the notable exceptions of the zooplankton, sponges and hydrozoans, which had similar isotope signatures during both studies (Table 5.1; Fig. 5.2).

Table 5.1. $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SD; ‰) of the zooplankton and benthic organisms collected during April 1999 (Kaehler *et al.*, 2000) and April 2009 (current study) around the Prince Edward Islands. The benthic community is separated into nearshore and inter-island (central) regions.

	2000		**2009**	
Taxonomic category or species	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Zooplankton				
Chaetognath				
Sagitta gazellae	-23.29 ± 0.45	3.05 ± 0.10	-22.87 ± 0.11	3.66 ± 0.13
Euphausiid				
Euphausia vallentini	-22.18 ± 2.00	3.40 ± 0.83	-22.49 ± 0.35	1.17 ± 0.17
Benthos: nearshore				
Deposit-feeder				
Polychaete				
Thelepus extensus	-17.41 ± 0.21	5.52 ± 0.53	-20.52 ± 0.17	5.78 ± 0.61
Benthos: inter-island				
Suspension-feeders				
Sponges	-21.80 ± 0.24	1.92 ± 1.22	-21.66 ± 0.46	3.37 ± 1.25
Brachiopod				
Magellania kerguelenensis	-18.47 ± 0.06	3.78 ± 0.33	-20.43	4.14
Hydrozoans	-22.35	2.50	-22.83	5.50
Scavengers/predators				
Ophiuroid				
Ophionotus hexactis	-16.71 ± 3.11	7.72 ± 0.44	-21.03 ± 0.54	6.04 ± 0.68
Ophiacantha vivipara	-18.59 ± 0.24	8.28 ± 0.11	-20.18 ± 0.49	8.38 ± 0.40
Asteroid				
Porania antarctica	-15.41 ± 0.10	6.00 ± 0.17	-20.11 ± 0.09	9.56 ± 0.10
Odonaster meridionalis	-19.93 ± 0.06	7.70 ± 0.22	-22.89 ± 0.13	5.59 ± 0.17

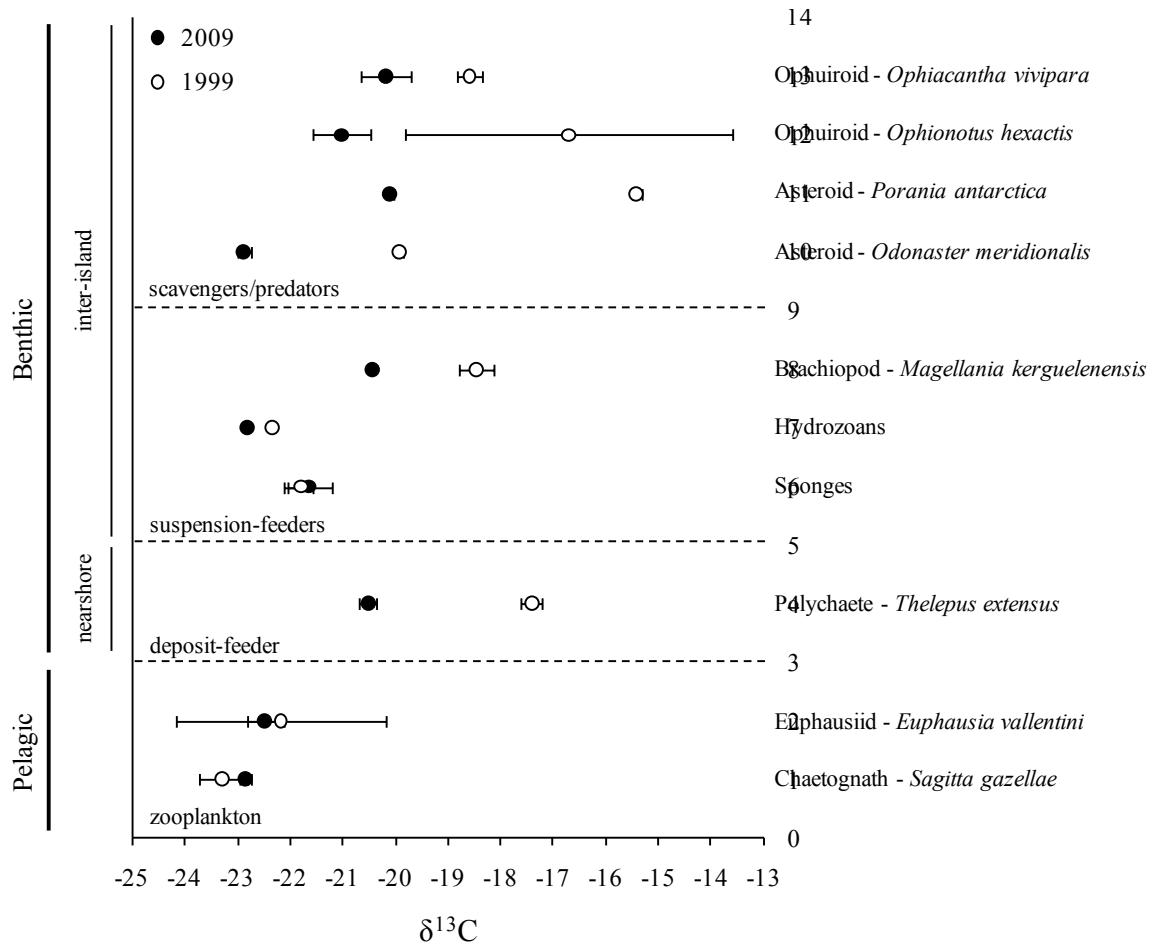

Figure 5.2. $\delta^{13}C$ signatures (‰) of zooplankton and benthic organisms collected from the nearshore and inter-island regions during April 1999 (Kaehler *et al.*, 2000) and April 2009 (current study) around the Prince Edward Islands.

Sea-surface temperature data, derived from monthly averages (MODIS-Terra.R1.1, NASA Giovanni), indicated that during March/April 2003, the SAF (8.0 to 8.5°C isotherms) was located far to the north of the islands (Fig. 5.3B). During April 2009 the SAF appeared to be immediately north of the PEI and less intense than in 2003 (Fig. 5.3D). During March/April 2003, the $\delta^{13}C$ values of the SPM between and within the lee of the PEI were more enriched than those upstream, i.e. east of the islands (-21.17 ± 0.68 ‰ and -23.51‰ ± 0.61 ‰, respectively; Fig. 5.3A). During April 2009, however, the $\delta^{13}C$ values of the SPM were similar between the regions (between: -24.33 ± 0.42 ‰, upstream: -24.16 ± 0.58 ‰; Fig. 5.3C). The $\delta^{13}C$ values recorded for the SPM between and within the lee of the islands during 2003 were also more enriched than those recorded during 2009 (2003: -21.17 ± 0.68 ‰, 2009: -24.33 ± 0.42 ‰; Figs. 5.3A and C).

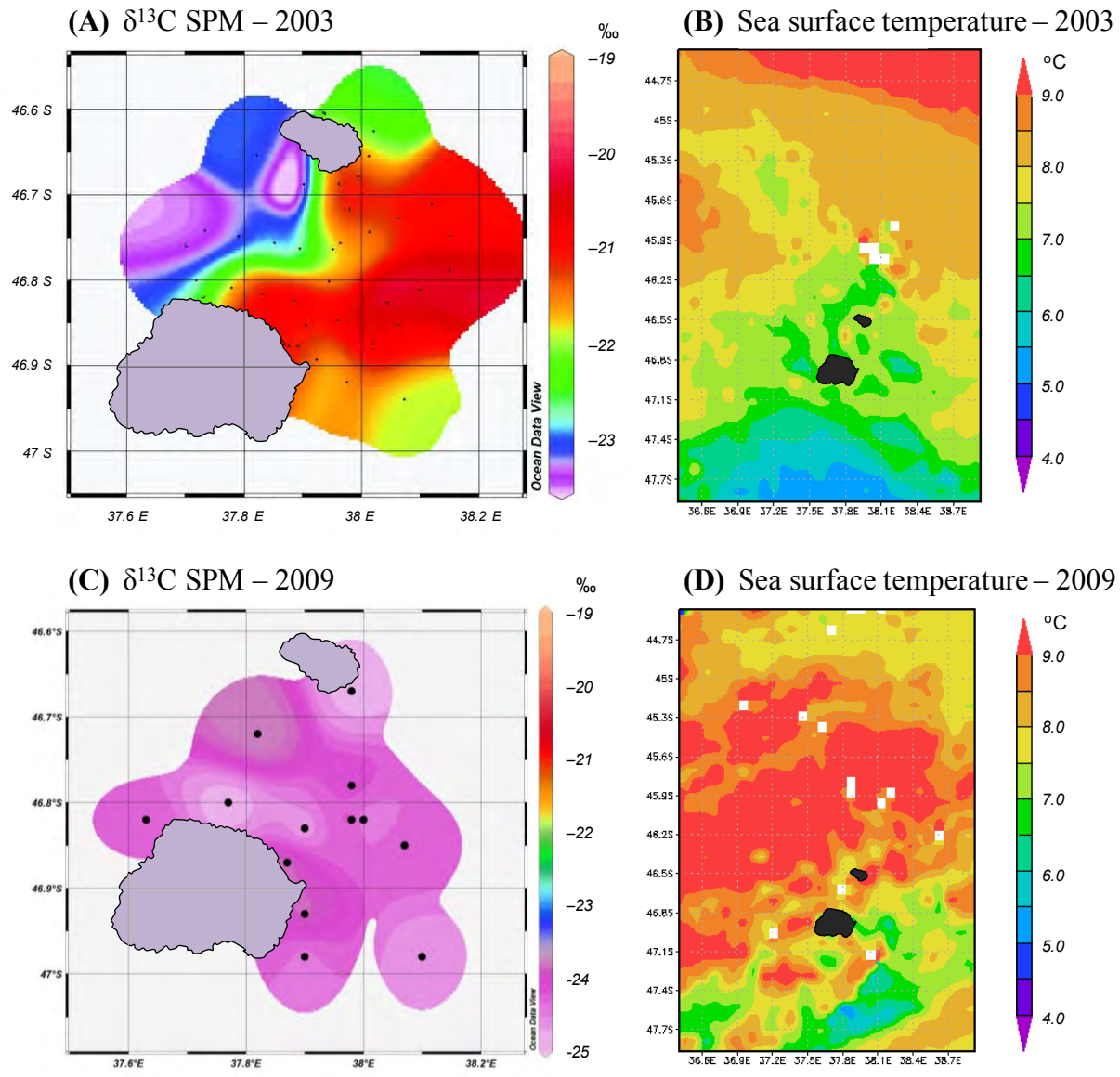

Figure 5.3. $\delta^{13}C$ signatures (‰) of the surface water suspended particulate matter (SPM) collected during March/April 2003 (Kaehler *et al.*, 2006; A) and April 2009 (current study; C) around the Prince Edward Islands. The sea-surface temperature data were derived from monthly averages (MODIS-Terra.R1.1, NASA Giovanni) for March/April 2003 (B) and April 2009 (D) in the vicinity of the Prince Edward Islands. The position of the sub-Antarctic Front was identified by the 8.0 to 8.5°C isotherms, as described by Uddstrom and Oien (1999).

5.4. DISCUSSION

Despite a high degree of inter-annual variation, Pakhomov *et al.* (2004) found an overall depletion in $\delta^{13}C$ signatures of *Nauticaris marionis* from 1984 to 2000. This pattern of depletion in the $\delta^{13}C$ signatures of *N. marionis* over time has subsequently continued as the shrimp collected in 2009 were substantially more ^{13}C-depleted relative to previous years (Figs. 5.1A and B). As *N. marionis* collected from stations close to the kelp beds tend to have substantially more enriched $\delta^{13}C$ values relative to those from the open shelf region (Fig. 5.1A *versus* Fig. 5.1B; Chapter 4), the more pronounced inter-annual variation observed by Pakhomov *et al.* (2004), compared to the current comparison (Fig. 5.1), likely results from the lack of separation of shrimp into regions i.e. nearshore and inter-island. As this pattern of ^{13}C-enrichment in *N. marionis* collected near the kelp beds of Marion Island was observed in both 2000 and 2009 (Chapter 4), this enrichment may be a permanent regional feature, most likely due to the local influence of kelp in the nearshore food webs.

The suspension- and deposit-feeders, and the higher benthic trophic levels (scavengers/ predators), have also demonstrated a substantial depletion in $\delta^{13}C$ values from 1999 to 2009 (Table 5.1; Fig. 5.2). There were, however, two groups of suspension-feeding organisms (sponges and hydrozoans) that showed no changes in their $\delta^{13}C$ signatures over time, which may be linked to their feeding modes. Since sponges can consume only a limited size range of particles, generally within the pico- and nano-size range (<20 μm; Reiswig, 1971, 1990; van de Vyver *et al.*, 1990; Pile *et al.*, 1996), they are unlikely to utilise the diatom blooms (>20 μm) that periodically occur between the islands. The position of the SAF relative to the PEI is a critical component that determines if and when phytoplankton blooms occur between the islands (Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 2000; Ansorge and Lutjeharms, 2002). The southward shift of the SAF, in response to global climate change (Pakhomov and Chown, 2003), is thought to promote a decrease in the frequency of occurrence of the "island mass effect" at the PEI due to unique flow-through hydrodynamics around the island (Pakhomov *et al.*, 2004; McQuaid and Froneman, 2008). The decreased frequency of occurrence of the "island mass effect" in response to global climate change is thus unlikely to impact on the feeding ecology of the sponges. As a result, the absence of any change in the $\delta^{13}C$ signatures of the sponges between 1999 and 2009 is not unexpected.

The $\delta^{13}C$ signatures of the hydrozoans demonstrated a trend of depletion between the two studies, although the extent of the change was minimal (~0.48 ‰; Table 5.1; Fig. 5.2). The

majority of hydrozoans are predominantly carnivorous and feed primarily on zooplankton (Gili and Hughes, 1995; Gili *et al.*, 1998; Cairns *et al.*, 2009). Hydrozoans are, however, able to feed on a variety of additional food sources including bacteria, protozoa, phytoplankton and detritus, and may even feed opportunistically, i.e. capture the most abundant food source available (Gili *et al.*, 1998). The hydrozoans collected in 2009 contained elevated proportions of the fatty acids 16:0 and 18:1ω9 (*Plumularia insignis*; see Table A9; Chapter 3), which are abundant in animal prey (Stevens *et al.*, 2004). Additionally, the hydrozoans had a carnivory index >3.0, suggesting a carnivorous diet (18:1ω9/18:1ω7; Arts *et al.*, 2001; Dalsgaard *et al.*, 2003). As a result, it is likely that the hydrozoans obtained a large proportion of their diet from animal prey such as zooplankton. The hydrozoans, like the sponges, may not utilise large amounts of diatom bloom production generated between the islands. The two species of zooplankton collected in the vicinity of the PEI had similar $\delta^{13}C$ signatures between 1999 and 2009, suggesting no large-scale changes in the productivity of the PFZ surrounding the PEI. As the zooplankton had similar $\delta^{13}C$ signatures between 1999 and 2009, the absence of any trend in the carbon signature of the hydrozoans is thus not unexpected.

The suspension-feeding brachiopod *Magellania kerguelenensis* and the deposit-feeding polychaete *Thelepus extensus* do not have restrictive feeding modes or specific food sources, and hence the depletion in their $\delta^{13}C$ signatures between 1999 and 2009 (Fig. 5.2) may reflect changes in the available food sources in the region of the islands. Organisms occupying higher trophic levels in the benthic community also showed a depletion in their $\delta^{13}C$ signatures over time (Fig. 5.2). Shifts in $\delta^{13}C$ signatures of scavengers/predators may result from their consumption of different food sources, or from changes in their feeding position in the food web. All the scavengers/predators around PEI demonstrated a substantial depletion in their $\delta^{13}C$ signatures over time (by 1.59 to 4.70 ‰), suggesting that their food sources have become ^{13}C-depleted. The depletion of $\delta^{13}C$ signatures in *M. kerguelenensis* (suspension-feeding brachiopod) and *T. extensus* (deposit-feeding polychaete) between 1999 and 2009 was similar to the depletion seen in *N. marionis* over the corresponding period (depletion: 1.96, 3.11 and 2.28 ‰, brachiopods, polychaetes and shrimps, respectively). Since *N. marionis* showed a continuing depletion in $\delta^{13}C$ signatures over 25 years (1984 to 2009), it is likely that the shifts in the benthic organisms over 10 years also reflect long-term changes in the ecosystem. As the fatty acid profiles of *N. marionis* showed that, at least indirectly, phytoplankton forms a vital component in the diet of these shrimp (Chapter 4), the continuing depletion in $\delta^{13}C$ signatures of both the benthic and hyperbenthic communities

over time indicates that the $\delta^{13}C$ signatures of the phytoplankton base of the food web are gradually shifting.

Variations in $\delta^{13}C$ signatures of phytoplankton have been linked with changes in isotopic fractionation due to alterations in water temperature, molecular CO_2 concentration and growth conditions (Bidigare *et al.*, 1997; Laws *et al.*, 1997; Rau *et al.*, 1997; Burkhardt *et al.*, 1999a, b). As marine $\delta^{13}C$ tends to decrease with increasing molecular CO_2 concentration (Rau *et al.*, 1997) increased atmospheric CO_2 due to burning of fossil fuels could account for some of the observed depletion $\delta^{13}C$ signatures. In subpolar regions, a decrease of ~-0.15 ‰ per decade has been calculated in $\delta^{13}C$ of marine dissolved inorganic carbon (Kroopnick, 1985). Over the period 1984 to 2009, this would result in a decrease of 0.38 ‰ in $\delta^{13}C$ signatures which cannot explain the depletion of -2.32 and -2.55 ‰ observed in the shrimp (nearshore and inter-island individuals, respectively). The lack of a consistent pattern in the $\delta^{13}C$ signatures of the pelagic and benthic organisms also suggests that the isotopic shifts at PEI could not result from changes in temperature or molecular CO_2 concentrations. As a result, changes in phytoplankton productivity in the vicinity of the PEI are more likely to be responsible for the observed changes. Phytoplankton growth rate has a strong negative relationship with carbon isotope fractionation, thus when phytoplankton grow more rapidly, their $\delta^{13}C$ values increase (Bidigare *et al.*, 1997; Laws *et al.*, 1997; Burkhardt *et al.*, 1999a, b). This pattern has been observed in the vicinity of the PEI, as diatom blooms had an enriched $\delta^{13}C$ value compared to a phytoplankton community dominated by small, slow growing cells indicative of the Polar Frontal Zone (PFZ; bloom: ~-23.3 ‰ *versus* small cells: ~-24.8 ‰; Kaehler *et al.*, 2000, 2006). The depletion of $\delta^{13}C$ signatures in *N. marionis* and various benthic invertebrates at the PEI over time therefore likely reflects a long-term decline in phytoplankton productivity in the vicinity of the islands. Over the period 1997 to present, total chlorophyll-*a* (chl-*a*) concentrations (monthly averages) of the PFZ upstream of the islands have remained relatively low ($\leq$0.3 $\mu g\ L^{-1}$), and showed no long-term changes (SeaWiFS.R2009, NASA Giovanni). Thus, the apparent decrease in phytoplankton productivity in the vicinity of the islands likely results from a decline in the frequency of occurrence of phytoplankton blooms in the vicinity of the PEI over time (Pakhomov *et al.*, 2004).

The increased frequency of occurrence of flow-through conditions between the islands may also effect the composition of the SPM. During the investigation in 2003, the $\delta^{13}C$ values for

the SPM between and within the lee of the islands were more enriched than those recorded in the upstream region (Fig. 5.3A). Conversely, during 2009 no spatial patterns in the $\delta^{13}C$ values of the SPM were evident (Fig. 5.3C; Chapter 3). Since SPM is composed of a mixture of phytoplankton, detritus and bacteria, the $\delta^{13}C$ values obtained during 2009 suggest that the SPM was largely comprised of phytoplankton (2009: -24.33 ± 0.42 ‰, mixed phytoplankton: from -24.84 to -23.51 ‰; Kaehler *et al.*, 2000, 2006). The SPM during 2003 appeared to comprise a mixture of phytoplankton with a more ^{13}C-enriched source such as kelp detrital POM (-17.50 ‰). Also during the 2003 investigation, large quantities of detrital fragments of the kelp *Macrocystis laevis* were present in the SPM, while large quantities of degrading kelp fronds were collected in the benthic trawls over the open shelf region (Kaehler *et al.*, 2006). During the 2009 investigation, however, degrading kelp fronds were only collected in the benthic trawls at stations adjacent to kelp beds (Station 8 and 5; see Table 2.1; Chapter 2). Sea-surface temperature data indicated that during March/April 2003, the SAF was located far to the north of the PEI, while during April 2009 the SAF was immediately north of the islands and was less intense than in 2003 (Figs. 5.3B and D; MODIS-Terra.R1.1, NASA Giovanni). The hydrodynamics around the PEI during 2003 likely promoted the retention of water between the islands, leading to increased rates of primary production. During 2009, however, a flow-through system probably predominated, resulting in low total chl-*a* concentrations and depleted $\delta^{13}C$ signatures of SPM in the vicinity of the islands, similar to those of the offshore region upstream of the islands (Chapter 3). The position of the SAF may therefore influence the retention of kelp detritus between the islands, thereby further affecting food webs around the islands.

