ECOSYSTEM FUNCTIONING IN NORTHEAST PACIFIC SOFT-SEDIMENTARY HABITATS: THE ROLES OF SPECIES DIVERSITY, FUNCTIONAL DIVERSITY, AND ENVIRONMENTAL VARIABLES

by

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Abstract

Previous studies indicate a central role for biodiversity and environment in marine ecosystem functioning, raising concerns about the potential consequences of biodiversity alteration. By combining marine biology and biogeochemistry approaches, and field and laboratory-based approaches I provide new information on biodiversity and environmental contributions to important ecosystem functions such as benthic flux variation and organic matter degradation. Using published benthic flux rate measurements and available environmental variables, I created global models and maps to identify predictors of benthic fluxes of oxygen and nutrients. By performing incubations of intact sediment cores and measuring benthic flux rates, I determined that, of the environmental variables examined, bottom water properties, organic matter quality, and sediment characteristics best explained benthic flux variation. By adding functional and species diversity metrics, I demonstrated that biodiversity and environment contribute about equally to these functions, and that functional richness was the most important predictor of benthic flux variation and organic matter degradation. In experimental incubations where I added phytodetritus to intact sediment cores, I determined that higher taxonomic diversity, and densities of detritivores and omnivores explained higher benthic flux rates in enriched sediment cores. These results point to the combined importance of biodiversity and environment in controlling ecosystem functioning and illustrate the need to combine established and novel approaches to evaluate more fully the consequences of anthropogenic impacts, such as biodiversity alteration and environmental change for ecosystem functioning.

I dedicate this thesis to my parents, Christian Belley and Françoise Gagnon, who passed to me their interest in nature and the desire to understand better the world we live in.

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Table of contents

List of Tables

List of Figures

List of common nomenclature and abbreviations

Term		Description
CTD	……	Conductivity temperature depth profiler
CHONe	……	Canadian Healthy Oceans Network
MUN	……	Memorial University of Newfoundland
NSERC	……	Natural Sciences and Research Council
OM	……	Organic matter
POC	……	Particulate organic carbon
POM	……	Particulate organic matter
O_2	……	Oxygen
NH_4^+	……	Ammonium
NO_3^-	……	Nitrate
NO_2^-	……	Nitrite
NOx	……	Nitrate + nitrite
DIN	……	Dissolved inorganic nitrogen
PO_4^{3-}	……	Phosphate
$Si(OH)_4$	……	Silicate

List of Appendices

Co-authorship statement

The research detailed in this thesis was designed and conceptualized by Rénald Belley, with assistance from committee members Drs. Paul Snelgrove, Philippe Archambault and Kim Juniper. All data were collected and analyzed by R. Belley. The Random Forests models and benthic flux prediction maps in Chapter 1 were jointly developed with Dr. Chih-Lin Wei. Chapter 2 was developed jointly with Drs. Paul Snelgrove, Philippe Archambault and Kim Juniper. Chapters 3 and 4 were developed with Dr. Paul Snelgrove. All manuscripts resulting from this research were composed by R. Belley, with editing assistance and creative direction from committee members and associated co-authors.

Chapter 1 — Seafloor ecosystem functioning: A global synthesis of sedimentary oxygen and nutrient exchange

1.1 Ecosystem functions in marine ecosystems

Oceans cover approximately 70% of the Earth's surface and sediments cover most of the seafloor (Snelgrove 1999). These sedimentary habitats harbour myriad organisms spanning from large-bodied megabenthic predators to smaller macrobenthic and meiobenthic organisms, to small-size bacteria and archaea (Rex et al. 2006). Interactions between these organisms and their habitat contribute significantly to ecosystem processes and functions in marine benthic environments (Stachowicz et al. 2007) by altering "energy and matter over time and space through biological activity" (Snelgrove et al. 2014). Nonetheless, biology alone does not fully control delivery of these functions, which acts in concert with environmental conditions (Hooper et al. 2005).

The many ecosystem processes mediated by benthic organisms (e.g. bioturbation) influence multiple ecosystem functions (e.g. carbon sequestration) that support different ecosystem services (e.g. climate regulation) that yield benefits to human populations (Costanza et al. 1997, Snelgrove et al. 2014).

Ever-increasing human use of marine resources (Halpern et al. 2008, Halpern et al. 2015) links directly to global alteration of marine species distributions and subsequent loss of biodiversity (Kappel 2005, Butchart et al. 2010, Barnosky et al.

2011). These biodiversity changes have led researchers to investigate potential effects of biodiversity loss on ecosystem functioning (Worm et al. 2006, Cardinale et al. 2012). These studies indicate an essential role for biodiversity, but point to a predominant role for functional traits in maintaining ecosystem functions (Solan et al. 2004). Functional traits are the biological characteristics of species that determine how species influence ecological processes (Bremner et al. 2006), whereas the value and range of species traits that influence ecosystem functioning defines functional diversity (Díaz & Cabido 2001, Tilman 2001). From marine coastal soft-sedimentary habitats (Braeckman et al. 2014) to the deep-sea (Danovaro et al. 2008), studies show that increases in functional diversity generally lead to increased ecosystem functioning. More precisely, Danovaro et al. (2008) reported an exponential increase in ecosystem functioning (prokaryote carbon production) with increases in deep-sea nematode diversity (Expected Species and trophic diversity traits).