The majority of studies aimed at assessing the impacts of climate change on benthic communities in polar regions have been focused on potential long-term effects due to increasing temperatures (Schiel *et al.*, 2004; Thatje, 2005; Clarke *et al.*, 2007; Smale and Barnes, 2008; Tatián *et al.*, 2008). To date, very few studies have focused on long-term changes related to shifts in food availability in both the sub-Antarctic/Antarctic region and the Arctic region (Clarke and Harris, 2003; Dunton *et al.*, 2005; Smith *et al.*, 2006; Clarke *et al.*, 2007). In the Arctic (Schell, 2000; Hirons *et al.*, 2001; Moore *et al.*, 2003; Hobson *et al.*, 2004) and Antarctic regions (Weimerskirch *et al.*, 2003; Hilton *et al.*, 2006; Lescroël and Bost, 2006) food web studies have instead focused on long-term changes in the population dynamics of top predators and how these link with changes in food availability and structure.

In the Alaskan waters, the populations of Steller sea lions, northern fur seals and harbor seals have undergone various degrees of decline over the last three decades (Pitcher, 1990; Hirons *et al.*, 2001). Over the period of 1951 to 1997 (Bering Sea and Gulf of Alaska), a significant depletion in $\delta^{13}C$ values (almost -2.0 ‰) was evident in Steller sea lions, while declining trends were evident in harbor seals and northern fur seals (Hirons *et al.*, 2001). As all three species exhibited no significant changes in $\delta^{15}N$ values during this period, this depletion in $\delta^{13}C$ values was more likely due to changes at the base of the food web rather than from shifts in their trophic level feeding (Hirons *et al.*, 2001). The diets of predators in the northern Bering and Chukchi Seas are dominated by benthic organisms such as bivalves and amphipods, thus benthic production is important to higher trophic levels including marine mammals and seabirds (Grebmeier and Dunton, 2000; Lovvorn *et al.*, 2003; Moore *et al.*, 2003; Simpkins *et al.*, 2003). It is therefore important to note that in this region, the predominant prey species for many top predators such as various pinnipeds (clupeid fish), grey whales (Ampeliscid amphipods) and spectacled eiders (clams), have also decreased in abundance (Merrick, 1997; Grebmeier and Dunton, 2000; Moore *et al.*, 2003). Bowhead whales from the Bering Sea, which feed exclusively on zooplankton (primarily euphausiids and large calanoid copepods), exhibited similar depletions in $\delta^{13}C$ values as Steller sea lions during a similar period (1947 to 1998; Schell, 2000). The depletion in $\delta^{13}C$ values of ~-2.7 ‰ (between 1966 and 1997) recorded from the baleen plates implied, using relationships described by Laws *et al.* (1995) and Bidigare *et al.* (1997), and assuming similar phytoplankton composition among years as well as relatively constant $\delta^{13}C$ values of dissolved free CO_2, that the ecosystem has experienced a decrease of between 30 to 40% in average seasonal primary productivity (Schell, 2000). In the mid 1970's, a rapid change in climate occurred in the Pacific Ocean (Hare and Mantua, 2000), resulting in changes in wind patterns/intensity, mixed layer depth, sea surface temperatures, sea-ice extent and depth of ocean current patterns (Trenberth and Hurrell, 1994; Freeland *et al.*, 1997). Thus, declines in the numbers of top predators in the Bering Sea and key benthic species, coupled with similar depletions in $\delta^{13}C$ values in Steller sea lions and Bowhead whales, highlights the impact that changes in primary production (resulting from changing oceanic conditions in response to climate change) can have on entire ecosystems.

Across the sub-Antarctic region, there have been gradual increases in sea surface and sub-surface temperatures (Levitus *et al.*, 2000; Gille, 2002), while at a similar time (time lag of 2 to 9 years) there have been substantial declines in the populations of most seabirds and seals

at several monitored breeding sites (with the notable exception of two species, King penguins and Amsterdam fur seals, that have increased; Weimerskirch *et al.*, 2003; Hilton *et al.*, 2006; Lescroël and Bost, 2006). In the southern Indian Ocean, there is evidence of a decline since the 1970's in total chl-*a* and zooplankton concentrations, suggesting a drop in primary productivity in the region accompanied by increased wind stress (Hunt *et al.*, 2001; Gregg *et al.*, 2003). The concurrent decreases in seabird and seal populations, coupled with apparent changes in primary productivity, were suggested to result from system shifts driven by climate change (Weimerskirch *et al.*, 2003). The population size of the Rockhopper penguin, a prominent top predator, has demonstrated distinct declines throughout the majority of its circumpolar breeding distribution coupled with an overall depletion in $\delta^{13}C$ signatures (at seven breeding sites) over time (Hilton *et al.*, 2006). The depletion in $\delta^{13}C$ values of these penguins and the decline of their population size may have resulted from decreases in primary productivity, and thus carrying capacity, of the ecosystem (Hilton *et al.*, 2006). There was also evidence of depletion in $\delta^{15}N$ values in penguins at some sites during warmer years, suggesting a dietary shift to prey at a lower trophic level during these periods (Hilton *et al.*, 2006).

5.5. CONCLUSION

The continuing depletion in $\delta^{13}C$ signatures of *Nauticaris marionis* from 1984 to 2009 suggests that temporal changes are occurring in the PEI marine ecosystem. The benthic community also had a depletion in $\delta^{13}C$ signatures from 1999 to 2009, except in organisms (sponges and hydrozoans) that are unable to utilise the diatom production generated between the islands. The suspension-feeding brachiopod and deposit-feeding polychaete showed relatively similar depletions of $\delta^{13}C$ signatures over the same time period, suggesting that shifts are occurring in the carbon signatures at the base of the food web. The observed depletions in $\delta^{13}C$ signatures in organisms around the PEI are likely due to decreases in the frequency and intensity of the "island mass effect" around PEI, related to a southward shift in the position of the SAF in response to global climate change. Flow-through conditions result in the export of large proportions of kelp production out of the PEI shallow shelf ecosystem eastward to the open waters of the PFZ.

6 GENERAL DISCUSSION

This study aimed to use a combination of both stable isotope and fatty acid analyses to provide a time-integrated view of the assimilated feeding history of selected components of the benthic community in the vicinity of the sub-Antarctic Prince Edward Islands (PEI). Although situated in a region of low productivity (Laubscher *et al.*, 1993; Froneman *et al.*, 2001), the PEI support a diverse and biomass-rich inter-island benthic community (Branch *et al.*, 1993a). The islands are also seasonally home to many land-based predators during their breeding seasons (Williams *et al.*, 1979; Condy, 1981; Ryan and Bester, 2008), with many species relying on allochthonous and/or autochthonous production in the shallow shelf waters around the islands, i.e. the inshore component of the life support system (Espitalier-Noël *et al.*, 1988; Adams and Klages, 1989; McQuaid and Froneman, 2004; Ryan and Bester, 2008).

6.1. TROPHODYNAMICS OF THE BENTHIC AND HYPERBENTHIC COMMUNITIES

The inshore component of PEI ecosystem was initially thought to be sustained by organic carbon derived from phytoplankton blooms associated with the "island mass effect" at the PEI (Perissinotto *et al.*, 1990; Perissinotto, 1992; Pakhomov and Froneman, 1999a). More recently, the importance of kelp-derived carbon in the diets of those benthic organisms in close proximity to kelp has been highlighted (Kaehler *et al.*, 2000, 2006). The stable isotope and fatty acid signatures of the benthic suspension- and deposit-feeding organisms generated during this study suggested that these two feeding guilds incorporated both phytoplankton and kelp into their diets (Chapter 3). Results from the simple mixing model for a two-source system ($\delta^{13}C$), coupled with elevated levels of the diatom (20:5ω3) and dinoflagellate (22:6ω3) fatty acids, all suggested that pelagic primary production contributed substantially to the diets of these organisms in all regions around the islands. Indeed, even those organisms living near the kelp beds with increased proportions of kelp in their diets, such as the polychaete *Thelepus extensus* and gastropod *Margarella expansa*, were also highly reliant on phytoplankton as a food source. Notable exceptions were the sponges and bryozoans, in which kelp and phytoplankton fatty acids were present in similar proportions, most likely

resulting from their particle size-restricted feeding mode. The suspension- and deposit-feeders collected from nearshore stations were generally more ^{13}C-enriched than those from the open shelf region, possibly due to an increased incorporation of enriched kelp detritus in their diets. This finding was in agreement with previous isotope studies at the PEI (Kaehler *et al.*, 2000, 2006). The target fatty acids (predominant food sources) in the benthic organisms, however, indicated no distinct spatial patterns between the inter-island (upstream, between and downstream) and nearshore regions, with the exception of the two species collected at Station 8. There was, however, strong evidence for increased food quality between and within the lee of the islands compared to upstream, as all *Lanice marionensis* (polychaete), *M. expansa* (gastropod) and *Thouarella variabilis* (gorgonian coral) collected upstream (Station 1 or 2) had substantially lower quantities of TFAs than those from nearshore, open shelf or downstream stations.

The hyperbenthic shrimp *Nauticaris marionis* is a key species of the inter-island ecosystem, representing an important food web link between the benthic community and land-based predators (Perissinotto and McQuaid, 1990). Even though these shrimp demonstrate a high degree of plasticity in their diet (Perissinotto and McQuaid, 1990; Pakhomov *et al.*, 1999; Vumazonke *et al.*, 2003), most likely in response to the variable supply of food within the region, their fatty acid profiles revealed no distinct ontogenetic or spatial patterns (Chapter 4). This result is in contrast to their stable isotope signatures, which demonstrated strong spatial and ontogenetic variation. The stable isotope ratios indicated that the nearshore shrimp, particularly those from Station 8 (near Marion Island kelp beds), were more ^{13}C-enriched than those from the inter-island region. This ^{13}C-enrichment was most likely due to increased kelp detritus entering the food web within these regions, in agreement with the findings from Chapter 3 and Kaehler *et al.* (2000, 2006). In addition, the subadult/adult shrimps showed enrichment in $\delta^{13}C$ and $\delta^{15}N$ signatures with an increase in size, resulting in a relatively distinct separation of size classes that reflected niche separation in their diet. Individuals in the smaller size class appeared to have a more restricted diet than larger individuals, and the largest individuals fed at a higher trophic level. Interestingly, all of the shrimps contained large proportions of PUFAs and EFAs, indicating that food quality was similar among the different size classes and regions despite the apparent niche separation and variation in carbon sources utilised. In addition, all the shrimp contained the diatom and dinoflagellate fatty acids (20:5ω3 and 22:6ω3, respectively) and 16:0 in large proportions, highlighting the importance of phytoplankton (indirectly) in their diet. This result provides

further evidence that phytoplankton is an important food source that may be transferred from the base of the food web to higher trophic levels through this key species. On the shelf off northeast Greenland, the fatty acid profile of the deep water prawn *Pandalus borealis*, which is an important prey item to several species of fish and marine mammals (Pedersen and Riget, 1993; Berenboim *et al.*, 2000; Nilssen *et al.*, 2000), also contained high proportions of 20:5ω3 and 22:6ω3 (Graeve *et al.*, 1997), further indicating the importance of these fatty acids in marine food webs. The different findings of each method highlights the merits of using these two techniques as a complementary approach in resolving trophodynamics in complex aquatic systems.

6.2. LONG-TERM EFFECTS OF GLOBAL CLIMATE CHANGE

There is growing evidence from a variety of sources that global climate change is having an impact on the terrestrial ecosystem of the PEI (Chown and Smith, 1993; Bergstrom and Chown, 1999; Chown *et al.*, 2002; le Roux and McGeoch, 2008). Evidence for the response of the marine ecosystem to this long-term trend is, however, generally lacking. The temporal investigation of changes in the isotope signatures of *Nauticaris marionis* at the PEI demonstrated an overall depletion in their $\delta^{13}C$ signatures over the period of 1984 to 2009 (Chapter 5). The depletion in the $\delta^{13}C$ signatures of the shrimp and in other selected components of the benthos over time suggests that long-term changes in the marine ecosystem of PEI are occurring.

In the Southern Ocean, global climate change, through increases in air and sea (surface and sub-surface) temperatures, is affecting oceanic circulation (Levitus *et al.*, 2000; Gille, 2002; le Roux, 2008), and causing shifts in the position and intensity of major frontal systems (Moore *et al.*, 1999; McQuaid and Froneman, 2008). Marion Island has experienced a decrease in annual precipitation since the mid 1960's (Smith, 2002; le Roux and McGeoch, 2008). As freshwater runoff is an important factor promoting phytoplankton growth between the islands through the input of nutrients and the promotion of water column stability, the decrease in precipitation is likely to affect the productivity of the marine ecosystem surrounding the islands. This freshwater input, however, needs to be retained between the islands for a minimum 15 days to enable the development of phytoplankton blooms (Perissinotto and Duncombe Rae, 1990). The position of the sub-Antarctic Front (SAF) relative to the islands plays a crucial role in the hydrodynamics around the islands (Perissinotto and Duncombe Rae, 1990; Ansorge and Lutjeharms, 2002). The southward shift

in the average position of this front (Pakhomov and Chown, 2003), most likely in response to global climate change (Moore *et al.*, 1999; le Roux, 2008), promotes the predominance of a flow-through system between the islands and a concomitant decreased frequency of occurrence of the "island mass effect" conditions (Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 2000; McQuaid and Froneman, 2008). A flow-through system between the islands also reduces the retention of kelp detritus within the inter-island and nearshore regions (Chapter 5). As a result, the benthic communities around the islands on the whole may become more reliant on the influx of primary production advected to the islands by the easterly flowing ACC. The depletion of $\delta^{13}C$ signatures in the benthos in the vicinity of the PEI most likely reflects decreases in productivity between the islands due to increased contributions of smaller phytoplankton cells in the diets of these organisms over time.

To date, there have been no additional quantitative studies on the biomass and abundance of the benthic community in the shallow inter-island shelf region of the PEI since the initial photographic assessments conducted between 1984 and 1989 (Branch *et al.*, 1993a). As a consequence, it is not possible to assess whether the perceived changes in the hydrodynamics in the region of the islands is associated with changes in benthic community population dynamics. As phytoplankton is an important base for the entire food web (Chapters 3 and 4), a decrease in the frequency of occurrence of diatom blooms between the islands is likely to have far-reaching consequences that reach the highest trophic levels. Essential fatty acids (EFAs) are important in organ functioning and are obtained from the diets of consumers (Arts *et al.*, 2001). As a consequence, EFAs act as fundamental drivers of ecosystem fitness and stability (Arts *et al.*, 2001). As diatoms and dinoflagellates are both important sources of EFAs (20:5ω3 and 22:6ω3, respectively), a decrease in the frequency of occurrence of "island mass effect" conditions in the vicinity of the islands may lead to a reduction in the overall nutritional fitness of the benthos in the PEI ecosystem. The PEI seasonally support up to five million land-based predators, including seals, flying seabirds and penguins, that come to the islands to breed and moult (Williams *et al.*, 1979; Condy, 1981; Ryan and Bester, 2008). As these activities are energetically expensive (Gales *et al.*, 1988; Wendeln and Becker, 1999) a reduction in ecosystem fitness could have a substantial impact on these top predators, particularly the inshore feeders. Continuous decreases in the population sizes of inshore pursuit-diving feeders such as Gentoo penguins, Rockhopper penguins and Crozet shags have been observed at the PEI over the last decade (Pakhomov and Chown, 2003; Ryan and Bester, 2008). On the other hand, the population sizes of those species with a

mixed inshore and offshore diet such as Macaroni penguins have remained relatively stable over the same period (Ryan and Bester, 2008). Adult *N. marionis* represent an important food source for Gentoo penguins and Crozet shags (Espitalier-Noël *et al.*, 1988; Adams and Klages, 1989), and periodically for Macaroni and Rockhopper penguins (Brown and Klages, 1987). As a result, these shrimp represent a crucial link between primary production and top predators. As lipid-rich organisms form high quality prey, any decreases in food quality (quantities of EFAs and TFAs) at the PEI mediated by global climate change could be reflected in the nutritional condition of the benthic community, which may ultimately result in changes in the overall fitness of the PEI ecosystem. Changes in the productivity of the PEI ecosystem may also result in decreased abundances of benthic species, which may have further impacts on higher trophic levels if there are changes in population dynamics of key species such as *N. marionis*.

It is generally accepted that ecosystems in the polar regions are particularly sensitive to global climate change (Clarke and Harris, 2003). Studies conducted in the open waters of the Southern Ocean and high Antarctic region have focused mainly on determining the potential long-term effects of increasing temperatures on benthic communities such as replacement of cold-water species by warm-water tolerant species (Schiel *et al.*, 2004; Clarke *et al.*, 2007), and range expansions by invasive species (Tavares and Melo, 2004; Thatje, 2005; Lee and Chown, 2007), and community changes resulting from increased sedimentation with glacial retreat (Smale and Barnes, 2008; Tatián *et al.*, 2008). Particle-flux studies conducted in a variety of shelf habitats indicated that between 6 and 60% of the annual primary production is exported to depth, where it provides an important food source for benthic communities (Valiela, 1984). As Antarctic and sub-Antarctic shelf waters generally support diverse and abundant benthic communities (Grebmeier and Barry, 1991; Arntz *et al.*, 1994; McQuaid and Froneman, 2004; Tatián *et al.*, 2008), these findings suggest that the transfer of water-column production to the benthos is important in the functioning of these ecosystems. Declines in populations of top predators and their predominant benthic prey species have already occurred in Arctic regions (Bering and Chukchi Seas; Merrick, 1997; Grebmeier and Dunton, 2000; Hirons *et al.*, 2001; Moore *et al.*, 2003). Over the period of 1947 to 1998, similar depletions in $\delta^{13}C$ values were recorded in benthic feeding Stellar sea lions (almost -2.0 ‰; Hirons *et al.*, 2001) and zooplankton-feeding (primarily euphausiids and large calanoid copepods) Bowhead whales (~-2.7 ‰; Schell, 2000), suggesting a change in carbon signatures at the phytoplankton base of these two food webs. These changes in pelagic

primary production may have resulted from changing oceanic conditions in response to climate change (Gregg *et al.*, 2003). Across the sub-Antarctic region, similar patterns have also been observed, with substantial declines in populations of many top predators, particularly seabirds and seals (Weimerskirch *et al.*, 2003; Hilton *et al.*, 2006; Lescroël and Bost, 2006). These population declines have been linked to reductions in ocean productivity mediated by climate change (Hunt *et al.*, 2001; Gregg *et al.*, 2003; Weimerskirch *et al.*, 2003). The Rockhopper penguin, which has demonstrated distinct population declines throughout the majority of its circumpolar breeding distribution, showed an overall depletion in $\delta^{13}C$ signatures over time, further suggesting decreases in primary productivity within their feeding regions (Hilton *et al.*, 2006). These findings highlight the potential impact that changes in primary production, predominantly in response to climate change, may have on Southern Ocean marine ecosystems.

6.3. FUTURE STUDIES

The results of this study have demonstrated the importance of determining the dominant carbon sources and pathways through the PEI ecosystem. This study also highlighted the complex interactions of hydrodynamics with the base of the food web, and indicates the importance of monitoring long-term changes in the components of this ecosystem. We urgently need to undertake a quantitative baseline study on the benthos in the shallow shelf waters of the PEI so that future changes in response to global climate change can be detected. Investigations of possible long-term changes in food sources to benthic communities of other sub-Antarctic islands such as Bouvet Island or the Crozet Islands will provide important information about the impacts of global climate change on food webs of other sub-Antarctic island systems.

Data on long-term patterns in the terrestrial ecosystem and the populations of top predators at the PEI and other sub-Antarctic islands are currently available (Inchausti *et al.*, 2003; Weimerskirch *et al.*, 2003; Hilton *et al.*, 2006; Lescroël and Bost, 2006; Trathan *et al.*, 2007; Ryan and Bester, 2008). However, information on the terrestrial/marine environment link is lacking, and comprehensive data regarding the top predators are also scarce. For example, limited information about shifts in diet (particularly through stable isotope ratios and fatty acid profiles) are available for inshore feeders such as Gentoo and Rockhopper penguins at the PEI. As these seabirds feed predominantly within the inshore region of the PEI, they will be greatly affected by any changes in the productivity of the PEI marine ecosystem.

REFERENCES

Adams NJ and Klages NT (1989) Temporal variation in the diet of the Gentoo Penguin *Pygoscelis papua* at sub-Antarctic Marion Island. *Colonial Waterbirds*, 12, 30-36.

Adams TS and Sterner RW (2000) The effect of dietary nitrogen content on trophic level ^{15}N enrichment. *Limnology and Oceanography*, 45, 601-607.

Allan EL, Ambrose ST, Richoux NB and Froneman PW (2010) Determining spatial changes in the diet of nearshore suspension-feeders along the South African coastline: Stable isotope and fatty acid signatures. *Estuarine*, *Coastal and Shelf Science*, 87, 463-471.

Allanson BR, Boden BP, Parker L and Duncombe Rae C (1985) A contribution to the oceanology of the Prince Edward Islands. In: Siegfried WR, Condy PR and Laws RM (eds.) *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin, pp. 38-45.

Ansorge IJ and Lutjeharms JRE (2002) The hydrography and dynamics of the ocean environment of the Prince Edward Islands (Southern Ocean). *Journal of Marine Systems*, 37, 107-127.

Ansorge IJ and Lutjeharms JRE (2003) Eddies originating from the South-West Indian Ridge. *Journal of Marine Systems*, 39, 1-18.

Ansorge IJ, Froneman PW, Pakhomov EA, Lutjeharms JRE, Van Ballegooyen R and Perissinotto R (1999) Physical-biological coupling in the waters surrounding the Prince Edward Islands (Southern Ocean). *Polar Biology*, 21, 135-145.

Ansorge IJ, Froneman PW, Lutjeharms JRE, Bernard KS, Lange L, Lukáč D, Backburg B, Blake J, Bland S, Burls N, Davies-Coleman MT, Gerber R, Gildenhuys S, Hayes-Foley P, Ludford A, Manzoni T, Robertson E, Southey D, Swart S, van Rensburg D and Wynne S (2004) An interdisciplinary cruise dedicated to understanding ocean eddies upstream of the Prince Edward Islands. *South African Journal of Science*, 100, 319-322.

Arntz WE, Brey T and Gallardo VA (1994) Antarctic zoobenthos. *Oceanography and Marine Biology: An Annual Review*, 32, 241-304.

Arrigo KR (1994) Impact of ozone depletion on phytoplankton growth in the Southern Ocean: large-scale spatial and temporal variability. *Marine Ecology Progress Series*, 114, 1-12.

Arts MT, Ackman RG and Holub BJ (2001) "Essential fatty acids" in aquatic ecosystems: a crucial link between diet and human health and evolution. *Canadian Journal of Fisheries and Aquatic Sciences*, 137, 122-137.

Attwood CG, Lucas MI, Probyn TA, McQuaid CD and Fielding PJ (1991) Production and standing stocks of the kelp *Macrocystis laevis* Hay at the Prince Edward Islands, Subantarctic. *Polar Biology*, 11, 129-133.

Balarin MG (2000) Size fractionated phytoplankton biomass and primary production in the Southern Ocean. MSc Thesis, Rhodes University, Grahamstown.

Båmstedt U, Gifford DJ, Irigoien X, Atkinson A and Roman M (2000) Feeding. In: Harris R, Wiebe P, Lenz J, Skjodal HR and Huntley M (eds.) *ICES Zooplankton Methodological Manual*. Academic Press, London, pp. 297-399.

Bautista B and Harris RP (1992) Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Marine Ecology Progress Series*, 82, 41-50.

Beckley LE and Branch GM (1992) A quantitative scuba-diving survey of the sublittoral macrobenthos at subantarctic Marion Island. *Polar Biology*, 11, 553-563.

Bell MV and Sargent JR (1985) Fatty acid analysis of phosphoglycerides from tissues of the clam *Chlamys islandica* (Muller) and the Starfish *Ctenodiscus crispatus* (Retzius) from Balsfjorden, Northern Norway. *Journal of Experimental Marine Biology and Ecology*, 58, 825-841.

Berenboim BI, Dolgov AV, Korzhev VA and Yaragina NA (2000) The impact of Cod on the dynamics of Barents Sea Shrimp (*Pandalus borealis*) as determined by multispecies models. *Journal of the Northwest Atlantic Fisheries Science*, 27, 69-75.

Bergstrom D and Chown SL (1999) Life at the front: history, ecology and change on southern ocean islands. *Trends in Ecology and Evolution*, 14, 472-477.

Bernard KS and Froneman PW (2002) Mesozooplankton community structure in the Southern Ocean upstream of the Prince Edward Islands. *Polar Biology*, 25, 597-604.

Bernard KS and Froneman PW (2003) Mesozooplankton community structure and grazing impact in the Polar Frontal Zone during austral autumn 2002. *Polar Biology*, 26, 268-275.

Bidigare RR, Fluegge A, Freeman KH, Hanson KL, Hayes JM, Hollander D, Jasper JP, King LL, Laws EA, Milder J, Millero FJ, Pancost R, Popp BN, Steiberg PA and Wakeham SG (1997) Consistent fractionation of ^{13}C in nature and in the laboratory: Growth-rate effects in some haptophyte algae. *Global Biochemistry Cycles*, 11, 279-292.

Blankley WO (1982) Feeding ecology of three inshore fish species at Marion Island (Southern Ocean). *South African Journal of Zoology*, 17, 164-170.

Bligh E and Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, 37, 911-917.

Boden BP (1988) Observations of the Island Mass Effect in the Prince Edward Archipelago. *Polar Biology*, 9, 61-68.

Boden BP and Parker LD (1986) The plankton of the Prince Edward Islands. *Polar Biology*, 5, 81-93.

Boyd CM, Heyraud M and Boyd CN (1984) Feeding of the Antarctic krill *Euphausia superba*. *Journal of Crustacean Biology*, 4, 123-141.

Bradford-Grieve JM, Markhaseva EL, Rocha CEF and Abiahy B (1999) Copepoda. In: Boltovskoy D (ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 869-1098.

Branch GM, Attwood CG, Gianakouras D and Branch ML (1993a) Patterns in the benthic communities on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biology*, 13, 23-34.

Branch ML (1994) The Polychaeta of sub-Antarctic Marion and Prince Edward Islands: illustrated keys to the species and results of the 1982-1989 University of Cape Town surveys. *South African Journal of Antarctic Research*, 24, 3-52.

Branch ML and Williams GC (1993) The Hydrozoa, Octocorallia and Scleractinia of sub-Antarctic Marion and Prince Edward Islands: illustrated keys to the species and results of the 1982-1989 University of Cape Town surveys. *South African Journal of Antarctic Research*, 23, 3-24.

Branch ML, Arnaud PM, Cantera J and Gianakouras D (1991) The benthic Mollusca and Brachiopoda of the sub-Antarctic Marion and Prince Edward Islands: 1) Illustrated keys to species 2) Records of the 1982-1989 University of Cape Town Surveys. *South African Journal of Antarctic Research*, 21, 45-64.

Branch ML, Jangoux M, Alvá V, Massin CI and Stampanato S (1993b) The Echinodermata of sub-Antarctic Marion & Prince Edward Islands. *South African Journal of Antarctic Research*, 23, 37–70.

Brown CR and Klages NTW (1987) Seasonal and annual variation in diets of Macaroni (*Eudyptes chrysolophus chrysolophus*) and Southern rockhopper (*E. chrysocome chrysocome*) penguins at sub-Antarctic Marion Island. *Journal of Zoology*, *London*, 212, 7-28.

Brown CR, Klages NTW and Adams NJ (1990) Short and medium term variations in the diets of penguins at Marion Island. *South African Journal of Antarctic Research*, 20, 13-20.

Bruland KW, Rue EL and Smith GJ (2001) Iron and macronutrients in California coastal upwelling regimes: Implications for diatom blooms. *Limnology and Oceanography*, 46, 1661-1674.

Bryden HL (1983) The Southern Ocean. In: Robinson AR (ed.) *Eddies in marine science*. Springer, Berlin, pp. 265-277.

Buda C, Dey I, Balogh N, Horvath LI, Maderspach K, Juhasz M, Yeo YK and Farkas T (1994) Structural order of membranes and composition of phospholipids in fish brain cells during thermal acclimatization. *Proceedings of the National Academy of Sciences of the USA*, 91, 8234-8238.

Budge SM and Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. *Organic Geochemistry*, 29, 1547-1559.

Budge SM and Parrish CC (1999) Lipid class and fatty acid composition of *Pseudonitzs chiamultiseries* and *Pseudonitzs chiapungens* and effects of lipolytic enzyme deactivation. *Phytochemistry*, 52, 561-566.

Budge SM, Iverson SJ and Koopman HN (2006) Studying trophic ecology in marine ecosystems using fatty acids: a primer on analysis and interpretation. *Marine Mammal Science*, 22, 759-801.

Budge SM, Springer AM, Iverson SJ and Sheffield G (2007) Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. *Marine Ecology Progress Series*, 336, 305-309.

Buhr KJ and Winter JE (1977) Distribution and maintenance of a *Lanice conchilega* association in the Weser Estuary (GFR), with special reference to the suspension-feeding behaviour of *Lanice conchilega*. In: Keegan BF, Ceidigh PO and Boaden PJS (eds.) *Biology of Benthic Organisms*. *11*. *European Symposium on Marine Biology*. Galway, Pergamon, pp. 101-113.

Burkhardt S, Riebesell U and Zondervan I (1999a) Effects of growth rate, CO_2 concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. *Geochimica et Cosmochimica Acta*, 63, 3729-3741.

Burkhardt S, Riebesell U and Zondervan I (1999b) Stable carbon isotope fractionation by marine phytoplankton in response to daylength, growth rate, and CO_2 availability. *Marine Ecology Progress Series*, 184, 31-41.

Cahalan JA, Siddall SE and Luckenbach MW (1989) Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops *Argopecten irradians*. *Journal of Experimental Marine Biology and Ecology*, 129, 45-60.

Cairns SD, Gershwin L-A, Brook FJ, Pugh P, Dawson EW, Ocaña O, Vervoort W, Williams G, Watson JE, Opresko DM, Schuchert P, Hine PM, Gordon DP, Campbell HJ, Wright AJ, Sánchez JA and Fautin DG (2009) Phylum CNIDARIA corals, medusae, hydroids, myxozoans. In: Gordon DP (ed.) *New Zealand Inventory of Biodiversity Volume One: Kingdom Animalia*. Cantebury University Press, Cantebury, pp. 59-101.

Casanova J-P (1999) Chaetognatha. In: Boltovskoy D (ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 1353-1374.

Chown SL and Froneman PW (2008) The Prince Edward Islands in a global context. In: Chown SL and Froneman PW (eds.) *The Prince Edward Islands: Land-sea interactions in a changing ecosystem*. Sun Press, Stellenbosch, pp. 1-16.

Chown SL and Smith VR (1993) Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edward Islands. *Oecologia*, 96, 508-516.

Chown SL, McGeoch MA and Marshall DJ (2002) Diversity and conservation of invertebrates on the sub-Antarctic Prince Edward Islands. *African Entomology*, 10, 67-82.

Clarke A (1996) Marine benthic populations in Antarctica: patterns and processes. *Antarctic Research Series*, 70, 373-388.

Clarke A and Harris CM (2003) Polar marine ecosystems: major threats and future change. *Environmental Conservation*, 30, 1-25.

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA and Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 149-166.

Condy PR (1981) Annual food consumption and seasonal fluctuations in biomass of seals at Marion Island. *Mammalia*, 45, 21-30.

Conley DJ, Schelske C and Stoermer E (1993) Modification of the biogeochemical cycle of silica with eutrophication. *Marine Ecology Progress Series*, 101, 179-192.

Cook HW and McMaster CR (2002) Fatty acid desaturation and chain elongation in eukaryotes. In: Vance DE and Vance JE (eds.) *Biochemistry of lipids, lipoproteins and membranes*. Elsevier, Amsterdam, pp. 181-204.

Copeman LA and Parrish CC (2003) Marine lipids in a cold coastal ecosystem: Gilbert Bay, Labrador. *Marine Biology*, 143, 1213-1227.

Corbisier TN, Petti MAV, Skowronski RSP and Brito TAS (2004) Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): $\delta^{13}C$ stable-isotope analysis. *Polar Biology*, 27, 75-82.

Crawford RJM, Cooper J, Dyer BM, Greyling MD, Klages NTW, Ryan PG, Petersen SL, Underhill LG, Upfold L, Wilkinson W, De Villiers MS, Du Plessis S, du Toit M, Leshoro TM, Makhado AB, Mason MS, Merkle D, Tshingana D, Ward VL and Whittington PA (2003a) Population of surface nesting birds at Marion island, 1994/95-2002/03. *African Journal of Marine Science*, 25, 427-440.

Crawford RJM, Cooper J, Dyer BM, Greyling MD, Klages NTW, Nel DC, Nel JL, Petersen SL and Wolfaardt AC (2003b) Decrease in numbers of the Eastern Rockhopper Penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science*, 25, 487-498.

Crawford RJM, Cooper J, du Toit M, Greyling MD, Hanise B, Holness CL, Keith DG, Nel JL, Petersen SL, Spencer K, Tshingana D and Wolfaardt AC (2003c) Population and breeding of the Gentoo Penguin *Pygoscelis papua* at Marion Island, 1994/95-2002/03. *African Journal of Marine Science*, 25, 463-474.

Cripps GC and Atkinson A (2000) Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1-7.

Dalsgaard J, St. John M, Kattner G, Müller-Navarra D and Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. *Advances in Marine Biology*, 46, 225-340.

Dayton PK and Oliver JS (1977) Antarctic soft bottom benthosin oligotrophic and eutrophic environments. *Science*, 197, 55-58.

de Bower JFC, de Deckere EMGT and Stal LJ (2003) Distribution of extracellular carbohydrates in three intertidal mudflats in Western Europe. *Estuarine*, *Coastal and Shelf Science*, 56, 313-324.

De Mol B, Huvenne V and Canals M (2009) Cold-water coral banks and submarine landslides: a review. *International Journal of Earth Sciences*, 98, 885-899.

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42, 495-506.

Dittel A, Epifanio C, Schwalm S, Fantle M and Fogel M (2000) Carbon and nitrogen sources for juvenile blue crabs *Callinectes sapidus* in coastal wetlands. *Marine Ecology Progress Series*, 194, 103-112.

Doi H, Matsumasa M, Toya T, Satoh N, Mizota C, Maki Y and Kikuchi E (2005) Spatial shifts in food sources for macrozoobenthos in an estuarine ecosystem: carbon and nitrogen stable isotope analyses. *Estuarine*, *Coastal and Shelf Science*, 64, 316-322.

Duggins DO, Simenstad CA and Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science*, 245, 170-173.

Duncombe Rae CM (1989a) Data report of the first cruise of the Marion Offshore Ecological Study (MOES-I). *South African National Science Progress Report*, 159, 384 pp.

Duncombe Rae CM (1989b) Frontal systems encountered between southern Africa and the Prince Edward Islands during April/May 1987. *South African Journal of Antarctic Research*, 19, 21-25.

Dunton KH and Dayton PK (1995) The biology of high latitude kelp. In: Skjoldal HR, Hopkins C, Erikstad KE and Leinaas HP (eds.) *Ecology of fjords and coastal waters*. Elsevier, Amsterdam, pp. 499-507.

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM and Maidment DR (2005) Multi-decadal synthesis of benthic-pelagic coupling in the western arctic: Role of cross-shelf advective processes. *Deep-Sea Research II*, 52, 3462-3477.

El-Sayed SZ, Benon P, David P, Grindley JR and Murail J-F (1979) Some aspects of the biology of the water column studies during the „Marion-Dufresne" cruise 08. *Comité National Française des Recherches Antarctiques*, 44, 127-134.

Espitalier-Noël G, Adams NJ and Klages NTW (1988) Diet of the imperial cormorant *Phalacrocorax atriceps* at sub-Antarctic Marion Island. *Emu*, 88, 43-46.

Fauchald K and Jumars P (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review*, 17, 193-284.

Fish JD and Fish S (1996) *A student's guide to the seashore*, *2nd edition*. Cambridge University Press, Cambridge, 564 pp.

Folch J, Lees M and Stanley GHS (1957) A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry*, 226, 497-509.

Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis. *Marine Ecology Progress Series*, 260, 71-81.

Freeland H, Denman K, Wong CS, Whitney F and Jacques R (1997) Evidence of change in the winter mixed layer in the Northeast Pacific Ocean. *Deep-Sea Research I*, 44, 2117-2129.

Frenot Y, Gloaguen JJ and Tréhen P (1997) Climate Change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa kerguelensis* and *P. annua*. In: Battaglia B, Valencia J and Walton DWH (eds.) *Antarctic Communities: species, structure and survival*. Cambridge University Press, Cambridge, pp. 358-366.

Froneman PW and Balarin MS (1998) Structure and grazing impact of the protozooplankton community in the waters surrounding the sub-Antarctic Prince Edward Islands. *Polar Biology*, 20, 198-205.

Froneman PW and Bernard KS (2004) Trophic cascading in the Polar Frontal Zone of the Southern Ocean during austral autumn 2002. *Polar Biology*, 27, 112-118.

Froneman PW and Pakhomov EA (1998) Biogeographic study of the planktonic communities of the Prince Edward Islands. *Journal of Plankton Research*, 20, 653-669.

Froneman PW, Ansorge IJ, Pakhomov EA and Lutjeharms JRE (1999) Plankton communities and the physical environment in the waters surrounding the Prince Edward Islands in late austral summer 1997. *Polar Biology*, 22, 145-155.

Froneman PW, Laubscher RK and McQuaid CD (2001) Size-fractionated primary production in the south Atlantic and Atlantic sectors of the Southern Ocean. *Journal of Plankton Research*, 23, 611-622.

Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography*, 33, 1182-1190.

Fry B and Sherr EB (1984) $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science*, 27, 13-47.

Fry B and Wainright SC (1991) Diatom sources of ^{13}C-rich carbon in marine food webs. *Marine Ecology Progress Series*, 76, 149-157.

Fry B, Scalan RS and Parker PL (1983) $^{13}C/^{12}C$ ratios in marine food webs of the Torres Strait, Queensland. *Australian Journal of Marine and Freshwater Research*, 34, 707-716.

Fullarton JG, Dando PR, Sargent JR, Southward AJ and Southward EC (1995) Fatty acids of hydrothermal vent *Ridgeia piscesae* and inshore bivalves containing symbiotic bacteria. *Journal of Marine Biological Association of United Kingdom*, 75, 455-468.

Fyfe JC, Saenko OA, Zickfeld K, Eby M and Weaver AJ (2007) The role of poleward-intensifying winds on Southern Ocean warming. *Journal of Climate*, 20, 5391-5400.

Gales R, Green B and Stahel C (1988) The energetics of free-living little penguins *Eudyptula minor* (Spheniscidae), during molt. *Australian Journal of Zoology,* 36, 159-167.

Gibbons MJ, Spiridonov VA and Tarling GA (1999) Euphausiacea. In: Boltovskoy D (ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 1241-1279.

Gille ST (2002) Warming of the Southern Ocean since the 1950‟s. *Science*, 295, 1275-1277.

Gili JM and Hughes RG (1995) The ecology of marine benthichydroids. *Oceanography and Marine Biology: An Annual Review*, 33, 351-426.

Gili JM, Alva V, Coma R, Orejas C, Pagès F, Ribes M, Zabala M, Arntz W, Bouillon J, Boero F, Hughes RG (1998) The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example. *Zoologische Verhandelingen*, 323, 99-105.

Glibert PM, Lipschultz F, McCarthy JJ and Altabet MA (1982) Isotope dilution models of uptake and remineralization of ammonium by marine plankton. *Limnology and Oceanography*, 27, 639-650.

Gorokhova E and Hansson S (1999) An experimental study on variations in stable carbon and nitrogen isotope fractionation during growth of *Mysis mixta* and *Neomysis integer*. *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 2203-2210.

Graeve M, Kattner G and Hagen W (1994) Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: Experimental evidence of trophic markers. *Journal of Experimental Marine Biology and Ecology*, 182, 97-110.

Graeve M, Kattner G and Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biology*, 18, 53-61.

Grebmeier JM and Barry JP (1991) The influence of oceanographic processes on pelagic-benthic coupling in polar regions: A benthic perspective. *Journal of Marine Systems*, 2, 495-518.