In addition to biological effects on ecosystem functions, environmental conditions also play an important role (Godbold 2012). Past studies identify bottom water temperature and particulate organic carbon (POC) flux to the seafloor as among the most important environmental variables. Increased organic matter remineralization on the seafloor links to increases in bottom water temperature (Hargrave 1969, Cowan et al. 1996, Alonso-Pérez & Castro 2014) and POC flux to the seafloor (Jahnke 1990, Berelson et al. 1996).

Soft-sedimentary habitats host many ecosystem functions necessary for the well-being of all marine ecosystems, including biomass (primary and secondary)

production, ecosystem metabolism (e.g. carbon mineralization), nutrient cycling (e.g. denitrification, nitrification, nitrogen fixation), and physical structuring (e.g. bioturbation, bio-irrigation). Among these, many studies recognize organic matter remineralization (included in ecosystem metabolism and nutrient cycling ecosystem functions) as a particularly important contribution of marine soft-sedimentary habitats to ecosystem functioning (Giller et al. 2004, Strong et al. 2015).

Organic matter remineralization can be quantified effectively by measuring oxygen and nutrient fluxes at the sediment-water interface (Giller et al. 2004). Different benthic flux measurement techniques include *in situ* benthic chambers deposited on the seafloor (Archer & Devol 1992, Devol & Christensen 1993, Berelson et al. 1996, Berelson et al. 2003, Berelson et al. 2013) and eddy-correlation (Glud 2008, Reimers et al. 2012), and *ex situ* sediment core incubations (Rowe & Phoel 1992, Link et al. 2013a). The latter technique provides reliable oxygen uptake estimates from sediments collected at depths < 1000 m (Glud et al. 1994).

This synthesis reviews current understanding of factors regulating benthic fluxes and predicts and maps global oxygen and nutrient fluxes on the seafloor based on available environmental variables, published benthic flux studies, and random forests modeling.

1.2 Global review of benthic fluxes

Coastal and continental margin sediments (<2000 m) cover approximately 16% of the oceans but contribute to more than 80% of global benthic mineralization

(Middelburg et al. 1997). Continental margins (200-2000 m) are important carbon and nitrogen hotspots (i.e. high seafloor recycling) (Walsh 1991) where the breakdown of organic matter on the seafloor results in fluxes of oxygen and nutrients that contribute to water column concentrations of key elements fuelling surface water productivity (Hammond et al. 1985, Denis & Grenz 2003).

1.2.1 Factors influencing organic matter degradation and benthic fluxes

On a fine scale (mm-cm), organic matter degradation at the seafloor follows the laws of thermodynamics and tends to maximal entropy (i.e., minimizing disorder). Therefore, diffusion patterns, in concert with drivers of ocean circulation (tides, currents) and biological processes (e.g. remineralization), result in spatial and temporal variation in fluxes of oxygen and nutrients (Schulz 2000). For example, penetration of dissolved oxygen from bottom water into the sediment follows a diffusion gradient, from highest values in the water column to lowest values in the sediment, noting that biological activity strongly influences this pattern (Aller 2014).

Microorganisms such as bacteria utilize oxygen and other electron acceptors to degrade organic material within the sediment and therefore increase chemical reaction rates by many orders of magnitude through enzymatic reactions. Hence, they generate nutrient fluxes directed either towards the water column or deeper in the sediment, depending on the specific chemical compound (Jorgensen 2006). Because oxic respiration yields the highest energy, prokaryotes preferentially utilize O_2 as an electron acceptor to degrade organic matter. However, in the absence of O_2,

prokaryotes use other electron acceptors to degrade organic matter following a predictable sequence, typically from the highest to the lowest energy yields (Table 1.1). Nonetheless, although some prokaryotes can utilise different electron acceptors depending on their availability and energy yields, other specialised forms can use only a single specific electron acceptor (e.g. sulphate reducing bacteria) (Jorgensen 2006).

Through their activities (e.g. feeding, tube-building) meio- and macro-organisms living within the sediment can enhance these fluxes and their impact may be particularly important on continental shelves characterized by relatively high faunal abundance and sedimentary organic matter (Schulz 2000). By measuring simultaneously sediment total oxygen uptake (TOU) using benthic chambers and the diffusive oxygen uptake (DOU), Glud et al. (1994) calculated TOU/DOU ratios and attributed the increase in oxygen uptake (by a factor of 1.1 to 4) to infaunal activities.

Many other factors influence benthic respiration and nutrient fluxes, including latitude (Jahnke 1996), depth (Smith 1987, Jahnke 1996, Christensen 2000), bottom water dissolved oxygen concentration (Seiter et al. 2005, Middelburg & Levin 2009, Nunnally et al. 2013), surface primary productivity (Christensen 1989, 2000) and the resulting particulate organic matter flux to the seafloor (Smith 1987, Jahnke 1996, Seiter et al. 2005, Berelson et al. 2013, Link et al. 2013a), and organic carbon burial (Jahnke 1996).