Grebmeier JM and Dunton KH (2000) Benthic processes in the northern Bering/Chukchi Seas: status and global change. In: Huntington HP (ed.) *Impacts of changes in sea ice and other environmental parameters in the Arctic*. US Marine Mammal Commission, Washington, pp. 80-93.

Gregg WW, Conkright ME, Ginoux P, O‟Reilly JE and Casey NW (2003) Ocean primary production and climate: global decadal changes. *Geophysical Research Letters*, 30, 1809.

Gurney LJ, Froneman PW, Pakhomov EA and McQuaid CD (2002) Diel feeding patterns in daily ration estimates of three sub-antarctic euphausiids in the vicinity of the Prince Edward Islands (Southern Ocean). *Deep-Sea Research II*, 49, 3207-3227.

Hall JM, Parrish CC and Thompson RJ (2002) Eicosapentaenoic acid regulates Scallop (*Placopecten magellanicus*) membrane fluidity in response to cold. *Biological Bulletin*, 202, 201-203.

Hammer Ø, Harper DAT and Ryan PD (2001) PAST: Palaeontological Statistics Software Package for education and data analysis. *Palaeontologia Electronica*, 4, 9 pp.

Hare SR and Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, 47, 103-146.

Harvey HR (1994) Fatty acids and sterols as source markers of organic matter in sediments of the North Carolina continental slope. *Deep-Sea Research II*, 41, 783-796.

Haxen PG and Grindley JR (1985) *Durvillaea antarctica* production in relation to nutrient cycling at Marion Island. In: Siegfried WR, Condy PR and Laws RM (eds.) *Antarctic nutrient cycles and food webs*. Springer, Berlin, pp. 637-640.

Hilton GM, Thompson DR, Sagar PM, Cuthbert RJ, Cherel Y and Bury SJ (2006) A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the Rockhopper Penguin *Eudyptes chrysocome*. *Global Change Biology*, 12, 611-625.

Hirons AC, Schell DM and Finney BP (2001) Temporal records of $\delta^{13}C$ and $\delta^{15}N$ in North Pacific pinnipeds: inferences regarding environmental change and diet. *Oecologia*, 129, 591-601.

Hobson KA (1993) Trophic relationships among high Arctic sea-birds: insights from tissue-dependent stable-isotope models. *Marine Ecology Progress Series*, 95, 7-18.

Hobson KA and Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$and $\delta^{15}N$ analysis. *Marine Ecology Progress Series*, 84, 9-18.

Hobson KA, Bowen GJ, Wassenaar LI, Ferrand Y and Lormee H (2004) Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, 141, 477-488.

Hofmeyr GJG, Bester MN, Makhado AB and Pistorius PA (2006) Population changes in Subantarctic and Antarctic Fur Seals at Marion Island. *South African Journal of Wildlife Research*, 36, 55-68.

Hopkins TL, Lancraft TM, Torres JJ and Donelly J (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea Marginal Ice Zone in Winter (1988). *Deep-Sea Research I*, 40, 81-105.

Hunt BPV, Pakhomov EA and McQuaid CD (2001) Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago. *Marine Biology*, 138, 369-381.

Iken K, Brey T, Wand U, Voigt J and Junghans P (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progress in Oceanography*, 50, 383-405.

Inchausti P, Guinet C, Koudil M, Durbec J-P, Barbraud C, Weimerskirch H, Cherel Y and Jouventin P (2003) Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology*, 34, 170-176.

Ismail HE (1990) Surface nutrients in the vicinity of the Prince Edward Islands during April/May 1989. *South African Journal of Antarctic Research*, 20, 33-36.

Jacob U, Brey T, Fetzer I, Kaehler S, Mintenbeck K, Dunton K, Beyer K, Struck U, Pakhomov EA and Arntz WE (2006) Towards the trophic structure of the Bouvet Island marine ecosystem. *Polar Biology*, 29, 106-113.

Jarre-Teichmann A, Brey T, Bathmann UV, Dahm C, Dieckmann GS, Gorny M, Klages M, Pagès F, Plötz J, Schnack-Schiel SB, Stiller M and Arntz WE (1997) Trophic flows in the benthic shelf community of the eastern Weddell Sea, Antarctica. In: Battaglia B, Valencia J and Walton DWH (eds.) *Antarctic Communities: Species*, *Structure and Survival*. Cambridge University Press, Cambridge, pp. 118-134.

Kaehler S and Pakhomov EA (2001) Effects of storage and preservation on the $\delta^{13}C$ and $\delta^{15}N$ signatures of selected marine organisms. *Marine Ecology Progress Series*, 219, 299-304.

Kaehler S, Pakhomov EA and McQuaid CD (2000) Trophic structure of the marine food web at the Prince Edward Islands (Southern Ocean) determined by $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series*, 208, 13-20.

Kaehler S, Pakhomov EA, Kalin RM and Davis S (2006) Trophic importance of kelp-derived suspended particulate matter in a through-flow sub-Antarctic system. *Marine Ecology Progress Series*, 316, 17-22.

Kattner G and Hagen W (1995) Polar herbivorous copepods-different pathways in lipid biosynthesis. *ICES Journal of Marine Science*, 52, 329-335.

Kattner G and Krause M (1987) Changes in lipids during the development of *Calanus finmarchicus* s.l. from copepodid I to adult. *Marine Biology*, 96, 511-518.

Kharlamenko VI, Zhukova NV, Khotimchenko SV, Svetashev VI and Kamenev GM (1995) Fatty acids as markers of food sources in a shallow-water hydrothermal ecosystem (Kraternaya Bight, Yankich Island, Kurile Islands). *Marine Ecology Progress Series*, 120, 231-241.

Kharlamenko VI, Kiyashko SI, Imbs AB and Vyshkvartzev DI (2001) Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Marine Ecology Progress Series*, 220, 103-117.

Kiyashko SI, Kharlamenko VI and Imbs AB (1998) Stable isotope ratios and fatty acids as food source markers of deposit-feeding invertebrates. *Russian Journal of Marine Biology*, 24, 170-174.

Kling GW, Fry B and O'Brian WJ (1992) Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology*, 73, 561-566.

Kroopnick PM (1985) The distribution of ^{13}C of ΣCO_2 in the world oceans. *Deep-Sea Research I*, 32, 57-84.

Laubscher RK, Perissinotto R and McQuaid CD (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology*, 13, 471-481.

Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO2]_{aq}$: theoretical considerations and experimental results. *Geochimica et Cosmochimica Acta*, 59, 1131-1138.

Laws EA, Bidigare RR and Popp BN (1997) Effect of growth rate and CO_2 concentration on carbon fractionation by the marine diatom *Phaeodactylum tricornutum*. *Limnology and Oceanography*, 42, 1552-1560.

le Roux PC (2008) Climate and climate change. In: Chown SL and Froneman PW (eds.) *The Prince Edward Islands: Land-sea interactions in a changing ecosystem*. Sun Press, Stellenbosch, pp. 39-64.

le Roux PC and McGeoch MA (2008) Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change*, 86, 309-329.

Lee JE and Chown SL (2007) *Mytilus* on the move: transport of an invasive bivalve to the Antarctic. *Marine Ecology Progress Series*, 339, 307-310.

Legeckis R (1977) Oceanic polar front in the Drake Passage - satellite observations during 1976. *Deep-Sea Research*, 24, 701-704.

Lescroël A and Bost C-A (2006) Recent decrease in Gentoo penguin populations at Iles Kerguelen. *Antarctic Science*, 18, 171-174.

Levinton J, Ward J and Shumway S (2002) Feeding responses of the bivalves *Crassostrea gigas* and *Mytilus trossulus* to chemical composition of fresh and aged kelp detritus. *Marine Biology*, 141, 367-376.

Levitus S, Antonov JI, Boyer TP and Stephens C (2000) Warming of the world ocean. *Science*, 287, 2225-2229.

Lovvorn JR, Richman SE, Grebmeier JM and Cooper LW (2003) Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. *Polar Biology*, 26, 259-267.

Lutjetiarms JRE (1985) Location of frontal systems between Africa and Antarctica: some preliminary results. *Deep-Sea Research I*, 32, 1499-1509.

Lutjeharms JRE (1990) Temperatuurstruktuur van die oseaanbolaag tussen Kaapstad en Marion-eiland. *South African Journal of Antarctic Research*, 20, 21-32.

Lutjeharms JRE and Valentine HR (1984) Southern Ocean thermal fronts south of Africa. *Deep-Sea Research I*, 31, 1461-1476.

Lutjeharms JRE, Shannon LV and Beekman LJ (1988) On the sea surface drift of the Southern Ocean. *Journal of Marine Research*, 64, 267-279.

MacIntyre HL, Geider RJ and Miller DC (1996) Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production, *Estuaries and Coasts*, 19, 186-201.

Mann KH (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnology and Oceanography*, 33, 910-930.

Mann KH (2000) *Ecology of coastal waters: with implications for management*. Blackwell Scientific Publications, Oxford. 406 pp.

Martin-Jézéquel V, Hildebrand M and Brzezinski M (2000) Review Silicon metabolism in diatoms: implications for growth. *Journal of Phycology*, 36, 821-840.

McConnaughey T and McRoy CP (1979) Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology*, 53, 257-262.

McKinney FK (1990) Feeding and associated colonial morphology in marine bryozoans. *Reviews in Aquatic Sciences*, 2, 255-280.

McQuaid CD and Froneman PW (2004) The Southern Ocean Group at Rhodes University: seventeen years of biological oceanography in the Southern Ocean reviewed. *South African Journal of Science*, 100, 571-578.

McQuaid CD and Froneman PW (2008) Biology in the oceanographic environment. In: Chown SL and Froneman PW (eds.) *The Prince Edward Islands: Land-sea interactions in a changing ecosystem*. Sun Press, Stellenbosch, pp. 97-120.

Mélice J-L, Lutjeharms JRE, Rouault M and Ansorge IJ (2003) Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science*, 99, 363-366.

Merrick RL, Chumbley MK and Byrd GV (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 1342-1348.

Michener RH and Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: Lajtha K and Michener RH (eds.) *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific, Oxford, pp. 138-158.

Miller CB, Frost BW, Batchedler HP, Clemons MJ and Conway RE (1984) Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the northeast Pacific. *Progress in Oceanography*, 13, 201-243.

Montoya JP and McCarthy JJ (1995) Isotopic fractionation during nitrate uptake by phytoplankton grown in continuous culture. *Journal of Plankton Research*, 17, 439-464.

Moore J, Abbott M and Richman J (1999) Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research*, 104, 3059-3073.

Moore SE, Grebmeier JM and Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. *Canadian Journal of Zoology*, 81, 734-742.

NagataY, Michida Y and Umimura Y (1988) Variation of positions and structures of the oceanic fronts in the Indian sector of the Southern Ocean in the period from 1965 to 1987. In: Sahrhage D (ed.) *Antarctic Ocean and Resources Variability*. Springer-Verlag, Berlin, pp. 92-98.

Napolitano GE, Pollero RJ, Gayoso AM, Macdonald BA and Thompson RJ, (1997) Fatty acids as trophic markers of phytoplankton blooms in the Bahia Blanca estuary (Buenos Aires, Argentina) and in Trinity Bay (Newfoundland, Canada). *Biochemical Systematics and Ecology*, 25, 739-755.

Needoba JA, Waser NA, Harrison PJ and Calvert SE (2003) Nitrogen isotope fractionation in 12 species of marine phytoplankton during growth on nitrate. *Marine Ecology Progress Series*, 255, 81-91.

Nel DC, Ryan PG, Crawford RJM, Cooper J and Huyser OAW (2002) Population trends of albatrosses and petrels breeding at sub-Antarctic Marion Island. *Polar Biology*, 25, 81-89.

Newell RC, Field JG and Griffiths CL (1982) Energy balance and significance of micro-organisms in a kelp bed community. *Marine Ecology Progress Series*, 8, 103-113.

Nilssen KT, Pedersen O-P, Folkow L and Haug T (2000) Food consumption estimates of Barents Sea harp seals. *NAMMCO Scientific Publication*, 2, 9-28.

Nowlin WD Jr and Klinck JM (1986) The physics of the Antarctic Circumpolar Current. *Reviews of Geophysics*, 24, 469-491.

Oke PR and England MH (2004) Oceanic response to changes in the latitude of the Southern Hemisphere subpolar westerly winds. *Journal of Climate*, 17, 1040-1054.

O'Loughlin PM, Paulay G, Davey N and Michonneau F (in press) The Antarctic region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers. *Deep-Sea Research II*, doi: 10.1016/j.dsr2.2010.10.011.

Olsen Y (1999) Lipids and essential fatty acids in aquatic food webs: what can freshwater ecologists learn from mariculture? In: Arts MT and Wainman BC (eds.) *Lipids in freshwater ecosystems*. Springer, New York, pp. 161-202.

Pakhomov EA and Chown SL (2003) The Prince Edward Islands: Southern Ocean oasis. *Ocean Yearbook*, 17, 348-379.

Pakhomov EA and Froneman PW (1999a) The Prince Edward Islands pelagic ecosystem, south Indian Ocean: a review of achievements, 1976-1990. *Journal of Marine Systems*, 18, 355-367.

Pakhomov EA and Froneman PW (1999b) Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean): new concept for the biomass build up for higher trophic levels. *Marine Biology*, 134, 501-515.

Pakhomov EA, Verheye HM, Atkinson A, Laubscher RK, Taunton-Clark J (1997) Structure and grazing impact of the mesozooplankton community during late summer 1994 near South Georgia Antarctica. *Polar Biology*, 18, 180-192.

Pakhomov EA, Froneman PW, Kuun PJ and Balarin M (1999) Feeding dynamics and respiration of the bottom-dwelling caridean shrimp *Nauticaris marionis* Bate, 1888 (Crustacea: Decapoda) in the vicinity of Marion Island (Southern Ocean). *Polar Biology*, 21, 112-121.

Pakhomov EA, Kuun P and McQuaid CD (2000a) Biology of the bottom-dwelling shrimp *Nauticaris marionis* Bate, 1888 at the sub-Antarctic Prince Edward Islands. *Polar Biology*, 23, 522-530.

Pakhomov EA, Ansorge IJ and Froneman PW (2000b) Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean). *Polar Biology*, 23, 593-603.

Pakhomov EA, Froneman PW and McQuaid CD (2001) Prince Edward Islands life support system and variability of living resource systems in the Southern Ocean. *Final report submitted to South African Committee on Antarctic Research*.

Pakhomov EA, Kaehler S and McQuaid CD (2002) Zooplankton community structure in the kelp beds of the sub-Antarctic Prince Edward Archipelago: are they a refuge for larval stages? *Polar Biology*, 25, 778-788.

Pakhomov EA, McClelland JW, Bernard KS, Kaehler S and Montoya JP (2004) Spatial and temporal shifts in stable isotope values of the bottom-dwelling shrimp *Nauticaris marionis* at the sub-Antarctic archipelago. *Marine Biology*, 144, 317-325.

Pakhomov EA, Kaehler S and Perissinotto R (2009) The Prince Edward Islands‟ life-support system: relative importance of local and advected sources. *Proceedings of the Kazan State University*, 151, 104-121.

Park YH, Gamberoni L and Charriaud E (1993) Frontal structure, water masses and circulation in the Crozet Basin. *Journal of Geophysical Research*, 98, 12361-12385.

Parker LD (1984) A contribution to the oceanology of the Prince Edward Islands. MSc Thesis. Rhodes University, Grahamstown.

Parrish CC (1999) Determination of total lipid, lipid classes, and fatty acids in aquatic samples. In: Arts MT and Wainman BC (eds.) *Lipids in Freshwater Ecosystems*. Springer, New York, pp. 4-20.

Parrish CC, Abrajano TA, Budge SM, Helleur RJ, Hudson ED, Pulchan K and Ramos C (2000) Chapter 8: Lipid and Phenolic Biomarkers in Marine Ecosystems: analysis and applications. In: Wangersky P (ed.) *The Handbook of Environmental Chemistry Vol*. 5 *Part D Marine Chemistry*. Springer-Verlag, Berlin, pp. 193-223.

Parrish CC, Deibel D and Thompson RJ (2009) Effect of sinking spring phytoplankton blooms on lipid content and composition in suprabenthic and benthic invertebrates in a cold ocean coastal environment. *Marine Ecology Progress Series*, 391, 33-51.

Parsons TR, Maita Y and Lalli CM (1984) *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford, 173 pp.

Pearse V, Pearse J, Buchsbaum M and Buchsbaum C (1987) *Living Invertebrates*. Blackwell Scientific Publishing, Palo Alto California, 848 pp.

Pedersen SA and Riget F (1993) Feeding habits of redfish (*Sebastes* spp.) and Greenland halibut (*Reinhardtius hippoglossoides*) in West Greenland waters. *ICES Journal of Marine Science*, 50, 445-459.

Perga M-E, Kainz M, Matthews B and Mazumder A (2006) Carbon pathways to zooplankton: insights from the combined use of stable isotope and fatty acid biomarkers. *Freshwater Biology*, 51, 2041-2051.

Perissinotto R (1992) Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern Ocean). *Marine Ecology Progress Series*, 79, 243-258.

Perissinotto R and Boden BP (1989) Zooplankton-phytoplankton relationships at the Prince Edward Islands during April/May 1985 and 1986. *South African Journal of Antarctic Research*, 19, 26-30.

Perissinotto R and Duncombe Rae CM (1990) Occurrence of anti-cyclonic eddies on the Prince Edward plateau (Southern Ocean): effects on phytoplankton productivity and biomass. *Deep-Sea Research I*, 37, 777-793.

Perissinotto R and McQuaid CD (1990) Role of the sub-Antarctic shrimp *Nauticaris marionis* in coupling benthic and pelagic food webs. *Marine Ecology Progress Series*, 64, 81-87.

Perissinotto R and McQuaid, CD (1992) Deep occurrence of the giant kelp *Macrocystis laevis* in the Southern Ocean. *Marine Ecology Progress Series*, 81, 89-95.

Perissinotto R, Allanson BR and Boden BP (1990) Trophic relations within the island seas of the Prince Edward Archipelago, Southern Ocean. In: Barnes M and Gibson RN (eds.) *Trophic Relationships in the Marine Environment*. Aberdeen University Press, Aberdeen, pp. 296-314.

Perissinotto R, Lutjeharms JRE and Van Ballegooyen RC (2000) Biological-physical interactions and pelagic productivity at the Prince Edward Islands, Southern Ocean. *Journal of Marine Systems*, 24, 327-341.

Peterson BJ (1999) Stable isotopes as tracers of organic matter input and transfer in benthic food webs: A review. *Acta Oecologica*, 20, 479-487.

Peterson BJ and Fry B (1987) Stable Isotopes in Ecosystem studies. *Annual Review of Ecology and Systematics*, 18, 293-320.

Peterson BJ, Howarth RW and Garritt RH (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science*, 227, 1361-1363.

Peterson W, Painting S and Barlow R (1990) Feeding rates of *Calanoides carinatus*: a comparison of five methods including evaluation of the gut fluorescence method. *Marine Ecology Progress Series*, 63, 85-92.

Pile A, Patterson MR, and Witman JD (1996) *In situ* grazing on plankton <10 μm by the boreal sponge *Mycale lingua*. *Marine Ecology Progress Series*, 141, 95-102.

Pitcher GC, Bolton JJ, Brown PC and Hutchings L (1993) The development of phytoplankton blooms in upwelled waters of the southern Benguela upwelling system as determined by microcosm experiments. *Journal of Experimental Marine Biology and Ecology*, 165, 171-189.

Pitcher KW (1990) Major decline in the number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science*, 6, 121-134.

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J and Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152, 179-189.

Rau GH, Riebesell U and Wolf-Gladrow D (1997) CO_{2aq}-dependent photosynthetic ^{13}C fractionation in the ocean: a model versus measurements. *Global Biochemical Cycles*, 11, 267-278.

Reiswig HM (1971) Particle feeding in natural populations of three marine demosponges. *Biological Bulletin*, 141, 568-591.

Reiswig HM (1990) *In situ* feeding in two shallow-water hexactinellid sponges. In: Rützler K (ed.) *New Perspectives in Sponge Biology*. Smithsonian Institution Press, Washington, pp. 504-510.

Richoux NB (in press) Trophic ecology of zooplankton at a frontal transition zone: fatty acid signatures at the subtropical convergence, Southern Ocean. *Journal of Plankton Research*.

Richoux NB and Froneman PW (2007) Assessment of spatial variation in carbon utilization by benthic and pelagic invertebrates in a temperate South African estuary using stable isotope signatures. *Estuarine*, *Coastal and Shelf Science*, 71, 545-558.

Richoux NB and Froneman PW (2008) Trophic ecology of dominant zooplankton and macrofauna in a temperate, oligotrophic South African estuary: a fatty acid approach. *Marine Ecology Progress Series*, 357, 121-137.

Richoux NB, Deibel D, Thompson RJ and Parrish CC (2005) Seasonal and developmental variation in the fatty acid composition of *Mysis mixta* (Mysidacea) and *Acanthostepheia malmgreni* (Amphipoda) from the hyperbenthos of a cold-ocean environment (Conception Bay, Newfoundland). *Journal of Plankton Research*, 27, 719-733.

Ryan PG and Bester MN (2008) Pelagic predators. In: Chown SL and Froneman PW (eds.) *The Prince Edward Islands: Land-sea interactions in a changing ecosystem*. Sun Press, Stellenbosch, pp. 121-164.

Sahade R, Tatián M, Kowalke J, Kühne S and Esnal G (1998) Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica. *Polar Biology*, 19, 85-91.

Saito H and Kotani Y (2000) Lipids of four boreal species of calanoid copepods: origin of monoene fats of marine animals at higher trophic levels in the grazing food chain in the subarctic ocean system. *Marine Chemistry*, 36, 233-248.

Sargent JR and Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. *Hydrobiologia*, 167/168, 101-l14.

Sargent JR and Henderson RJ (1986) Lipids. In: Comer EDS and O'Hara SCM (eds.) *The Biological Chemistry of Marine Copepods*. Oxford Scientific Publications, Clarendon Press, Oxford, pp. 59-108.

Sargent JR, Bell MV, Henderson RJ and Tocher DR (1989) The lipids. In: Halver J (ed.) *Fish nutrition*. Academic, New York, pp. 153-218.

Schell DM (2000) Declining carrying capacity in the Bering Sea: isotopic evidence from whale baleen. *Limnology and Oceanography*, 45, 459-462.

Schiel DR, Steinbeck JR and Foster MS (2004) Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*, 85, 1833-1839.

Schlitzer R (2010) Ocean Data View, http://odv.awi.de

Schmidt K, Atkinson A, Stübing D, McClelland JW, Montoya JP and Voss M (2003) Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. *Limnology and Oceanography*, 48, 277-289.

Scott CL, Falk-Petersen S, Gulliksen B, Lønne OJ and Sargent JR (2001) Lipid indicators of the diet of the sympagic amphipod *Gammarus wilkitzkii* in the Marginal Ice Zone and in open waters of Svalbard (Arctic). *Polar Biology*, 24, 572-576.

Simpkins MA, Hiruki-Raring LM, Sheffield G, Grebmeier JM and Bengston JL (2003) Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska. *Polar Biology*, 26, 577-586.

Smale DA and Barnes DKA (2008) Likely responses of the Antarctic benthos to climate-related changes in physical disturbance during the 21st century, based primarily on evidence from the West Antarctic Peninsula region. *Ecography*, 31, 289-305.

Smith CR, Mincks S and DeMaster DJ (2006) A synthesis of bentho-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. *Deep-Sea Research II*, 53, 875-894.

Smith VR (2002) Climate change in the sub-Antarctic: an illustration from Marion Island. *Climatic Change*, 52, 345-357.

Smith VR, Steenkamp M and Gremmen NJM (2001) Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany*, 67, 641-654.

Smith WO Jr and Nelson DM (1986) Importance of ice edge phytoplankton production in the Southern Ocean. *BioScience*, 36, 251-257.

Stevens CJ, Deibel D and Parrish CC (2004) Copepod omnivory in the North Water Polynya (Baffin Bay) during autumn: Spatial patterns in lipid composition. *Deep-Sea Research I*, 51, 1637-1658.

Subba Rao DV and Platt T (1984) Primary production of Arctic waters. *Polar Biology*, 3, 191-201.

Sumner PD, Meiklejohn KI, Boelhouwers JC and Hedding DW (2004) Climate change melts Marion Island"s snow and ice. *South African Journal of Science*, 100, 395-398.

Sweeting CJ, Barry J, Barnes C, Polunin NVC and Jennings S (2007) Effects of body size and environment on diet-tissue $\delta^{15}N$ fractionation in fishes. *Journal of Experimental Marine Biology and Ecology*, 340, 1-10.

Tatián M, Sahade R, Mercuri G, Fuentes VL, Antacli JC, Stellfeldt AE, Graciela B (2008) Feeding ecology of benthic filter-feeders at Potter Cove, an Antarctic coastal ecosystem. *Polar Biology*, 81, 509-517.

Tavares M and De Melo GAS (2004) Discovery of the first known benthic invasive species in the Southern Ocean: the North Atlantic spidercrab *Hyasaraneus* found in the Antarctic Peninsula. *Antarctic Science*, 16, 129-131.

Thatje S (2005) The future fate of the Antarctic marine biota? *Trends in Ecology and Evolution*, 20, 418-419.

Thompson DWJ and Solomon S (2002) Interpretation of Recent Southern Hemisphere Climate Change. *Science*, 296, 895-899.

Thost D and Allison I (2005) The climate of Heard Island. In: Green K and Woehler EJ (eds.) *Heard Island: Southern Ocean Sentinel*. Surrey Beatty and Sons, Sydney, pp. 62-68.

Tieszen L, Boutton TW, Tesdahl K and Slade N (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. *Oecologia*, 57, 32-37.

Tocher DR (2003) Metabolism and functions of lipids and fatty acids in teleost fish. *Reviews in Fisheries Science*, 11, 107-184.

Trathan PN, Forcada J and Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 2351-2365.

Trenberth KE and Hurrell JW (1994) Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics*, 9, 303-319.

Tweedie CE and Bergstrom D (2000) A climate change scenario for surface air temperature at Subantarctic Macquarie Island. In: Davison W, Howard-Williams C and Broady P (eds.) *Antarctic Ecosystems: Models for Wider Ecological Understanding*. New Zealand Natural Sciences, Christchurch, pp. 272-281.

Tyrrell, T and Lucas MI (2002) Geochemical evidence of denitrification in the Benguela upwelling system. *Continental Shelf Research*, 22, 2497-2511.

Uddstrom MJ and Oien NA (1999) On the use of high-resolution satellite data to describe the spatial and temporal variability of sea surface temperatures in the New Zealand region. *Journal of Geophysical Research*, 104, 20729-20751.

Valentine HR and Lutjeharms JRE (1983) Oceanic thermal fronts in the Southern Ocean. *CSIR Research Report 558*, CSIR, Stellenbosch, 187 pp.

Valiela I (1984) *Marine Ecological Processes*. Springer, New York, 546 pp.

Van Ballegooyen RC, Perissonotto R, Ismail A, Boden BR, Lucas M, Allanson BR and Lutjeharms JRE (1989) Data report of the second cruise of the Marion Offshore Ecological Study (MOES-II). *CSIR Report EMA-D 8910*, 398 pp.

van de Vyver G, Vray B, Belaouane S and Toussaint D (1990) Efficiency and selectivity of micro-organism retention by *Ephydatia fluviatilis*. In: Rützler K (ed.) *New Perspectives in Sponge Biology*. Smithsonian Institute Press, Washington, pp. 511-515.

van der Spoel S and Dadon JR (1999) Pteropoda. In: Boltovskoy D (ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 649-706.

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ and Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. *Climate Change*, 60, 243-274.

Vinogradov G (1999) Amphipoda. In: Boltovskoy D (ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, pp. 1141-1240.

Vumazonke L, Pakhomov EA, Froneman PW and McQuaid CD (2003) Diet and daily ration of male and female caridean shrimp *Nauticaris marionis* at the Prince Edward Archipelago. *Polar Biology*, 26, 420-422.

Walsh JJ (1971) Relative importance of habitat variables in predicting the distribution of phytoplankton at the ecotone of the Antarctic upwelling ecosystem. *Ecological Monographs*, 41, 291-309.

Weimerskirch H, Inchausti P, Guinet C and Barbraud C (2003) Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science*, 15, 249-256.

Wendeln H and Becker PH (1999) Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology*, 68, 205-214.

Williams AJ, Siegfried WR, Burger AE and Berruti A (1979) The Prince Edward Islands: a sanctuary for seabirds in the Southern Ocean. *Biological Conservation*, 15, 59-71.

Winter J (1978) A review of the knowledge of suspension-feeding in Lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture*, 13, 1-33.

Table A1. Fatty acid composition (mean % TFA ± SD) of the surface water suspended particulate matter (SPM) in the vicinity and in the surrounding offshore region of the Prince Edward Islands. Data represent all fatty acids at concentrations >1% TFA in at least one sample (n = 1 per station).

Fatty acid	Vicinity of the Prince Edward Islands									
	Inter-island							Nearshore		
	upstream			between			downstream			
	St 1	St 2	St 3	St 4	St 5	St 6	St 7	St 8	St 9	St 10
14:0	6.9	6.3	10.5	4.5	7.6	6.6	2.2	3.4	5.4	6.5
15:0	1.5	1.0	0.8	0.9	0.7	0.9	0.4	0.7	1.0	1.1
16:0	32.3	34.7	33.8	32.1	27.7	34.1	25.9	25.1	30.7	29.6
17:0	0.7	1.1	0.7	0.7	0.8	0.8	0.7	0.8	0.8	0.7
18:0	33.4	35.9	28.4	32.6	25.7	31.8	58.5	23.2	31.6	23.1
20:0	1.1	1.1	1.2	1.3	1.2	1.2	1.6	1.7	1.1	1.5
22:0	1.1	0.6	1.0	1.3	1.1	0.8	0.6	1.6	1.1	3.0
24:0	0.4	0.0	0.4	0.4	0.4	0.0	0.2	0.6	0.4	1.3
Σ SFA	77.8	81.1	77.2	74.3	65.9	76.7	90.4	57.6	72.9	68.1
14:1ω5	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
16:1ω7	1.4	2.8	2.2	2.2	1.7	1.7	0.7	2.1	1.9	2.2
16:1ω9	0.9	1.3	1.3	0.9	0.8	0.8	0.7	1.0	1.9	1.0
18:1ω7	0.0	0.8	0.0	0.8	1.1	0.9	0.3	1.0	0.6	0.0
18:1ω9	9.9	6.6	8.2	7.8	10.5	9.5	3.4	8.7	10.3	10.2
20:1ω9	4.1	0.0	4.0	0.0	4.9	3.0	0.6	1.9	4.9	6.8
20:1ω11	0.7	1.2	0.8	5.4	1.8	0.0	0.3	0.7	0.9	0.7
22:1ω9	0.4	0.0	0.5	0.6	0.6	0.4	0.2	6.0	0.0	1.0
Σ MUFA	17.3	12.7	17.2	17.7	21.4	16.3	6.4	22.3	20.6	21.9
18:2ω6	1.9	1.6	1.9	2.4	2.3	1.8	1.2	2.9	2.5	4.7
18:4ω3	0.0	1.0	0.5	1.0	1.7	1.1	0.3	1.7	0.8	0.0
20:2ω9	1.2	0.8	0.0	1.2	2.2	1.0	0.2	0.0	0.0	1.9
20:5ω3	0.6	1.3	0.9	1.3	2.6	1.4	0.5	5.1	1.2	1.5
22:6ω3	0.6	0.9	0.7	0.8	1.9	1.0	0.4	7.9	0.9	1.2
Σ PUFA	4.9	6.2	5.6	8.0	12.7	7.0	3.2	20.2	6.5	10.0
Σ EFA	1.2	2.2	1.6	2.2	4.8	2.3	1.0	13.3	2.2	2.7
Σ BAFA	2.5	2.6	1.9	2.1	1.8	2.2	1.3	2.0	2.3	2.8
Σ HPFA	1.9	2.2	2.2	3.0	3.0	2.2	1.5	3.5	3.0	4.7
Σ TFA	9.7	12.1	6.7	11.2	7.1	7.4	24.6	4.9	13.8	3.6

Table A1. (cont.)

Fatty acid	Surrounding offshore region							
	Upstream			Downstream				
	St i	St ii	St iii	St iv	St v	St vi	St vii	St viii
14:0	14.3	20.5	10.0	4.7	19.8	10.6	21.2	28.3
15:0	1.0	1.4	3.5	0.4	3.3	2.7	3.7	1.9
16:0	41.0	31.9	34.6	33.1	38.8	43.0	36.3	34.8
17:0	0.0	0.9	0.8	0.6	0.7	1.5	0.0	1.4
18:0	27.2	25.3	31.2	27.5	17.7	31.9	20.3	12.3
20:0	0.0	0.7	0.7	1.0	0.0	0.6	0.0	0.5
22:0	0.7	1.3	0.8	1.0	1.3	0.9	0.8	0.5
24:0	0.0	0.5	0.0	0.3	0.0	0.0	0.0	0.0
Σ SFA	84.2	82.7	82.0	68.9	81.6	91.1	82.3	80.5
14:1ω5	0.0	0.7	1.0	0.0	1.5	0.6	0.0	0.8
16:1ω7	3.1	3.6	2.4	2.4	3.4	1.9	5.1	6.8
16:1ω9	0.0	1.3	1.0	0.8	1.2	0.0	0.9	0.0
18:1ω7	0.0	0.0	0.5	0.7	0.5	0.4	0.3	0.0
18:1ω9	10.9	7.7	6.8	16.8	5.9	3.6	7.9	5.6
20:1ω9	0.0	0.0	0.0	4.0	0.0	0.0	0.0	0.0
20:1ω11	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
22:1ω9	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0
Σ MUFA	14.0	13.9	11.7	25.5	12.5	6.5	14.2	13.2
18:2ω6	0.8	1.7	3.3	3.3	2.0	0.9	2.3	2.5
18:4ω3	0.0	0.4	0.0	0.3	0.0	0.0	0.0	1.0
20:2ω9	0.9	0.0	2.5	0.0	3.5	1.4	0.0	1.5
20:5ω3	0.0	0.7	0.5	0.6	0.4	0.0	1.2	1.3
22:6ω3	0.0	0.5	0.0	0.4	0.0	0.0	0.0	0.0
Σ PUFA	1.8	3.4	6.3	5.6	5.9	2.4	3.5	6.3
Σ EFA	0.0	1.2	0.5	1.0	0.4	0.0	1.2	1.3
Σ BAFA	1.0	2.3	4.7	1.3	4.0	4.1	3.7	4.1
Σ HPFA	0.8	1.7	3.3	3.5	2.0	0.9	2.3	2.5
Σ TFA	4.1	6.9	6.5	6.3	4.5	6.1	5.5	6.4

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (μg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A2. Fatty acid composition (mean % TFA ± SD) of the kelp *Macrocystis laevis*. Fresh and degraded fronds, and degraded kelp particulate organic matter (POM) and the suspended particulate matter (SPM) obtained from within the kelp beds near Marion Island. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

	Fresh	Degraded		Kelp bed
Fatty acid	frond	frond	POM	SPM
	M. laevis	*M. laevis*		
14:0	12.8 ± 6.5	8.7 ± 2.0	3.9	2.7
i-15:0	0.2 ± 0.3	2.0 ± 0.1	0.3	0.6
16:0	19.5 ± 0.6	16.5 ± 0.9	21.8	34.3
i-17:0	0.4 ± 0.5	1.2 ± 0.3	0.7	0
17:0	0	0	0	1.5
18:0	1.1 ± 0.5	0.9 ± 0.2	2.3	28.5
20:0	0.4 ± 0.5	0.4 ± 0.1	0	1.8
22:0	0	0	0	3.6
Σ SFA	34.5 ± 6.0	30.1 ± 5.6	29.4	75.0
16:1ω7	0.6 ± 0.3	6.6 ± 0.5	34.4	2.1
18:1ω5	0	0	0	7.0
18:1ω7	0	0.6 ± 0.1	17.7	2.4
18:1ω9	17.9 ± 4.9	11.3 ± 1.8	4.0	4.6
Σ MUFA	18.5 ± 4.6	18.6 ± 2.5	56.1	9.9
16:4ω1	0	0	0	1.2
18:2ω6	7.1 ± 1.0	4.7 ± 1.3	1.8	0
18:3ω3	5.4 ± 2.2	6.9 ± 2.7	3.2	0
18:4ω3	6.7 ± 3.7	10.7 ± 3.0	2.5	0
20:2ω9	0	0	0	5.9
20:4ω3	1.0 ± 0.6	1.2 ± 0.4	0.3	0
20:4ω6	18.6 ± 0.3	15.0 ± 0.6	3.4	0
20:5ω3	7.0 ± 3.2	12.1 ± 4.3	2.8	1.0
Σ PUFA	47.0 ± 10.6	51.4 ± 7.0	14.5	15.1
Σ EFA	25.6 ± 3.5	27.1 ± 4.6	6.2	1.0
Σ BAFA	0.7 ± 1.0	3.6 ± 0.4	1.4	2.6
Σ HPFA	12.5 ± 3.2	11.6 ± 2.9	5.0	0
Σ TFA	14.2 ± 1.3	43.9 ± 5.2	20.4	1.7

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A3. Fatty acid composition (mean % TFA ± SD) of the four species of sponge at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

	Inter-island	Nearshore	Inter-island	Nearshore	Inter-island	Nearshore	Inter-island	Nearshore
	Between		Between		Between		Between	
Fatty acid	St 4	St 9	St 6	St 9	St 6	St 9	St 6	St 10
	sp. 1	sp. 1	sp. 2	sp. 2	sp. 3	sp. 3	sp. 4	sp. 4
14:0	0.8 ± 0.3	2.4 ± 0.6	1.3 ± 0.2	1.3 ± 0.1	1.0 ± 0.2	0.8 ± 0.1	1.8 ± 0.5	2.0 ± 0.5
i-15:0	1.0 ± 0.2	0.3 ± 0.1	3.2 ± 0.7	2.9 ± 0.9	0.3 ± 0.1	0.2 ± 0.1	1.9 ± 0.5	4.7 ± 2.2
ai-15:0	0	0	0.3 ± 0.3	0.2 ± 0.1	0	0	13.4 ± 1.9	11.4 ± 3.8
15:0	2.8 ± 0.0	0.6 ± 0.2	0.2 ± 0.2	0.4 ± 0.1	0.8 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.3
i-16:0	1.7 ± 0.2	0.4 ± 0.1	1.3 ± 0.1	1.3 ± 0.4	0	0	1.0 ± 0.2	1.8 ± 0.2
16:0	15.2 ± 0.3	11.3 ± 2.2	14.9 ± 0.8	14.4 ± 1.5	14.8 ± 3.1	14.4 ± 1.2	7.6 ± 0.9	13.7 ± 2.0
i-17:0	7.3 ± 0.2	2.8 ± 1.1	5.6 ± 0.1	5.0 ± 0.4	1.1 ± 0.2	1.3 ± 0.6	0.2 ± 0.4	0.8 ± 0.7
ai-17:0	1.1 ± 0.3	1.4 ± 0.4	1.7 ± 0.5	1.3 ± 0.1	0	0	4.6 ± 1.2	4.2 ± 0.7
17:0	1.4 ± 0.5	0.7 ± 0.6	0	0	1.3 ± 0.1	1.1 ± 0.4	0.5 ± 0.2	0.2 ± 0.3
18:0	9.1 ± 0.4	6.1 ± 0.9	1.5 ± 0.4	1.4 ± 0.2	6.7 ± 0.4	6.1 ± 0.5	8.5 ± 0.2	12.0 ± 1.0
20:0	1.2 ± 0.0	3.5 ± 0.3	0.2 ± 0.2	0.8 ± 0.8	1.3 ± 0.3	0.5 ± 0.7	1.3 ± 0.1	1.1 ± 0.1
21:0	1.1 ± 0.2	1.9 ± 0.1	0.2 ± 0.0	0.1 ± 0.1	0.9 ± 0.3	1.3 ± 0.6	2.0 ± 0.4	1.4 ± 0.2
22:0	2.4 ± 0.1	4.7 ± 0.3	0.8 ± 0.1	0.4 ± 0.4	2.9 ± 0.9	1.5 ± 0.3	5.1 ± 1.4	3.2 ± 0.7
24:0	1.0 ± 0.1	3.8 ± 0.3	16.7 ± 1.3	18.2 ± 1.9	1.8 ± 0.9	1.1 ± 0.3	1.3 ± 0.4	0.6 ± 0.2
Σ SFA	46.2 ± 0.8	39.6 ± 1.5	48.0 ± 2.1	47.7 ± 0.7	33.0 ± 1.5	28.8 ± 0.4	49.5 ± 2.9	57.3 ± 3.2
16:1ω3	0	0	0	0	10.1 ± 2.6	9.8 ± 0.8	0	0.5 ± 0.5
16:1ω7	3.9 ± 0.3	7.7 ± 2.3	6.2 ± 0.4	6.2 ± 0.7	7.2 ± 1.7	9.3 ± 0.7	5.2 ± 1.1	5.7 ± 0.8
16:1ω9	0	0	0.5 ± 0.5	0.3 ± 0.4	0	0	2.2 ± 0.4	2.0 ± 0.2
18:1ω7	5.8 ± 0.1	7.7 ± 0.1	4.5 ± 0.1	4.3 ± 0.0	6.0 ± 0.6	6.3 ± 0.2	9.3 ± 0.4	10.5 ± 1.0
18:1ω9	3.4 ± 0.8	2.3 ± 0.4	1.0 ± 0.0	0.9 ± 0.1	0	0	4.0 ± 0.1	4.0 ± 0.6
20:1ω7	0	0.4 ± 0.3	0	0	0	0	1.9 ± 0.3	1.7 ± 0.1
20:1ω9	1.4 ± 0.6	5.4 ± 0.3	5.7 ± 1.1	5.5 ± 1.0	0	0	0.2 ± 0.2	0.1 ± 0.2
20:1ω11	0	0.1 ± 0.1	0.2 ± 0.2	0	0	0	0.4 ± 0.3	0.8 ± 0.3

Table A3. (cont.)