1.2.2 Oxygen uptake

Several studies have examined O_2 and nutrient fluxes on the seafloor but benthic flux studies have focused mostly on oxygen uptake, with a strong focus on the Northeast Pacific region of the United States (US). Consequently, most of the general observations summarized here draw from these studies.

The oxygen demand across the United States Northeast Pacific shelf sediment (between 90-200 m depth) varies only by 30% among sites in Oregon, and Northern and Central California. These relatively consistent benthic O_2 uptake rates range between 2.3-18.3 mmol m^{-2} d^{-1} (factor of 9 difference) and their mean values vary by a factor of 2 (Berelson et al. 2013). In these regions, one study estimated O_2 uptake by aerobic respiration at less than 50% of organic carbon remineralization (Berelson et al. 2013). Moreover, calculations of the impact of benthic O_2 uptake on water column hypoxia indicate a minimal role in increasing hypoxia because O_2 uptake decreases oxygen only a few μM over tens of meters of the water column (Berelson et al. 2013).

Early attempts to measure sediment oxygen uptake indicated a large disparity between measurements from shallow shelf to abyssal depths. Measurements using a free vehicle respirometer in the Northwest Atlantic indicated oxygen uptake from sediments in shallow waters up to three orders of magnitude higher than values measured at 5,200 m (Smith et al. 1976). The magnitude of particulate organic carbon (POC) rain to the seafloor strongly influences oxygen uptake rates, and direct oxygen flux measurements have been used to estimate POC flux to the deep sea (≥ 1000 m) (Jahnke 1996, Seiter et al. 2005). The increased

presence of infaunal and epifaunal organisms on the continental shelf, however, complicates prediction of O_2 uptake. In California, where an oxygen minimum zone (OMZ) occurs between 500 and 1500 m, oxygen uptake rates were constant at sites between 700 and 3500 m depth, and 3-10 times lower than at sites on the continental shelf (Berelson et al. 1996). The authors attributed this large difference in O_2 flux rates to higher abundances and biomass of macrofauna on the continental shelf rather than to differences in bottom water O_2 concentrations. Whereas diffusive O_2 uptake (DOU) measured using microsensors and total O_2 uptake (TOU) measured by whole core incubations or flux chambers both decreased with increasing water depth, the TOU to DOU ratio indicative of infaunal-mediated O_2 uptake, decreased from 3 to 4 on continental shelves to 1 at deeper sites (Wenzhöfer & Glud 2002). Moreover, Rowe and Phoel (1992) reported excellent relationships between TOU and macrofaunal biomass (R^2=0.98) and Hammond et al. (1985) attributed variation of up to 30% in flux measurements over a few meters to tens of meters to differences in benthic fauna.

Other environmental variables can contribute to benthic oxygen uptake rates. For instance, Hammond et al. (1985) reported an increase by a factor of 2-3 in O_2 uptakes following increased water temperature during the spring bloom in San Francisco Bay. Moreover, rates of oxygen uptake sometimes correlate strongly with bottom water oxygen concentrations (Berelson et al. 1987), however, not in all cases. Studies indicate insensitivity of sediment community oxygen consumption rates to bottom water oxygen concentrations or to organic carbon content in surficial sediments (Berelson et al. 1996).

Sedimentary oxygen uptake rates may also be used to estimate carbon remineralization rate at the sediment surface (Wenzhöfer & Glud 2002, Link et al. 2011, Song et al. 2016) and to build simple organic carbon budgets.

1.2.3 Nitrogen compounds

The marine nitrogen cycle is one of the most complex of all biochemical cycles in the ocean (Gruber 2008) (Figure 1.1). In seawater at pH 8, salinity of 35 ppm and 6 °C, only about 1% of ammonical nitrogen ($NH_3 + NH_4^+$) occurs as ammonia (NH_3). Therefore, most researchers use the general term ammonium (NH_4^+) (Aminot & Chaussepied 1983). Ammonium can be nitrified within the upper few millimeters of the sediment, although both nitrification and denitrification can occur in sediments (Denis & Grenz 2003). The ammonium diffusing upward from deeper sediments can be partially oxidized to nitrate in the sediment column (i.e., nitrification). The nitrate can then diffuse downward and be reduced to N_2, or infaunal bio-irrigation can also transport nitrate downward (Hammond et al. 1985).

Ammonium generally dominates sediment-water nitrogen fluxes and shallow water sediments occasionally act as a nutrient sink possibly because of the presence of benthic algal mats that increase nutrient uptake (Hammond et al. 1985). Ammonium concentration can vary greatly spatially and temporally. Highly variable ammonium fluxes prevented Denis & Grenz (2003) from drawing conclusions on causation in the Gulf of Lions. However, they reported high effluxes of ammonium in incubations with high oxygen uptake rates, possibly indicative of large infaunal organisms.

Nitrate uptakes typically exceed ammonium effluxes in continental shelf sediments of Oregon and California, indicating that sediments represent a net sink for nitrogen fixed in the water column (Berelson et al. 2013).