Fatty acid	Inter-island Between St 4 sp. 1	Nearshore St 9 sp. 1	Inter-island Between St 6 sp. 2	Nearshore St 9 sp. 2	Inter-island Between St 6 sp. 3	Nearshore St 9 sp. 3	Inter-island Between St 6 sp. 4	Nearshore St 10 sp. 4
22:1ω7	1.9 ± 0.1	1.3 ± 0.2	6.8 ± 0.5	6.9 ± 0.8	3.5 ± 0.9	1.0 ± 0.2	0.9 ± 0.7	0.5 ± 0.1
24:1ω9	2.4 ± 0.0	0.9 ± 0.8	2.5 ± 0.3	2.6 ± 0.3	2.4 ± 1.0	1.2 ± 0.6	0.7 ± 0.1	0.3 ± 0.3
Σ MUFA	18.8 ± 0.8	25.8 ± 2.3	27.5 ± 0.7	26.7 ± 0.8	29.1 ± 3.0	27.6 ± 1.2	24.8 ± 0.9	26.3 ± 2.2
16:3ω3	0	0	10.8 ± 0.7	10.5 ± 0.9	5.1 ± 0.9	5.0 ± 0.5	0	0
18:2ω6	0	0	0	0	0	0.2 ± 0.0	1.4 ± 0.1	1.1 ± 0.0
18:3ω6	1.5 ± 0.1	0.5 ± 0.4	0	0	0.8 ± 0.0	0.4 ± 0.5	0.7 ± 0.0	0.7 ± 0.1
18:4ω3	0.3 ± 0.3	4.1 ± 0.6	0.9 ± 0.1	1.0 ± 0.1	1.0 ± 0.2	0.7 ± 0.0	0.9 ± 0.2	0.7 ± 0.1
20:2ω6	4.5 ± 0.2	1.6 ± 0.2	3.4 ± 0.8	3.3 ± 0.1	0	0	1.7 ± 0.2	0.7 ± 0.1
20:2ω9	0.2 ± 0.2	0	0.7 ± 0.1	0.6 ± 0.2	2.9 ± 0.8	2.5 ± 0.1	0	0
20:3ω3	1.5 ± 0.1	0.5 ± 0.4	0	0	3.6 ± 0.4	5.5 ± 0.6	0.1 ± 0.1	0
20:4ω3	0.3 ± 0.2	1.4 ± 0.1	1.0 ± 1.2	1.2 ± 1.2	0.4 ± 0.2	0.2 ± 0.0	1.7 ± 0.4	0.9 ± 0.1
20:4ω6	4.5 ± 0.2	2.5 ± 0.1	2.0 ± 0.1	2.2 ± 0.1	8.5 ± 0.6	10.8 ± 0.2	1.4 ± 0.1	1.3 ± 0.1
20:5ω3	8.3 ± 0.2	5.0 ± 0.2	1.0 ± 0.1	1.1 ± 0.1	5.3 ± 0.5	5.6 ± 0.3	2.0 ± 0.1	1.8 ± 0.2
22:3ω6	0.1 ± 0.2	0.2 ± 0.2	0	0	0.4 ± 0.1	0	2.8 ± 0.2	2.3 ± 0.5
22:4ω6	0	0	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	2.6 ± 0.7	1.2 ± 0.2
22:5ω3	0.8 ± 0.1	0.5 ± 0.1	0	0	1.2 ± 0.3	1.0 ± 0.0	0.3 ± 0.2	0
22:5ω6	0.6 ± 0.1	0.6 ± 0.3	1.4 ± 0.1	1.6 ± 0.2	1.0 ± 0.2	1.2 ± 0.2	1.5 ± 0.5	1.0 ± 0.2
22:6ω3	12.3 ± 0.7	16.6 ± 2.3	2.9 ± 0.2	3.6 ± 0.4	7.2 ± 1.5	8.5 ± 1.4	6.7 ± 1.0	4.4 ± 0.7
Σ PUFA	35.0 ± 0.3	33.4 ± 3.5	24.2 ± 1.5	25.2 ± 0.5	37.4 ± 4.2	41.9 ± 2.8	23.7 ± 3.1	16.3 ± 2.0
Σ EFA	25.2 ± 0.7	24.0 ± 2.5	5.9 ± 0.5	6.9 ± 0.6	20.9 ± 2.6	25.0 ± 1.9	10.1 ± 1.2	7.5 ± 1.0
Σ BAFA	15.3 ± 0.6	5.9 ± 2.2	12.3 ± 0.5	11.1 ± 1.6	3.6 ± 0.3	3.0 ± 0.7	21.9 ± 3.4	23.4 ± 6.6
Σ HPFA	0	0	0	0	0	0.2 ± 0.0	1.4 ± 0.1	1.3 ± 0.2
Σ TFA	4.8 ± 0.4	9.6 ± 1.9	13.8 ± 0.3	14.2 ± 2.1	6.3 ± 2.9	5.6 ± 1.0	6.3 ± 1.3	18.1 ± 3.0

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (μg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A4. Fatty acid composition (mean % TFA ± SD) of the two species of bryozoan at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

	Inter-island			Nearshore		Inter-island	
	Upstream	Between				Between	Downstream
Fatty acid	St 3	St 4	St 6	St 9	St 10	St 6	St 7
	sp. 1	sp. 1	sp. 1	sp. 1	sp. 1	sp. 2	sp. 2
14:0	2.7	1.6	2.7 ± 0.8	2.4 ± 0.9	3.3 ± 0.3	2.8 ± 0.7	0.9 ± 0.1
i-15:0	0.6	0.6	0.7 ± 0.1	0.8 ± 0.4	0.7 ± 0.1	0.4 ± 0.3	0.2 ± 0.2
15:0	1.6	0.9	2.1 ± 0.5	0.8 ± 0.1	1.4 ± 0.4	1.5 ± 0.2	0.7 ± 0.1
16:0	23.4	12.9	15.1 ± 2.2	13.5 ± 0.3	19.7 ± 4.6	20.3 ± 0.2	16.5 ± 2.3
i-17:0	1.0	0	1.6 ± 0.2	0.4 ± 0.8	0.5 ± 0.9	0	1.4 ± 0.3
17:0	4.6	3.7	3.2 ± 0.0	2.4 ± 0.7	3.2 ± 1.4	2.7 ± 0.0	1.4 ± 0.3
18:0	11.1	7.2	6.5 ± 1.2	7.1 ± 2.1	8.5 ± 2.5	7.1 ± 1.5	5.3 ± 1.1
22:0	0.4	0	0.5 ± 0.1	0.5 ± 0.4	0.9 ± 0.3	0.8 ± 0.2	0.1 ± 0.1
Σ SFA	45.4	27.0	32.3 ± 3.0	28.0 ± 1.6	38.3 ± 8.0	35.7 ± 1.2	26.6 ± 3.8
16:1ω7	5.0	2.5	3.8 ± 0.7	3.2 ± 0.5	4.3 ± 0.8	1.3 ± 0.4	2.1 ± 0.4
18:1ω7	2.8	2.6	2.8 ± 0.9	2.3 ± 0.1	3.8 ± 0.3	1.5 ± 0.0	2.3 ± 0.7
18:1ω9	2.4	3.0	3.1 ± 0.7	2.9 ± 0.1	3.4 ± 0.7	3.5 ± 0.4	5.3 ± 1.1
18:1ω11	0.7	0	1.3 ± 0.2	0	0	0	0
20:1ω7	0	0	0	0	0	0.8 ± 0.0	1.2 ± 0.2
20:1ω9	1.2	0	0	0.4 ± 0.6	1.0 ± 0.9	1.7 ± 0.3	2.4 ± 0.5
22:1ω9	0	0	0	0	0	1.1 ± 0.1	1.4 ± 0.1
Σ MUFA	12.2	8.1	11.1 ± 2.4	8.9 ± 1.0	12.5 ± 2.6	10.0 ± 0.2	14.7 ± 1.5
18:2ω6	0.7	3.0	4.0 ± 0.5	3.3 ± 2.0	3.0 ± 1.1	3.7 ± 0.1	0
18:4ω3	0.7	1.0	1.0 ± 0.3	1.0 ± 0.0	0.7 ± 0.1	0.5 ± 0.0	0.2 ± 0.2
20:2ω6	1.7	2.1	1.6 ± 0.0	1.7 ± 0.2	1.7 ± 0.2	2.3 ± 0.2	3.7 ± 0.1
20:2 NMI	10.7	8.5	8.6 ± 1.1	8.4 ± 0.2	7.3 ± 2.7	1.0 ± 0.2	2.0 ± 0.2
20:4ω3	0.7	0	0.4 ± 0.1	0.5 ± 0.5	1.3 ± 0.4	1.0 ± 0.4	0.3 ± 0.3
20:4ω6	4.4	2.8	5.3 ± 1.4	5.5 ± 0.2	8.6 ± 5.3	12.0 ± 0.4	9.6 ± 0.1
20:5ω3	5.3	7.7	6.5 ± 0.6	7.2 ± 0.6	5.3 ± 0.6	9.5 ± 0.6	11.7 ± 0.9
22:2 NMI 1	1.3	0	0.1 ± 0.1	0.2 ± 0.2	1.2 ± 0.2	1.7 ± 0.0	2.4 ± 0.5
22:2 NMI 2	0.3	1.6	1.3 ± 0.3	1.4 ± 0.6	0	3.8 ± 0.1	4.7 ± 1.0
22:3ω6	3.2	0.9	0.5 ± 0.1	0.5 ± 0.5	2.8 ± 0.6	0.6 ± 0.0	0
22:4ω6	1.6	2.8	1.9 ± 0.4	2.2 ± 0.2	1.8 ± 0.1	0.4 ± 0.1	0.7 ± 0.1
22:5ω3	1.2	2.6	2.0 ± 0.1	2.4 ± 0.3	1.3 ± 0.0	0.9 ± 0.1	2.5 ± 0.6
22:5ω6	0.8	2.5	1.6 ± 0.4	2.0 ± 0.3	1.1 ± 0.2	1.1 ± 0.0	1.9 ± 0.4
22:6ω3	8.8	26.7	19.7 ± 1.7	24.0 ± 0.9	10.3 ± 0.2	14.4 ± 1.1	18.4 ± 3.1
Σ PUFA	41.2	62.2	54.4 ± 4.5	60.3 ± 1.9	46.6 ± 4.0	52.9 ± 2.0	58.1 ± 5.1
Σ EFA	18.5	37.2	31.5 ± 2.5	36.7 ± 1.4	24.2 ± 6.2	35.9 ± 1.3	39.7 ± 2.4
Σ BAFA	7.9	5.2	7.5 ± 0.5	4.5 ± 1.1	5.8 ± 1.5	4.6 ± 0.1	3.7 ± 0.4
Σ HPFA	0.7	3.0	4.0 ± 0.5	3.3 ± 2.0	3.0 ± 1.1	3.7 ± 0.1	0
Σ TFA	2.4	1.1	1.4 ± 0.0	1.1 ± 0.2	1.6 ± 0.7	0.6 ± 0.1	0.4 ± 0.2

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (μg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A5. Fatty acid composition (mean % TFA ± SD) of the brachiopod *Magellania kerguelenensis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Inter-island				Nearshore
	Upstream	Between			
	St 3	St 4	St 5	St 6	St 10
16:0	25.4	20.4 ± 1.8	21.9	23.5 ± 2.1	22.4 ± 3.2
i-17:0	1.0	2.1 ± 0.8	0	2.4 ± 0.8	1.1 ± 0.3
17:0	1.9	1.8 ± 0.6	1.4	2.0 ± 0.4	1.6 ± 0.4
18:0	14.1	12.2 ± 1.1	17.2	12.4 ± 1.4	13.9 ± 1.0
20:0	1.4	0	0.9	0	0
21:0	1.9	0	1.3	0	0
22:0	5.0	0.5 ± 0.0	2.5	0	0.6 ± 0.1
Σ SFA	50.8	37.0 ± 1.1	45.3	40.3 ± 1.3	39.6 ± 1.2
16:1ω5	0.2	1.1 ± 0.3	0.7	1.5 ± 0.3	0.3 ± 0.0
18:1ω7	7.7	2.6 ± 0.4	2.2	1.2 ± 0.5	2.8 ± 0.8
18:1ω9	2.3	1.2 ± 0.7	1.3	0.9 ± 0.2	1.5 ± 0.7
20:1ω9	0.7	1.1 ± 0.1	0	0.7 ± 0.1	1.2 ± 0.2
20:1ω11	2.4	4.8 ± 0.7	2.7	4.3 ± 0.3	4.2 ± 0.8
Σ MUFA	13.3	10.8 ± 0.4	6.8	8.6 ± 0.4	10.0 ± 0.3
20:2ω6	1.5	1.6 ± 0.4	1.8	1.4 ± 0.3	1.9 ± 0.4
20:2ω9	8.3	4.9 ± 0.9	4.9	4.6 ± 1.0	5.3 ± 1.0
20:4ω3	0.5	1.6 ± 0.7	1.3	1.4 ± 0.2	1.3 ± 0.3
20:4ω6	3.0	5.4 ± 0.9	3.2	5.3 ± 0.5	5.3 ± 0.7
20:5ω3	6.7	13.0 ± 1.2	13.0	11.3 ± 1.0	13.4 ± 1.4
22:2 NMI 1	1.9	3.5 ± 0.5	2.2	3.9 ± 1.3	3.3 ± 1.0
22:4ω6	0.7	1.4 ± 0.7	1.1	1.6 ± 0.7	1.4 ± 0.8
22:5ω3	0.9	1.7 ± 0.7	1.6	2.0 ± 0.4	1.6 ± 0.2
22:5ω6	0.7	1.2 ± 0.6	0.9	1.2 ± 0.5	1.3 ± 0.2
22:6ω3	8.1	16.0 ± 1.0	16.6	17.3 ± 1.0	14.5 ± 0.9
Σ PUFA	32.3	50.3 ± 1.8	46.4	50.0 ± 1.5	49.2 ± 1.5
Σ EFA	17.7	34.4 ± 1.6	32.8	33.9 ± 1.2	33.2 ± 1.3
Σ BAFA	3.0	3.9 ± 0.2	1.4	4.4 ± 0.4	2.7 ± 0.3
Σ HPFA	0	0	0	0	0
Σ TFA	26.1	17.0 ± 0.9	21.2	10.8 ± 0.4	12.3 ± 0.6

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A6. Fatty acid composition (mean % TFA ± SD) of the bivalves *Limatula pygmaea* and *Thracia meridionalis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

	Inter-island				Inter-island
	Upstream		Between	Downstream	Upstream
Fatty acid	St 1	St 3	St 5	St 7	St 1
	L. pygmaea				*T. meridionalis*
14:0	3.6 ± 0.3	2.8	1.0	4.4	3.2
15:0	2.0 ± 0.1	1.3	0.8	0.7	1.1
16:0	21.3 ± 3.0	18.7	14.6	27.5	20.0
i-17:0	1.4 ± 0.2	0.8	0.7	1.0	0.6
17:0	1.1 ± 0.4	1.0	1.2	1.9	2.1
18:0	9.2 ± 2.3	9.1	13.0	8.4	11.4
Σ SFA	38.5 ± 3.0	33.6	31.3	43.9	38.4
16:1ω5	1.2 ± 0.2	1.0	1.0	0.3	0
16:1ω7	0.4 ± 0.0	1.2	0.4	1.4	1.2
18:1ω7	1.2 ± 0.1	1.7	1.6	4.5	1.3
18:1ω9	0.9 ± 0.1	1.5	1.5	2.4	2.0
20:1ω7	6.7 ± 0.5	5.9	6.3	1.4	3.0
20:1ω11	5.4 ± 0.3	5.5	3.1	1.6	4.9
Σ MUFA	15.9 ± 1.3	16.8	13.9	11.6	12.4
20:2 NMI	1.3 ± 0.1	1.6	1.1	0	0
20:4ω6	3.1 ± 0.2	3.5	3.8	2.5	3.9
20:5ω3	10.4 ± 2.0	11.6	12.6	11.0	11.8
22:2 NMI 1	0	0	0	0	2.3
22:2 NMI 2	1.2 ± 0.3	1.7	0.8	0	7.9
22:3ω6	0.5 ± 0.0	0.6	0.7	0.6	1.9
22:5ω3	1.0 ± 0.1	1.1	1.2	2.8	1.3
22:6ω3	27.2 ± 1.6	26.8	28.0	26.5	15.4
Σ PUFA	44.2 ± 3.7	46.2	47.4	42.9	44.5
Σ EFA	40.7 ± 2.8	41.9	44.3	40.1	31.1
Σ BAFA	4.4 ± 0.4	3.0	2.7	3.6	3.8
Σ HPFA	0	0	0	0	0
Σ TFA	35.7 ± 2.2	36.3	32.2	40.5	39.7

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A7. Fatty acid composition (mean % TFA ± SD) of the polychaete *Serpula vermicularis vermicularis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Nearshore	
	St 9	St 10
14:0	0.5	1.5
16:0	10.8	17.1
i-17:0	1.1	1.4
17:0	1.9	2.2
18:0	8.5	8.7
Σ SFA	22.9	30.8
16:1ω7	4.1	7.7
18:1ω7	1.7	2.1
18:1ω9	2.1	1.6
20:1ω11	13.2	12.4
Σ MUFA	21.1	23.9
18:4ω3	1.9	1.5
20:4ω6	3.9	2.9
20:5ω3	17.7	16.1
22:3ω6	0.8	1.2
22:5ω3	1.5	0.8
22:6ω3	25.7	19.4
Σ PUFA	51.6	41.9
Σ EFA	47.3	38.4
Σ BAFA	3.1	3.6
Σ HPFA	0	0
Σ TFA	40.5	60.9

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A8. Fatty acid composition (mean % TFA ± SD) of the holothurians *Pseudocnus laevigatus and Psolus paradubiosus* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

	Inter-island	Nearshore	Inter-island
	Between		Between
Fatty acid	St 5	St 10	St 6
	P. laevigatus		*P. paradubiosus*
14:0	2.6	10.5	3.6 ± 1.7
ai-15:0	1.3	4.1	5.2 ± 1.4
i-16:0	0	0	3.1 ± 0.3
16:0	4.3	4.4	5.0 ± 0.8
18:0	4.7	4.5	6.0 ± 1.7
20:0	1.9	1.8	1.5 ± 1.1
21:0	0	0	2.1 ± 1.8
22:0	0.8	0.8	2.7 ± 2.4
24:0	0	0	0.8 ± 0.7
Σ SFA	15.5	26.1	30.1 ± 3.4
16:1ω3	0.5	0	1.1 ± 0.1
16:1ω7	9.2	10.2	2.6 ± 0.9
18:1ω7	5.1	4.4	6.0 ± 1.6
18:1ω9	10.7	10.0	3.1 ± 0.6
20:1ω9	3.7	2.8	6.6 ± 0.2
20:1ω11	1.0	1.1	1.5 ± 2.2
22:1ω9	1.7	1.3	1.3 ± 0.9
24:1ω9	1.4	2.2	3.3 ± 2.7
Σ MUFA	33.3	32.0	25.5 ± 2.7
18:2ω6	1.3	0.5	0.3 ± 0.4
18:4ω3	3.9	3.3	1.1 ± 0.8
20:2 NMI	2.4	3.0	6.2 ± 1.5
20:2ω6	1.0	1.0	1.4 ± 0.1
20:4ω3	1.7	1.2	0.4 ± 0.6
20:4ω6	2.4	1.8	6.1 ± 1.6
20:5ω3	29.2	25.9	20.0 ± 2.3
22:5ω6	0	0	1.2 ± 1.3
22:6ω3	4.1	3.1	3.8 ± 0.8
Σ PUFA	46.1	39.7	40.5 ± 6.6
Σ EFA	35.8	30.8	29.9 ± 4.7
Σ BAFA	1.3	4.1	8.3 ± 1.7
Σ HPFA	1.3	0.5	0.3 ± 0.4
Σ TFA	96.1	53.9	2.9 ± 0.5

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (μg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A9. Fatty acid composition (mean % TFA ± SD) of the hydrozoan *Plumularia insignis*, gorgonian coral *Thouarella variabilis* and the sea pen *Pennatula inflata* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

	Inter-island	Inter-island		Inter-island
	Downstream	Upstream	Downstream	Upstream
Fatty acid	St 7	St 2	St 7	St 2
	P. insignis	*T. variabilis*		*P.inflata*
14:0	6.9	2.6	1.7	2.3
16:0	22.0	20.8	8.8	15.1
18:0	6.7	7.5	9.2	3.9
Σ SFA	35.6	30.9	19.6	21.3
16:1ω7	5.0	3.2	3.7	1.5
18:1ω7	3.8	3.2	1.5	2.7
18:1ω9	14.1	10.5	14.9	10.8
20:1ω7	0.3	0.9	2.0	1.5
20:1ω9	3.0	2.3	9.1	6.9
22:1ω9	0.3	0.4	0.9	3.2
22:1ω11	0.8	1.0	1.1	2.2
Σ MUFA	27.2	21.3	33.3	28.8
18:2ω6	1.6	0	0.8	0.5
18:4ω3	3.5	0.9	2.0	0.7
20:3ω3	0	0	0	0
20:4ω3	1.0	0	1.5	0.3
20:4ω6	3.1	5.7	2.4	4.6
20:5ω3	10.2	22.1	19.5	26.5
22:6ω3	11.9	2.1	3.2	4.1
24:6ω3	0	15.4	11.8	9.8
Σ PUFA	31.3	46.1	41.2	46.5
Σ EFA	25.2	29.8	25.1	35.3
Σ BAFA	0	0	0	0
Σ HPFA	1.6	0	0.8	0.5
18:1ω9/18:1ω7	3.7	3.3	9.9	4.1
Σ 22:1ω11+20:1ω9	3.8	3.3	10.2	9.1
Σ TFA	58.9	4.9	14.2	45.7

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A10. Fatty acid composition (mean % TFA ± SD) of the polychaete *Thelepus extensus* at the station where it was collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Nearshore
	St 8
14:0	2.7 ± 0.3
16:0	20.1 ± 1.1
i-17:0	1.6 ± 0.3
18:0	2.9 ± 0.2
Σ SFA	27.3 ± 1.1
16:1ω7	3.9 ± 0.5
18:1ω7	16.5 ± 1.8
18:1ω9	2.3 ± 0.1
18:1ω11	1.8 ± 0.0
20:1ω11	4.1 ± 0.3
Σ MUFA	28.6 ± 2.3
20:2ω9	2.0 ± 0.3
20:4ω6	2.8 ± 0.4
20:5ω3	24.4 ± 0.3
22:5ω3	2.4 ± 0.2
22:6ω3	5.3 ± 1.2
Σ PUFA	36.9 ± 1.6
Σ EFA	32.5 ± 1.8
Σ BAFA	1.6 ± 0.3
Σ HPFA	0
Σ TFA	67.2 ± 5.9

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A11. Fatty acid composition (mean % TFA ± SD) of the polychaete *Lanice marionensis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Inter-island						Nearshore
	Upstream		Between			Downstream	
	St 1	St 3	St 4	St 5	St 6	St 7	St 9
14:0	7.3 ± 0.3	19.4 ± 2.3	13.6	6.0	22.3	5.0	11.8 ± 1.6
15:0	0.5 ± 0.1	1.2 ± 0.2	0.8	0.4	1.7	1.0	0.9 ± 0.1
16:0	18.2 ± 2.1	28.4 ± 3.1	16.2	16.0	21.5	16.9	16.6 ± 1.4
i-17:0	1.3 ± 0.4	1.0 ± 0.1	1.2	0.7	1.2	1.3	1.1 ± 0.2
18:0	5.4 ± 0.9	4.2 ± 0.3	5.0	6.8	4.0	4.8	3.7 ± 0.5
Σ SFA	32.6 ± 1.8	54.1 ± 3.4	36.9	29.8	50.7	29.0	34.1 ± 2.4
16:1ω7	8.4 ± 0.8	14.5 ± 0.5	6.6	6.7	9.8	4.0	9.2 ± 1.1
18:1ω7	4.5 ± 1.0	3.8 ± 0.7	4.5	4.7	3.7	5.2	4.0 ± 0.8
18:1ω9	1.9 ± 0.6	1.8 ± 0.3	1.6	1.8	1.8	4.1	2.1 ± 0.3
18:1ω11	1.6 ± 0.4	1.3 ± 0.2	1.4	1.9	1.2	1.1	1.2 ± 0.1
20:1ω9	1.0 ± 0.2	0.5 ± 0.1	0.6	0.6	0	1.4	0.7 ± 0.3
20:1ω11	1.3 ± 0.4	0.6 ± 0.3	1.0	0.8	0	0.8	0.9 ± 0.3
Σ MUFA	18.7 ± 1.4	22.5 ± 3.0	15.7	16.6	16.5	16.7	18.0 ± 1.1
18:4ω3	1.2 ± 0.5	0.9 ± 0.1	1.1	1.6	1.1	0.9	1.8 ± 0.6
20:2ω9	0.2 ± 0.0	0	0	1.3	0	0.5	0
20:4ω3	0.9 ± 0.4	0.8 ± 0.1	1.1	1.0	1.5	1.1	1.0 ± 0.2
20:4ω6	0.7 ± 0.1	0.4 ± 0.0	1.1	1.3	0	1.3	0.7 ± 0.1
20:5ω3	18.5 ± 1.0	10.6 ± 1.2	20.7	25.4	16.5	18.2	21.4 ± 1.9
22:4ω6	1.6 ± 0.8	0.5 ± 0.1	1.7	1.2	0.8	1.5	1.1 ± 0.3
22:5ω3	11.2 ± 2.6	3.6 ± 1.4	8.6	8.5	5.4	8.2	8.5 ± 1.0
22:5ω6	0.4 ± 0.1	0.0 ± 0.0	0.5	0.3	0	1.1	0.4 ± 0.0
22:6ω3	9.1 ± 1.6	2.7 ± 0.2	8.3	8.3	5.5	15.5	8.1 ± 2.0
Σ PUFA	44.0 ± 3.3	19.4 ± 1.4	43.0	48.9	30.6	48.5	42.9 ± 3.0
Σ EFA	28.4 ± 2.4	13.7 ± 1.3	30.1	34.9	21.9	35.0	30.2 ± 1.8
Σ BAFA	1.7 ± 0.3	2.2 ± 0.2	2.0	1.0	2.9	2.3	2.0 ± 0.1
Σ HPFA	0	0	0	0	0	0	0
Σ TFA	39.3 ± 2.5	147.8 ± 7.1	81.4	118.3	107.6	73.0	94.7 ± 4.8

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A12. Fatty acid composition (mean % TFA ± SD) of the gastropod *Margarella expansa* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Inter-island	Nearshore
	Upstream	
	St 1	St 8
14:0	0.8	1.1
16:0	9.0	19.1
i-17:0	1.1	1.5
17:0	1.4	1.6
18:0	8.8	6.0
20:0	1.1	0
Σ SFA	25.4	31.4
16:1ω7	1.0	6.0
18:1ω7	4.5	13.3
18:1ω9	2.1	4.6
20:1ω7	1.0	0.9
20:1ω11	1.9	2.3
Σ MUFA	11.9	28.0
18:2ω6	3.6	2.2
20:2ω6	2.2	1.3
20:4ω6	10.4	6.7
20:5ω3	18.6	17.9
22:2 NMI 1	3.7	0.6
22:2 NMI 2	5.0	2.8
22:4ω6	1.3	0.4
22:5ω3	4.6	3.0
22:6ω3	9.7	4.0
Σ PUFA	62.6	40.6
Σ EFA	38.6	28.6
Σ BAFA	5.3	4.8
Σ HPFA	3.6	2.7
Σ TFA	15.3	43.4

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A13. Fatty acid composition (mean % TFA ± SD) of the size classes of the hyperbenthic shrimp *Nauticaris marionis* at the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Inter-island						
	Upstream						
	St 1			St 3			
	III 7.0-8.0 mm	IV 8.5-9.5 mm	V 10.0-11.0 mm	II 5.5-6.5 mm	III 7.0-8.0 mm	IV 8.5-9.5 mm	V 10.0-11.0 mm
14:0	1.1 ± 0.1	1.4 ± 0.3	1 ± 0.1	1.2 ± 0.3	1.8 ± 0.5	1.9 ± 0.5	1 ± 0.3
15:0	0.7 ± 0.1	0.6 ± 0.2	0.6 ± 0	0.5 ± 0	0.7 ± 0.1	0.6 ± 0.1	0.7 ± 0.2
16:0	23.6 ± 1.2	20 ± 0.3	21.7 ± 1.3	21.4 ± 1.8	23.2 ± 0.1	22.4 ± 0.6	22.2 ± 1.1
i-17:0	0.7 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	0.5 ± 0	0.7 ± 0.1	0.7 ± 0.1	0.3 ± 0.5
17:0	0.9 ± 0.1	0.7 ± 0.2	0.8 ± 0.2	1 ± 0.1	0.9 ± 0	1 ± 0.2	0.9 ± 0.1
18:0	4.1 ± 0.1	4.1 ± 0.2	4.8 ± 0.6	4.5 ± 0.5	5.4 ± 0.9	4.8 ± 0.8	3.8 ± 0.4
22:0	0.4 ± 0.6	0.4 ± 0.7	0.8 ± 0.4	0.5 ± 0.1	0 ± 0	0.5 ± 0.2	0.3 ± 0.5
Σ SFA	32.2 ± 1.5	28.2 ± 0.5	31.3 ± 2.2	30.7 ± 2.8	33 ± 1	32.8 ± 0.7	29.4 ± 0.9
16:1ω7	5.3 ± 0.7	3.3 ± 0.3	4.9 ± 0.6	4.6 ± 0.5	4.7 ± 0.4	3.9 ± 0.6	4 ± 0.1
18:1ω7	7.3 ± 1	6.6 ± 0.5	6.8 ± 0.7	6 ± 0.9	7.2 ± 0.2	6.6 ± 0.5	7.8 ± 0.4
18:1ω9	5.6 ± 4.4	9.5 ± 0.9	9.5 ± 1.8	9.3 ± 1.2	10.9 ± 0	10.4 ± 0.6	9.8 ± 1
20:1ω7	0.4 ± 0	0 ± 0	0.5 ± 0.1	0.2 ± 0.4	0 ± 0	0.4 ± 0.1	0.2 ± 0.4
Σ MUFA	19.7 ± 3.1	20.7 ± 2.1	22.8 ± 2.7	20.6 ± 2.8	23.1 ± 0.3	22 ± 1.6	23 ± 1.7
18:2ω6	0.7 ± 0.3	1.3 ± 0.3	0.8 ± 0.6	1.1 ± 0.1	1.1 ± 0.2	1 ± 0.1	1.1 ± 0.1
20:4ω6	5.7 ± 1.3	4.2 ± 0.7	4.9 ± 0.5	5.6 ± 0.4	4.1 ± 0	2.7 ± 0.1	4.8 ± 1.1
20:5ω3	20.3 ± 0.6	20 ± 1	18.8 ± 1.3	19.4 ± 1.3	20.4 ± 0.6	20.9 ± 0.5	19.2 ± 1.3
22:4ω6	0.2 ± 0.4	0.2 ± 0.4	0.2 ± 0.3	0.1 ± 0.2	0.2 ± 0.3	0.1 ± 0.2	0.2 ± 0.4
22:5ω3	2.2 ± 0.2	4.1 ± 0.1	1.6 ± 0	2.3 ± 0.7	1.9 ± 0.2	2.2 ± 0.3	1.7 ± 0.4
22:5ω6	1.1 ± 0.5	0.8 ± 0.3	0.9 ± 0.1	1.1 ± 0.1	0.2 ± 0.4	0.6 ± 0.3	0.6 ± 0
22:6ω3	16 ± 1	19.6 ± 0.1	17.2 ± 1.5	17.6 ± 1.4	14.9 ± 0.2	16 ± 1.6	18.1 ± 0.9
Σ PUFA	47.4 ± 1.7	50.6 ± 1.8	45.4 ± 0.6	47.9 ± 0.7	43.2 ± 1.4	44.7 ± 1.2	46.7 ± 2.2
Σ EFA	42.1 ± 2.9	43.8 ± 1.7	40.9 ± 2.3	42.6 ± 0.3	39.4 ± 0.4	39.6 ± 1	42.1 ± 3.3
Σ BAFA	2.9 ± 0.5	2.1 ± 0	2.4 ± 0.3	2.5 ± 0.2	2.4 ± 0.1	2.5 ± 0.7	1.9 ± 0.7
Σ HPFA	0.7 ± 0.3	1.3 ± 0.3	0.8 ± 0.6	1.1 ± 0.1	1.1 ± 0.2	1.2 ± 0.2	1.1 ± 0.1
18:1ω9/18:1ω7	0.8 ± 0.7	1.4 ± 0	1.4 ± 0.1	1.6 ± 0	1.5 ± 0	1.6 ± 0	1.3 ± 0.2
Σ 22:1ω11+20:1ω9	0.6 ± 0.2	0.8 ± 0	0.6 ± 0.2	0.2 ± 0.4	0 ± 0	0.6 ± 0	0.4 ± 0
Σ TFA	47.6 ± 1.7	44.4 ± 1	33.7 ± 0.3	52.1 ± 8.4	64.2 ± 6.5	58.6 ± 11.8	33.7 ± 2.4

Table A13. (cont.)

Fatty acid	Inter-island						
	Between						
	St 4				St 5		
	II	III	IV	V	II	III	IV
	5.5-6.5 mm	7.0-8.0 mm	8.5-9.5 mm	10.0-11.0 mm	5.5-6.5 mm	7.0-8.0 mm	8.5-9.5 mm
14:0	2.5 ± 0.3	2.5 ± 0.5	2.6 ± 0.4	2.3 ± 0.4	1.2 ± 0.3	1.8 ± 0.7	1.5 ± 0.5
15:0	0.4 ± 0.1	0.8 ± 0.3	0.8 ± 0.2	0.7 ± 0.2	0.5 ± 0.2	0.7 ± 0.2	0.6 ± 0.2
16:0	21.3 ± 0.8	24.3 ± 0.7	22.0 ± 1.0	19.8 ± 0.8	20.3 ± 0	23.1 ± 1.7	20.7 ± 1
i-17:0	0.8 ± 0.2	0.6 ± 0.2	0.6 ± 0.2	0.8 ± 0.1	0.1 ± 0.1	0.5 ± 0.2	0.3 ± 0.5
17:0	0.8 ± 0.2	0.9 ± 0.1	0.8 ± 0.2	1 ± 0.1	0.8 ± 0	0.9 ± 0.1	0.9 ± 0
18:0	4.2 ± 0.3	4.2 ± 0.4	4.3 ± 0.3	3.8 ± 0.3	4.6 ± 0.3	5.1 ± 0.5	5.7 ± 1.4
22:0	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0	0.3 ± 0.1	0.4 ± 0.3	0 ± 0.1	0.2 ± 0.3
Σ SFA	30.4 ± 1	33 ± 1.1	31.5 ± 0.6	29 ± 1.9	29.6 ± 3.3	33 ± 4	30.5 ± 2.4
16:1ω7	3.8 ± 0.7	4.1 ± 0.5	4.9 ± 0.4	4.9 ± 0.8	4.5 ± 0.6	5.3 ± 0.2	5.6 ± 0.1
18:1ω7	6.8 ± 0.6	7.7 ± 0.4	7.5 ± 0.5	7.5 ± 0.9	5.6 ± 2.1	7.2 ± 0.5	7.4 ± 0.3
18:1ω9	8.4 ± 0.3	9.1 ± 0.6	10 ± 0.6	9.9 ± 0.5	8.9 ± 1.1	10.2 ± 0.4	9.8 ± 0.5
20:1ω7	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	0.6 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.2
Σ MUFA	19.5 ± 1.3	21.3 ± 0.6	22.9 ± 0.7	23.4 ± 2.6	19.8 ± 4.2	23.8 ± 1.2	23.1 ± 0.8
18:2ω6	0.8 ± 0.4	0.9 ± 0.2	0.9 ± 0.1	0.9 ± 0.1	0.8 ± 0.6	1.2 ± 0.1	1.4 ± 0.3
20:4ω6	4.5 ± 0.5	4.3 ± 0.3	5 ± 0.5	6 ± 0.4	5 ± 0.1	4.3 ± 1.3	5.4 ± 0.2
20:5ω3	20.5 ± 0.6	19.9 ± 1	19.6 ± 1.3	19.1 ± 0.4	24.7 ± 2.4	19.8 ± 1.1	21.5 ± 0.3
22:4ω6	0.2 ± 0.3	0.3 ± 0.2	0.2 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.2	0.4 ± 0.7
22:5ω3	3.6 ± 0.4	2.5 ± 0.4	1.7 ± 0.3	1.4 ± 0.2	0.5 ± 0.7	1.3 ± 0.1	0.4 ± 0.7
22:5ω6	0.4 ± 0.2	0.3 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.7 ± 0.2	0.6 ± 0	0.6 ± 0.2
22:6ω3	16.5 ± 0.5	14.2 ± 1	15.4 ± 0.6	15.2 ± 1.2	17.3 ± 1.4	14 ± 1.6	14.5 ± 0.4
Σ PUFA	46.9 ± 2	39.8 ± 3.7	40.2 ± 4.3	43.6 ± 2	50.5 ± 1	42.6 ± 5.1	45 ± 2.1
Σ EFA	41.4 ± 1.6	35.5 ± 2.4	36.7 ± 3.4	40.3 ± 1.3	47 ± 3.6	38 ± 4	41.5 ± 0.5
Σ BAFA	2.1 ± 0.2	1.8 ± 0.7	2.3 ± 0.3	2.6 ± 0.4	2 ± 1.3	2.7 ± 1.1	1.8 ± 0.7
Σ HPFA	0.9 ± 0.5	1 ± 0.3	1 ± 0.2	1 ± 0.2	1.1 ± 0.7	1.3 ± 0.3	1.6 ± 0.2
18:1ω9/18:1ω7	1.3 ± 0.1	1.2 ± 0.1	1.3 ± 0.2	1.3 ± 0.1	1.7 ± 0.4	1.4 ± 0	1.3 ± 0.1
Σ 22:1ω11+20:1ω9	0.6 ± 0.3	0.6 ± 0.1	0.6 ± 0.2	0.7 ± 0.3	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.3
Σ TFA	58.6 ± 11.8	52.1 ± 8.4	64.2 ± 6.5	33.7 ± 2.4	64.7 ± 11.7	73.1 ± 9	52 ± 12.3

Table A13. (cont.)