Ammonium concentrations in oceanic waters rarely exceed 1 μmol L^{-1}, whereas deep waters usually don't contain ammonium. Four day lander deployments in central equatorial north Pacific sediments indicated no change in ammonium, with ammonium levels remaining consistently below the 13 μmol detection limit (Berelson et al. 1990). However, elevated concentrations have been reported in anoxic waters (Aminot & Chaussepied 1983). For example, ammonium concentrations up to 100 μmol L^{-1} can occur in the deep water of the Black Sea, and studies report increased nitrate uptake with decreasing bottom water oxygen concentration (Berelson et al. 1987). Similarly, OMZs such as those in the eastern tropical South Pacific, the Arabian Sea, and the eastern tropical Pacific, are active sites of water column denitrification and nitrogen loss through anammox, heterotrophic denitrification, and nitrate reductions (Horak et al. 2016). Nitrate efflux from the sediment (or uptake from the water column) is termed direct denitrification and occurs occasionally, especially in locations with reduced oxidation of organic carbon (Berelson et al. 2003). In contrast, nitrate uptake from the sediment increases with increased flux of OC to the seafloor and oxidation of organic matter (Berelson et al. 2003), often leading to decreased bottom water oxygen concentration (Levin et al. 2009).

Ammonium efflux rates from sediments can also vary temporally as a function of export of phytoplankton productivity and bottom temperature. The

earliest measurements of nutrient flux pointed to the importance of primary production export to the sediment surface (Rowe et al. 1975), as well as a 4-5 times increase in ammonium effluxes following the spring bloom and increased bottom temperature in San Francisco Bay (Hammond et al. 1985).

1.2.4 Silicate

Inputs of biogenic silica to the sediment surface primarily originate from sinking diatom frustules. Silica undergoes dissolution processes that vary with temperature and pH. Therefore, physical rather than biological factors primarily mediate the dissolution of silica. Dissolved silicate, which accumulates in surface sediments, diffuses upward into the water column and becomes available to primary producers (Conley et al. 1988, Conley et al. 1993, Denis & Grenz 2003).

Denis & Grenz (2003) linked temporal difference in silicate effluxes to the timing of the phytoplankton bloom, which resulted from high nutrient input from the Rhône River and coastal water mass circulation. Similarly, high phytoplankton productivity and bio-irrigation were linked with a 3-10 fold increase in silicate effluxes (Hammond et al. 1985). Sediment resuspension by groundfish in Saanich Inlet also corresponded to a tripling in dissolved silica export from the sediment to the water column, suggesting an important role for sediment resuspension by groundfish in the silica cycle (Katz et al. 2009).

1.2.5 Phosphate

Many factors influence phosphate fluxes on the seafloor, which can vary widely from net sediment uptake to net release. In brief, bacterial decomposition of organic matter on the seafloor regenerates phosphate that may be released from the sediment to the overlying water, re-precipitated within the sediment, or adsorbed by other sediment constituents such as iron oxides. Within the sediment, iron oxides adsorb phosphates in the oxidizing zone. Sedimentation and biological mixing can bring this adsorbed phosphate into the reducing zone of the sediment where desorption and potential release may occur. Alternatively, phosphate may diffuse back to the oxic sediment layer, enhanced by bioturbation and bio-irrigation, and potentially repeating the cycle several times. The flux of phosphate depends on the phosphate production rate, the sediment buffering capacity, and the diffusive layer thickness at the sediment-water interface (Sundby 1992).

Although phosphate fluxes on the seafloor generally increase following phytoplankton bloom deposition (Nixon et al. 1980), they sometimes lack seasonality (Berelson et al. 2003). Oxygen penetration depth within the sediment (OPD), bottom water dissolved oxygen concentration (DO), sediment porosity and mineral bound inorganic phosphorous all influence phosphate benthic fluxes (Almroth-Rosell et al. 2015).

1.2.6 Benthic fluxes in deep-sea sediments

As with benthic flux measurements on the continental shelf, the majority of benthic flux observations reported here for deep-sea sediments refer to O_2 uptake in

the Pacific Ocean. High primary productivity characterizes equatorial Pacific surface waters, decreasing with increasing latitude (Chavez & Barber 1987). This high productivity leads to high particulate organic matter (POM) export to the seafloor (Hammond et al. 1996). The flux of relatively labile POM in the equatorial region may persist for a few months or less, and benthic response to surface primary productivity variation occurs within days (Witte et al. 2003) to a few months (Hammond et al. 1996).