Fatty acid	Inter-island						
	Between					Downstream	
	St 6					St 7	
	I	II	III	IV	V	II	V
	4.0-5.0 mm	5.5-6.5 mm	7.0-8.0 mm	8.5-9.5 mm	10.0-11.0 mm	5.5-6.5 mm	10.0-11.0 mm
14:0	2.4	2 ± 0.1	2.8 ± 0.4	2.5 ± 0	2.5 ± 1.1	2.1	1.5 ± 0.3
15:0	0.7	0.7 ± 0.2	0.7 ± 0.2	0.8 ± 0.2	0.7 ± 0.2	2.6	0.7 ± 0.3
16:0	23.1	18.9 ± 1.3	20.6 ± 1.7	21.1 ± 1.7	25.7 ± 0.6	20.4	23 ± 0.8
i-17:0	0.7	0.9 ± 0	0.7 ± 0.1	1.3 ± 0.6	0.7 ± 0.2	0.8	0.7 ± 0.3
17:0	0.9	1.1 ± 0.5	1.1 ± 0.3	2 ± 1	0.9 ± 0.3	1.4	1 ± 0.1
18:0	4.3	4.9 ± 1.5	7 ± 2.5	4.4 ± 0.4	4.2 ± 0.8	4.5	5.3 ± 1.5
22:0	0.3	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 1	0.2 ± 0.2	0.0	0.5 ± 0.1
Σ SFA	32.7	30.4 ± 4.8	35 ± 2.9	33.4 ± 2.4	35.3 ± 1	32.6	33.6 ± 4
16:1ω7	3.5	3.4 ± 0.2	4.8 ± 0.3	4.1 ± 0.5	4.9 ± 1	5.4	4.3 ± 1.6
18:1ω7	6.1	5.8 ± 0.5	6.3 ± 0.8	5.5 ± 0.8	7.1 ± 1.1	8.0	6.5 ± 1.5
18:1ω9	7.8	7.4 ± 0.4	9.3 ± 1.3	9.3 ± 0.8	10.5 ± 1.2	10.4	8.5 ± 1.8
20:1ω7	0.1	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.2	0.1 ± 0.2	0.0	0 ± 0
Σ MUFA	18.8	20.1 ± 0.2	22.1 ± 2.5	20.4 ± 2.1	23.8 ± 2.7	24.6	19.6 ± 2
18:2ω6	0.7	0.4 ± 0.2	0.2 ± 0.4	0.5 ± 0.5	0.7 ± 0.1	1.0	0.5 ± 0.7
20:4ω6	3.7	3 ± 0.2	4.2 ± 0.7	3.3 ± 0.5	3.3 ± 0.6	4.0	5.4 ± 0
20:5ω3	20.4	19.3 ± 0.3	18 ± 1	18.5 ± 0.3	17.4 ± 1.5	20.2	19.6 ± 0.8
22:4ω6	0.5	0.3 ± 0.5	0.2 ± 0.3	0.2 ± 0.3	0.4 ± 0.1	0.0	0.3 ± 0.4
22:5ω3	3.9	5.5 ± 0.6	2.8 ± 0.3	2.8 ± 0.3	2.2 ± 0.5	0.7	1.7 ± 0.2
22:5ω6	0.8	1 ± 0.1	0.8 ± 0.2	0.8 ± 0.2	0.7 ± 0.3	0.0	0.5 ± 0.6
22:6ω3	17.1	19.3 ± 1.7	15.1 ± 0.9	18.7 ± 0.7	15.4 ± 2	16.2	18.5 ± 0.4
Σ PUFA	48.6	49.5 ± 4.5	42.1 ± 1.1	45 ± 0.8	40.8 ± 2.1	42.9	46.8 ± 2
Σ EFA	41.2	41.5 ± 2.1	37.3 ± 0.6	40.5 ± 0.2	36.2 ± 2.1	40.4	43.5 ± 1.2
Σ BAFA	2.6	3.6 ± 1.3	3.2 ± 0.9	4.5 ± 2.1	2.6 ± 1	5.5	3.1 ± 1.6
Σ HPFA	1.1	0.5 ± 0.4	0.3 ± 0.6	0.5 ± 0.5	0.8 ± 0.2	1.0	0.6 ± 0.8
18:1ω9/18:1ω7	1.3	1.3 ± 0	1.5 ± 0	1.7 ± 0.1	1.5 ± 0.3	1.3	1.3 ± 0
Σ 22:1ω11+20:1ω9	0.9	1.1 ± 0.2	0.6 ± 0.3	0.9 ± 0	0.7 ± 0.1	0.5	0.3 ± 0.4
Σ TFA	47.4	45.7 ± 13.2	61 ± 5.8	40.9 ± 5.3	34.2 ± 1.5	59.0	33 ± 4.5

Table A13. (cont.)

Fatty acid	Nearshore						
	St 8				St 9		
	I 4.0-5.0 mm	II 5.5-6.5 mm	IV 8.5-9.5 mm	V 10.0-11.0 mm	II 5.5-6.5 mm	III 7.0-8.0 mm	IV 8.5-9.5 mm
14:0	1.9	1.5 ± 0.2	1.6 ± 0.5	1.4 ± 0.1	2.9 ± 0.3	3.2 ± 0.4	2.3 ± 0.2
15:0	0.7	0.6 ± 0.1	0.7 ± 0	0.8 ± 0.1	0.7 ± 0.1	0.9 ± 0	0.8 ± 0.1
16:0	16.1	21.6 ± 2.1	23.3 ± 2.4	21.1 ± 0.8	23.1 ± 1.4	23.4 ± 1	14.7 ± 0.9
i-17:0	0.7	0.6 ± 0.2	0.5 ± 0.2	0.7 ± 0.1	0.7 ± 0.1	0.8 ± 0	0.7 ± 0.3
17:0	0.9	0.9 ± 0.2	0.2 ± 0.3	1.2 ± 0.3	1 ± 0.1	1 ± 0	0.8 ± 0
18:0	4.1	4.3 ± 0.2	3.3 ± 2.8	4.3 ± 1.1	4.4 ± 1	4.1 ± 0.4	3.5 ± 0.4
22:0	0.5	0.2 ± 0.1	0.2 ± 0.3	0.4 ± 0.2	0.5 ± 0.2	0 ± 0	0.6 ± 0.1
Σ SFA	26.5	30.2 ± 2	30.4 ± 4.7	31 ± 3	34.5 ± 1.5	34.5 ± 1.3	25.1 ± 1.5
16:1ω7	6.3	5.5 ± 0.6	4.6 ± 0.2	4.2 ± 0.2	4.6 ± 0.5	4.4 ± 0.4	4.4 ± 0.3
18:1ω7	7.5	7.3 ± 0.3	7.6 ± 0.8	7.1 ± 0.1	6.4 ± 0	6.2 ± 0.4	5.2 ± 0.6
18:1ω9	8.8	10.7 ± 0.4	10.5 ± 0.8	10.7 ± 1	8.2 ± 0.9	8.9 ± 1.3	8.2 ± 1.3
20:1ω7	0.8	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.2	0 ± 0	0.1 ± 0.1	0.2 ± 0
Σ MUFA	25.5	24.6 ± 1	22.9 ± 2.2	22.6 ± 0.4	20 ± 0.3	19.9 ± 2.6	18.9 ± 2.3
18:2ω6	1.5	2 ± 0.2	1.1 ± 0.3	1.3 ± 0	0.9 ± 0.1	0.3 ± 0.6	0.7 ± 0.2
20:4ω6	5.1	5.2 ± 0.1	5.7 ± 0.6	4.4 ± 0.3	3.2 ± 0.2	4 ± 0.4	3.7 ± 0.2
20:5ω3	17.7	20.1 ± 0.9	20.6 ± 1.3	19.1 ± 1.8	19.4 ± 0.4	19.9 ± 0.5	22 ± 0.8
22:4ω6	0.4	0.3 ± 0.1	0.3 ± 0.5	0.5 ± 0.1	0.1 ± 0.2	0.1 ± 0.2	0.2 ± 0.3
22:5ω3	0.9	0.7 ± 0.1	1.2 ± 0.1	0.9 ± 0.1	2.2 ± 0.1	2 ± 0.1	3 ± 0.2
22:5ω6	0.6	0.4 ± 0.1	0.5 ± 0.2	0.7 ± 0.2	0.8 ± 0.2	0.8 ± 0.2	0.9 ± 0
22:6ω3	18.4	13.8 ± 1.7	13.6 ± 0.8	17.4 ± 1.4	17.6 ± 0.2	16.5 ± 1	23.7 ± 0.5
Σ PUFA	47.9	45.2 ± 2.9	44.2 ± 1.5	45.6 ± 3.1	44.8 ± 1.3	44.3 ± 1.8	55.1 ± 1.2
Σ EFA	41.3	39.2 ± 2.6	39.9 ± 0.1	40.8 ± 2.8	40.2 ± 0.5	40.4 ± 1.9	49.4 ± 1.1
Σ BAFA	3.2	2.2 ± 0.1	1.5 ± 0.3	3.2 ± 0.8	3.3 ± 1	3.2 ± 0.4	3.3 ± 1.3
Σ HPFA	2.1	2.7 ± 0.2	1.2 ± 0.5	1.5 ± 0.3	1 ± 0.3	0.4 ± 0.7	0.8 ± 0.3
18:1ω9/18:1ω7	1.2	1.5 ± 0	1.4 ± 0.1	1.5 ± 0.2	1.3 ± 0.1	1.4 ± 0.1	1.6 ± 0.1
Σ 22:1ω11+20:1ω9	1.0	0.4 ± 0.1	0.1 ± 0.2	0.1 ± 0.2	0.5 ± 0.2	0.2 ± 0.3	0.5 ± 0.3
Σ TFA	67.0	72.6 ± 15.8	81 ± 15.1	34.1 ± 1.3	64.8 ± 12.5	55.4 ± 1.8	33.4 ± 8.8

Table A13. (cont.)

Fatty acid	Nearshore		
	St 10		
	II	III	IV
	5.5-6.5 mm	7.0-8.0 mm	8.5-9.5 mm
14:0	1.5 ± 0.3	1.3 ± 0.2	1.4 ± 0
15:0	1.1 ± 0.5	0.7 ± 0.1	0.8 ± 0.1
16:0	22.1 ± 0.2	23.4 ± 1	18.8 ± 1.4
i-17:0	0.8 ± 0.3	0.5 ± 0.1	0.7 ± 0.2
17:0	1.2 ± 0.1	0.9 ± 0.4	0.9 ± 0.1
18:0	4.5 ± 1	3.6 ± 0.1	3.1 ± 0.1
22:0	0.6 ± 0.1	0.4 ± 0.1	0.1 ± 0.3
Σ SFA	32.8 ± 2	31.2 ± 0.5	26.7 ± 1.4
16:1ω7	3.4 ± 0.1	4.7 ± 0.3	4.5 ± 0.3
18:1ω7	6.1 ± 0.2	5.5 ± 1.1	7.6 ± 0.8
18:1ω9	8.4 ± 0.1	9.3 ± 0.1	9.7 ± 1.2
20:1ω7	0.1 ± 0.2	0.9 ± 0.5	0.5 ± 0
Σ MUFA	18.6 ± 1.6	21.2 ± 0.6	23.6 ± 2.3
18:2ω6	1.4 ± 0.1	1.4 ± 0	1.3 ± 0.1
20:4ω6	5 ± 0.1	5.5 ± 1.1	4.5 ± 0.2
20:5ω3	19 ± 1.6	20.2 ± 0.3	19.4 ± 0.4
22:4ω6	0.2 ± 0.3	0.1 ± 0.2	0 ± 0
22:5ω3	2.6 ± 0.3	2 ± 0.3	2.1 ± 0
22:5ω6	1.2 ± 0.4	0.7 ± 0	0.6 ± 0.1
22:6ω3	17.7 ± 1	15.5 ± 0.2	20.3 ± 0.1
Σ PUFA	47.9 ± 0.7	47 ± 0.9	49.4 ± 1
Σ EFA	41.7 ± 0.5	41.2 ± 1	44.2 ± 0.3
Σ BAFA	3.5 ± 0.7	2.4 ± 1.1	2.8 ± 0.2
Σ HPFA	1.4 ± 0.1	1.4 ± 0	1.3 ± 0.1
18:1ω9/18:1ω7	1.4 ± 0	1.8 ± 0.4	1.3 ± 0
Σ 22:1ω11+20:1ω9	0.1 ± 0.3	0.6 ± 0.1	0.6 ± 0
Σ TFA	43.1 ± 5.5	58.2 ± 8.7	42.1 ± 6.6

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A14. Fatty acid composition (mean % TFA ± SD) of the detritus at the stations where it was collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Inter-island				Nearshore	
	Upstream		Between			
	St 1	St 3	St 5	St 6	St 9	St 10
14:0	2.5 ± 0.7	3.3 ± 0.5	2.3 ± 0.7	2.1 ± 0.3	2.1 ± 1.0	2.3 ± 0.6
i-15:0	0.7 ± 0.1	3.2 ± 0.7	0.4 ± 0.1	0.7 ± 0.2	0.5 ± 0.1	0.5 ± 0.1
15:0	1.4 ± 0.4	2.1 ± 0.4	1.3 ± 0.4	1.4 ± 0.2	1.2 ± 0.3	0.9 ± 0.3
16:0	10.4 ± 1.0	17.6 ± 1.2	5.8 ± 0.4	10.9 ± 0.7	4.7 ± 0.4	12.3 ± 0.9
i-17:0	1.0 ± 0.1	1.9 ± 0.4	0	2.5 ± 0.4	0.6 ± 0.2	1.5 ± 0.3
17:0	1.1 ± 0.3	0	0.5 ± 0.1	1.6 ± 0.3	0.6 ± 0.0	1.4 ± 0.3
i-18:0	1.1 ± 0.2	0	0.7 ± 0.4	1.0 ± 0.3	0.5 ± 0.2	0
18:0	8.8 ± 0.8	5.7 ± 0.3	4.7 ± 0.2	7.4 ± 0.4	6.6 ± 0.4	5 ± 0.3
20:0	1.4 ± 0.3	0	1.2 ± 0.2	3.2 ± 0.2	0.7 ± 0.1	0
22:0	0.6 ± 0.1	0	0.5 ± 0.0	1.8 ± 0.3	0	0
Σ SFA	29.7 ± 3.4	33.7 ± 3.6	17.7 ± 2.2	33.2 ± 3.4	19.4 ± 2	24.3 ± 2.3
16:1ω7	3.4 ± 1.1	3.1 ± 0.5	2.9 ± 1.1	3.4 ± 1.6	1.1 ± 0.3	4.1 ± 2.3
18:1ω7	2.2 ± 0.6	2.5 ± 0.7	0.8 ± 0.2	3.2 ± 0.9	0.7 ± 0.1	2.8 ± 0.9
18:1ω9	3.0 ± 0.9	2.1 ± 0.6	1.0 ± 0.3	2.2 ± 0.8	1.4 ± 0.4	2.1 ± 0.6
18:1ω11	0	0	0	0	0	1.4 ± 0.7
20:1ω9	0.8 ± 0.2	0.6 ± 0.1	0.3 ± 0.0	1.0 ± 0.3	0	1.4 ± 0.4
20:1ω11	1.1 ± 0.5	1.0 ± 0.5	0.6 ± 0.3	2.3 ± 0.8	0	1.9 ± 0.8
Σ MUFA	12.2 ± 2.3	9.4 ± 2.1	6.7 ± 0.9	15.3 ± 2.6	3.2 ± 0.7	13.7 ± 3.3
16:2ω6	1.2 ± 0.3	0	0.7 ± 0.2	2.0 ± 0.4	0	1.3 ± 0.2
18:2ω6	1.1 ± 0.4	0	1.0 ± 0.2	0	1.1 ± 0.2	0
18:4ω3	1.0 ± 0.2	0	1.0 ± 0.2	1.1 ± 0.3	0	1.3 ± 0.2
20:2 NMI	1.3 ± 0.8	3.2 ± 1.8	0.4 ± 0.2	2.7 ± 1.6	0	4.9 ± 1.7
20:2ω6	0.9 ± 0.2	0	0	2.0 ± 0.6	0	2.0 ± 0.4
20:3ω6	0	0	0	0.6 ± 0.4	0	1.7 ± 0.9
20:4ω3	0	0	0	0	0	2.4 ± 0.6
20:4ω6	15.5 ± 2.2	21.8 ± 3.4	30.2 ± 5.6	9.5 ± 2	41.3 ± 9.2	6.6 ± 1.1
20:5ω3	8.7 ± 0.9	9.7 ± 1.0	12.2 ± 1.0	6.0 ± 0.9	6.9 ± 0.5	9.8 ± 1.2
22:2 NMI 1	0.6 ± 0.2	0	0	3.3 ± 0.7	0	3 ± 0.6
22:2 NMI 2	0	0	0	1.1 ± 0.8	0	0
22:2ω6	0	0	0	0	1.7 ± 0.6	0
22:3ω6	0	0	0	1.1 ± 0.6	0	0
22:4ω6	1.9 ± 0.8	1.7 ± 0.5	1.6 ± 0.7	2.5 ± 0.9	1.8 ± 0.3	2.1 ± 0.6
22:5ω3	2.6 ± 1.0	1.4 ± 0.7	1.2 ± 0.6	1.9 ± 0.3	1.4 ± 0.3	2.5 ± 0.9
22:5ω6	4.0 ± 1.5	2.9 ± 1.3	6.7 ± 1.1	4.5 ± 1.0	5.7 ± 1.0	2.1 ± 0.9
22:6ω3	18.8 ± 1.6	16.1 ± 1.5	20 ± 2.0	12.2 ± 2.1	16.8 ± 1.5	22.2 ± 1.9
Σ PUFA	58.1 ± 10.4	56.9 ± 9.6	75.6 ± 11.4	51.5 ± 12.1	77.4 ± 13.9	62.0 ± 10.5
Σ EFA	42.9 ± 5.0	47.6 ± 5.7	62.4 ± 7.8	27.8 ± 5.0	65 ± 10.1	38.6 ± 4.4
Σ BAFA	6.0 ± 0.4	7.2 ± 1.1	3.3 ± 0.5	7.9 ± 0.9	4.2 ± 0.5	4.6 ± 0.4
Σ HPFA	1.1 ± 0.4	0	1.0 ± 0.4	0	1.1 ± 0.5	0
Σ TFA	2 ± 0.3	4.6 ± 0.8	6 ± 1.2	0.9 ± 0.1	3.6 ± 0.8	1.3 ± 0.3

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (μg FA mg^{-1} DM); NMI: nonmethylene interrupted

Table A15. Fatty acid composition (mean % TFA ± SD) of the three size fractions of zooplankton for the stations where they were collected. Data represent all fatty acids at concentrations >1% TFA in at least one sample.

Fatty acid	Inter-island		
	small <500 µm	medium 500-1500 µm	large >1500 µm
14:0	9.8 ± 6.1	2.9 ± 0.7	1.6 ± 0.2
i-15:0	1.8 ± 0.7	0.3 ± 0.1	0.2 ± 0.0
15:0	2.7 ± 1.5	0.5 ± 0.1	0.4 ± 0.1
16:0	47.4 ± 11.4	14.6 ± 4.7	13.7 ± 1.6
i-17:0	0.9 ± 0.6	0.4 ± 0.3	0.3 ± 0.1
17:0	3.0 ± 0.9	0.6 ± 0.2	0.7 ± 0.2
i-18:0	1.2 ± 0.1	0.4 ± 0.1	0.4 ± 0.1
18:0	15.2 ± 5.5	3.6 ± 0.8	2.5 ± 0.6
20:0	2.1 ± 1.1	0.9 ± 0.2	0.8 ± 0.3
22:0	6.1 ± 6.7	0.6 ± 0.1	0.5 ± 0.2
24:0	2.8 ± 3.9	0	0
Σ SFA	95.6 ± 1.6	25.2 ± 7.0	21.2 ± 2.9
16:1ω7	0	3.9 ± 1.0	4.0 ± 0.2
17:1ω7	0	0.9 ± 0.4	0.7 ± 0.1
18:1ω7	0	1.7 ± 0.6	1.9 ± 0.4
18:1ω9	0	6.8 ± 1.7	6.9 ± 0.4
20:1ω7	0	0.9 ± 0.3	0.2 ± 0.2
20:1ω9	0	1.3 ± 0.5	1.1 ± 0.2
22:1ω9	0.5 ± 0.7	4.2 ± 2.1	4.5 ± 1.4
22:1ω11	0	8.0 ± 3.7	8.6 ± 2.7
24:1ω9	0	1.6 ± 0.6	2.8 ± 0.2
Σ MUFA	0.9 ± 0.1	30.3 ± 3.2	30.6 ± 5.8
18:2ω6	0	1.1 ± 0.1	1.4 ± 0.2
18:4ω3	1.8 ± 0.8	1.4 ± 0.2	1.5 ± 0.1
20:4ω6	0	0.8 ± 0.0	0.8 ± 0.2
20:5ω3	0	15.0 ± 0.2	15.2 ± 5.3
22:5ω3	1.2 ± 0.1	0.9 ± 0.0	3.8 ± 5.3
22:6ω3	0	23.8 ± 3.4	24.1 ± 5.0
Σ PUFA	3.5 ± 1.7	44.5 ± 3.8	48.3 ± 8.3
Σ EFA	0	39.6 ± 3.6	40.2 ± 10.6
Σ BAFA	10.4 ± 3.0	2.6 ± 0.8	2.1 ± 0.3
Σ HPFA	0	1.1 ± 0.1	1.4 ± 0.2
18:1ω9/18:1ω7	0	4.1 ± 0.5	3.7 ± 0.9
Σ 22:1ω11+20:1ω9	0	9.4 ± 4.2	9.7 ± 2.8
Σ TFA	8.6 ± 1.5	20.6 ± 0.7	51.0 ± 8.8

SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; EFA: essential fatty acids; BAFA: bacterial fatty acids; HPFA: higher plant fatty acids; TFA: total fatty acids (µg FA mg^{-1} DM); NMI: nonmethylene interrupted