Oxygen fluxes vary spatially, with generally higher values in the equatorial region than at higher latitude, but with minimal longitudinal variation along the equator (between 102°W and 140°W). The largest fluxes were measured between 2°N and 2°S, and declined by a factor of ~5 between 9°N and 12°S (Hammond et al. 1996). Despite relatively small longitudinal variation along the equator (between 100°W and 14O°W) Hammond et al. (1996) reported a factor of two temporal variation in O_2 uptake near the equator. They related this variation to changes in sea-surface temperature (SST) that could indicate changes in upwelling and surface water productivity. They also proposed the use of SST as a proxy for POM flux to the seafloor in this region, coupling benthic carbon remineralization to export on a timescale of few months (Hammond et al. 1996). However, they noted large uncertainties in their benthic fluxes measurements and emphasized the need for more data to determine whether POM flux can effectively predict benthic nutrient fluxes. In the Central and Northeast Pacific, Smith & Baldwin (1984) reported two-fold seasonal variation in benthic fluxes of O_2 in the deep Pacific. Overall, carbon respiration on the Pacific margins is about four times higher than rates near the

equator but Pacific deep-sea sediments nonetheless contribute significantly to the global benthic carbon cycle (Hammond et al. 1996).

In the deep North Atlantic, a seasonal increase of POM fluxes to the seafloor increased sedimentary O_2 uptake by a factor of four (Pfannkuche 1993). However, Sayles et al. (1994) found no significant seasonal variation in O_2 uptake in the deep (≈4400m) Atlantic near Bermuda, indicating relative stability in sedimentary O_2 uptake over a large portion on the deep seafloor. They attributed this consistency to the lower reactivity or "quality" of the POM reaching the oligotrophic deep North Atlantic region near Bermuda compared to the deep Pacific seafloor near the equator.

Nitrate efflux from sediments to the overlying water follows a similar latitudinal pattern, with higher fluxes in the Pacific equatorial region (Berelson et al. 1990). As noted previously, deep waters rarely contain ammonium and no change in ammonium was measured over the four day lander deployments in central equatorial North Pacific sediments where ammonia levels were consistently below the 13 μmol m^{-2} L^{-1} detection limit (Berelson et al. 1990). Despite high uncertainties in their measurements of phosphate flux, Hammond et al. (1996) noted phosphate efflux varied widely, with some very low values and some very high values, possibly indicating heterogeneous phosphate sources or contamination.

In another study based on benthic chamber deployments in the deep central equatorial North Pacific, Berelson et al. (1990) noted no significant spatial differences in nitrate (or O_2, or silicate) fluxes along a transect through this biologically productive region at depths between 4440 m and 4910 m.

1.2.7 Effect of riverine inputs

Riverine input can affect benthic respiration and nutrient fluxes by delivering large quantities of sediments and nutrients onto the continental shelf. For example, the Mississippi and Atchafalaya rivers in the Gulf of Mexico (Nunnally et al. 2013), and the Eel and Umpqua rivers in California and Oregon, respectively, significantly increase benthic respiration and nutrient fluxes on the adjacent continental shelf (Berelson et al. 2013).

In the Northwest Mediterranean Sea, Denis & Grenz (2003) reported O_2 flux near the Rhône river exceeded the nearby continental shelf break by a factor or two, although they considered the Gulf of Lions continental shelf to be relatively homogenous. Higher O_2 flux correlated positively with the organic carbon (OC) content of the surface sediments. They also indicated higher phosphate effluxes near the Rhône river mouth.

In the Adriatic Sea, Tahey et al. (1996) observed higher effluxes of silicate and ammonium at northern stations near the Po river and lower fluxes at more distant southern stations. They also reported that the highest ammonium fluxes near the Po River coincided with high sediment O_2 uptake, and that the latter decreased with distance and depth, and increased with temperature and phytodetritus content.

1.2.8 Effects of benthic community

Many studies report enhanced benthic flux rates and organic matter degradation as a function of the local benthic community. In general, the presence of bioturbators and bio-irrigators increase benthic flux rates and organic matter degradation (Aller 1982, Aller & Aller 1998, Aller 2014). Indeed, Archer and Devol (1992) attributed a 3-4 times increase in O_2 uptake on the Washington continental shelf relative to the slope to infaunal bio-irrigation. Devol and Christensen (1993) also compared benthic fluxes measured using an *in situ* benthic tripod and fluxes predicted by molecular diffusion in Northeastern Pacific sediments. They attributed 3-times increases in O_2, nitrate, and silicate fluxes measured with the benthic tripod relative to fluxes predicted by molecular diffusion to macrobenthic irrigation of sediments.

Bioturbation activities of spatangoid urchins also exert large and positive impacts on benthic fluxes (Lohrer et al. 2004). Maldanid polychaete worms have been proposed as geochemical keystone species because of their feeding and irrigation activities (Levin et al. 1997, Waldbusser et al. 2004). In their study of the three-dimensional organization of *Maldane sarsi* tubes, Dufour et al. (2008) observed higher concentrations of bacteria, organic carbon, Fe and Mn adjacent to the tubes, possibly resulting from feeding activities, irrigation, and mucous secretion. Sediment resuspension created primarily by the flatfish *Lyopsetta exilis* strongly influenced ammonium, phosphate, and silica cycles in Saanich Inlet (Yahel et al. 2008, Katz et al. 2012).

Relatively few studies have specifically addressed the effects of faunal functional diversity on benthic fluxes and organic matter degradation. The few that have investigated this topic link higher functional richness to increased benthic fluxes and organic matter remineralization (Link et al. 2013b, Braeckman et al. 2014).

1.3 Global predictions of sedimentary oxygen and nutrient exchange

A recent surge of interest in marine ecosystem functioning prompts a need to begin global mapping of key seafloor functions such as cycling of organic matter and related oxygen and nutrient fluxes at the sediment-water interface. Understanding carbon, nitrogen, and other nutrient cycles linked to the seafloor require these measurements. The section below presents the first global predictions of oxygen and nutrient fluxes at the sediment-water interface by modeling the contributions of available environmental variables and published regional flux data. These predictions enhance understanding of benthic fluxes across different environments on a global scale, and generate a framework in which to test biodiversity-function relationships over broad spatial scales.

Previous studies have developed models to predict different sediment-water fluxes. For example, Christensen (1989) developed a power curve regression to determine total oxygen consumption rates (ORC = 199.485 $X^{-0.7169}$, ml O_2 m^{-2} h^{-1}) based on water column depth for sediment depths between 40 and 300 m. More recently, Almroth-Rosell et al. (2015) developed a model to predict phosphate fluxes

in the Baltic Sea based on oxygen penetration depth within the sediment, bottom water dissolved oxygen concentration, sediment porosity, and mineral bound inorganic phosphorous. Others have taken a different approach and developed models to predict global POC flux to the seafloor based on sediment diffusive oxygen uptake (DOU) and total organic carbon (TOC) measurements (Seiter et al. 2005). Jahnke (1996) used a similar approach to estimate global POC fluxes below 1000 m depth.

Here I develop global models to predict benthic flux rates. I chose to incorporate these global models in the introductory chapter of my thesis because the information provided by these new analyses knits together the findings of past studies included in the literature review presented here. In the following sections, I describe the: 1) data collection process, (2) statistical analyses, 3) results of the prediction models for oxygen, nutrients (ammonium, nitrate, nitrite, NOx, DIN, phosphate and silicate) fluxes, and multifunctionality, and 4) implications of these results. I hypothesize that for these global models: (i) the variables influencing benthic flux rates across study sites corresponds to those identified with specific regions in previous studies (e.g. surface water primary productivity, POM flux to the seafloor, bottom depth), and (ii) predicted benthic flux rate will be generally highest in shallower regions with high primary productivity abundances.

1.3.1 Data collection

Data for oxygen (O_2) uptake, and fluxes of ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), nitrate+nitrite (NOx), dissolved inorganic nitrogen (DIN = $NH_4^+ + NO_3^-$

+ NO_2^-), silicate ($Si(OH)_4$) and phosphate (PO_4^{3-}) were collated from 22 different published sources and separated into 13 different regions (Table 1.2). I included only data from on-board (<1000 m) and *in situ* incubation studies because benthic fluxes calculated from pore water profiles (whole-core squeeze and centrifuged sediments) are believed to be less accurate (Hammond et al. 1985), in that they contain ammonium and nitrate artefacts upon recovery from deep sites (Berelson et al. 1990). Likewise, diffusive O_2 flux estimated for the continental shelf using microelectrodes are 40% lower than those calculated using chambers and the eddy correlation technique because diffusive flux does not account for bio-irrigation which enhances total flux (Berelson et al. 2013). Therefore, my benthic flux measurements required no correction because on-board (<1000 m) and *in situ* incubation results from the studies used in my analyses yielded similar results. I also removed flux measurements from sites near large output of organic matter (e.g. sewage outfalls) and containing obvious large outliers. Where benthic flux data were only available in figures or sampling locations only on maps, I obtained numerical data using the software Plot Digitizer 2.6.6 (http://plotdigitizer.sourceforge.net/).

Topographic data were derived from the Cell/pixel-registered ETOPO1 bedrock global relief model (https://www.ngdc.noaa.gov/mgg/global/global.html), reducing the grid resolution from 1 to 5 minutes by averaging. Derived terrain characteristics included slope and aspect of terrain in radians degrees, Topographic Position Index (TPI, mean of the absolute differences between the value of a cell and the value of its 8 surrounding cells), Terrain Ruggedness Index (TRI, difference

between the value of a cell and the mean value of its 8 surrounding cells) and roughness (difference between the maximum and the minimum value of a cell and its 8 surrounding cells). Decadal (1955-2012) seafloor mean temperature and salinity (1/4 degree resolution), as well as oxygen (Figure 1.2), nitrate, phosphate and silicate concentrations (1 degree grid) were downloaded from the World Ocean Atlas 2013 v2 (https://www.nodc.noaa.gov/OC5/woa13/woa13data.html). I calculated export POC flux (Lutz_POC) at the seafloor based on Lutz et al. (2007), using the mean and seasonality (svi=sd/mean) of primary production, as well as the mean export depth below the euphotic layer over the 16-year period (1998-2014). I estimated euphotic depth using the Morel and Berthon (1989) Case I model based on mean surface chlorophyll *a* concentrations, and calculated export depth by subtracting euphotic depth from water depth. The global climatological monthly mean SeaWiFS (1998-2002) and MODIS (form 2003-2014) Level-3 chlorophyll *a* (Chl_mean) concentration and Level-4 Vertical General Production (VGPM_mean) ocean primary productivity data (Behrenfeld & Falkowski 1997) (5 minutes grids) were downloaded from http://www.science.oregonstate.edu/ocean.productivity/. The projected seafloor living standing stocks (1 degree grids), including abundance and biomass of prokaryotes, meiofauna, macrofauna, and megafauna, were derived from Wei et al. (2010a).

1.3.2 Statistical analyses

I used Random Forests (RF) (Breiman 2001) to fit oxygen and nutrient fluxes with multiple environmental variables (Table 1.3), randomly selecting 2/3 of flux

data to construct the prediction model, and retaining the other 1/3 of the data to validate model accuracy and calculate the variation explained (R^2). These resampling (with replacement) procedures were repeated 5000 times in order to calculate an average R^2. Data from similar sites collected at different time of the year likely increased variation in each flux. Environmental variables were normalized before the analyses. To extrapolate oxygen and nutrient fluxes to unsampled areas, I calculated average predicted values by inserting multi-layers of seafloor environmental factors into each of the 5000 models.

Variable importance was assessed by randomly shuffling the environmental data corresponding to the 1/3 of flux data retained to validate the predicted model. By shuffling one variable at a time I mimicked the absence of that particular variable and repeated the process for each of the 5000 model iterations. The relative increase of mean squared error (MSE) then provided an objective measure of the importance of each variable in the RF model. To this end, I used a "conditional permutation" algorithm (Strobl et al. 2008) which permutes predictor values within partitions of values of correlated predictors ($\rho > 0.5$, Pearson's correlation). This algorithm reduces the bias of spurious correlations by correcting for the assumption of independence of predictors.

Statistical analyses and predictive maps were completed using R software (R Core Team 2016), whereas RF models were created using the "randomForest" function implemented in the R "randomForest" package (Liaw & Wiener 2002).

1.3.3 Model predictions and variable importance

Overall, model accuracy and variance explained varied between $R^2 = 0.82$ and $R^2 = 0.39$ (Table 1.4). However, other than for O_2 uptake for which more data were available, I extrapolated global maps of nutrients from limited data. Therefore, the O_2 uptake prediction model proved most accurate ($R^2 = 0.80$, Table 1.4).

The most important variables for total benthic fluxes identified by RF models can be grouped into seafloor, bottom water and biological predictors. Important seafloor characteristics include depth (Elevation), topographic position index (TPI), terrain ruggedness index (TRI), and slope. Important predictors of benthic fluxes include bottom water dissolved oxygen and silicate concentrations. Finally, important biological predictors encompass variables from the ocean surface to the seafloor. These include surface water chlorophyll-*a* concentrations (Chl_mean), particulate organic carbon flux to the seafloor (Lutz_POC), the vertically generalized production models (VGPM_SVI and VGPM_mean), which all estimate net primary production, as well as mean sedimentary bacterial and megafaunal biomass (Bact.biom.mean and Mega.biom.mean, respectively, Table 1.4).

1.3.3.1 Oxygen uptake

O_2 uptake produced the second best RF model ($R^2 = 0.80$) where key predictors included decreasing sediment O_2 uptake with increasing depth (elevation), and the net primary production seasonal variation index (VGPM_SVI), and decreasing POC flux to the seafloor (Lutz_POC) (Figure 1.3, Table 1.4). Predicted O_2 uptake also increased with increasing water temperature (4^{th} most important

variable, results not presented). Although past studies show a strong correlation between macrofaunal biomass and O_2 uptake rates ($R^2 = 0.98$) (Rowe & Phoel 1992), my results suggest that depth, net primary productivity, and POC flux to the seafloor are better predictors of O_2 flux variation. Discrepancies between the macrofaunal biomass model used and real values may explain this difference, or it may be that these three variables are simply better predictors of O_2 flux variation.

The global predictive map indicates generally higher sediment O_2 uptake in shallow regions along continental shelves, and decreasing uptake with depth (Figure 1.4). The predictive map also indicates high O_2 uptake rates in regions with high calculated POC fluxes to the seafloor. Predicted O_2 uptakes are especially high in regions such as the South China Sea and Arafura Sea (north of Australia) (Figure 1.4), as well as the East China Sea, Northern Russia, Scandinavia and Europe, Persian Gulf, North Sea, Northeastern Americas, Argentina and West coast of Alaska. My model predicted relatively low values along the Northeast Pacific, although my analysis included many data from this region which suggest generally high uptakes. This discrepancy can be explained by the fact that model predictions represent yearly averages whereas benthic flux measurements are usually performed during summer months or after phytoplankton blooms, where higher water temperature and POC flux to the seafloor are expected to increase benthic fluxes.

1.3.3.2 Ammonium

The best RF model for ammonium ($R^2 = 0.45$) indicates increasing effluxes with increasing mean megafaunal abundance (Mega.biom.mean), and decreasing

bottom water O_2 concentration (BWO_2) and topographic position index (TPI) (Figure 1.3, Table 1.4). Predicted ammonium effluxes also decreased with depth (4th most important variable, results not presented).

As in the global predictive map for O_2 uptake, my model predicted generally higher effluxes of ammonium in shallow regions with high BWO_2 such as in the East China Sea and northeastern Americas (Figure 1.5). The model also predicted high ammonium effluxes in the South China Sea, Arafura Sea (north of Australia), Persian Gulf, Red Sea, North Sea, northern Brazil, and Argentina (Figure 1.5). The model also predicted no or very low values of ammonium efflux in deep-sea sediments, a pattern consistent with previous studies (Berelson et al. 1990).

1.3.3.3 Nitrate

The best RF model for nitrate (R^2 = 0.71) predicted decreasing nitrate fluxes (i.e., higher nitrate uptake from the sediment) with increasing mean productivity (VGPM_mean), bottom slope, and POC export to the seafloor (Lutz_POC) (Figure 1.3, Table 1.4).

Again the model predicted low to no fluxes of nitrate in deep-sea sediments (Figure 1.6), possibly reflecting the lower calculated POC flux to the deep seafloor. Therefore, the global predictive map for nitrate generally indicates higher nitrate sediment uptake in productive shallow regions and low to no uptake in deeper regions with lower POC export to the seafloor (Figure 1.6). Low nitrate efflux values predicted in some deep-sea regions may result from model prediction inaccuracies, which become more evident at very low values.

1.3.3.4 Nitrite

The best model for nitrite (R^2 = 0.61) indicates that seafloor characteristics influence fluxes most strongly. Specifically, the model predicted increasing nitrite flux with increasing topographic position index (TPI), bottom slope, and terrain ruggedness index (TRI) (Figure 1.3, Table 1.4). The global predictive map of nitrite generally indicates nitrite sediment uptakes on the shallow parts of the continental shelves and no or low release from sediments in deeper regions (Figure 1.7).

1.3.3.5 NOx

The best model for NOx (R^2 = 0.75) predicted decreasing fluxes (i.e., higher NOx uptake from the sediment) with increasing bottom slope, and mean and seasonal variation in productivity (VGPM_mean and VGPM_svi, respectively) (Figure 1.3, Table 1.4).

Given that NOx data represent the sum of nitrate and nitrite flux, and that nitrate fluxes typically greatly exceed those for nitrite (generally an order of magnitude), the best model and global predictive map of NOx were similar to those for nitrate. Therefore, once again low predicted fluxes of NOx in deep-sea sediments (Figure 1.8), possibly reflect the reduced surface productivity reaching the deep seafloor, and higher sediment uptakes in productive shallow regions of the continental shelves (Figure 1.8).

1.3.3.6 DIN

The best model for DIN (R^2 = 0.46) predicts increased effluxes from the sediment with increased predicted bacterial biomass (bact.biom.mean) and bottom water silicate concentration (Silicate), and decreased at high levels of mean predicted productivity (VGPM_mean) (Figure 1.3, Table 1.4). Predicted DIN efflux also decreased with depth (4th most important variable, results not presented).

Given that DIN data represents the sum of ammonium, nitrate, and nitrite flux, and that ammonium efflux generally dominates nitrate and nitrite fluxes, the best model and global predictive map of DIN closely resembles those for ammonium. Therefore, the model predicts generally higher DIN effluxes in shallow regions with intermediate predicted productivity, and elevated bacterial biomass, and silicate concentration such as in the East China Sea and Arafura Sea (north of Australia) where the model predicted highest DIN effluxes (Figure 1.9). The model also predicted high DIN effluxes for the South China Sea, Northern Russia, Scandinavia and Europe, Persian Gulf, North Sea, Northeastern Americas, Argentina, and west coast of Alaska. (Figure 1.9). As in the ammonium model, the DIN model predicted no or very low DIN fluxes in deep-sea sediments.

1.3.3.7 Silicate

Silicate produced the best RF model overall (R^2 = 0.82), indicating increased sediment releases with increasing primary productivity (Chl_mean), terrain ruggedness index (TRI), and POC flux to the seafloor (Lutz_POC) (Figure 1.3, Table 1.4).

The global predictive map of silicate indicates generally higher effluxes in shallow continental shelf regions with high primary productivity and POC flux to the seafloor, such as the East and South China Seas, Arafura Sea (north of Australia), Northern Russia, Scandinavia and Europe, Persian Gulf, North Sea, African west coast, Northeastern Americas, Northern Brazil, Argentina, and Alaskan west coast (Figure 1.10).

1.3.3.8 Phosphate

Finally, the best model for phosphate (R^2 = 0.39) indicates decreasing sediment release with decreasing bottom water O_2 concentration and topographic position index (TPI), and increasing with increasing mean megafaunal biomass (Mega.biom.mean) (Figure 1.3, Table 1.4). The global predictive map of phosphate predicts generally higher phosphate efflux in shallower regions, possibly with high-predicted mean megafaunal biomass (Figure 1.11), such as the East and South China Seas, North Sea, Persian Gulf, Northeastern Americas and Argentina (Figure 1.11).

1.3.3.9 Multiple ecosystem functions predictive map

The global predictive map of multiple ecosystem functions identified regions with similar benthic flux based on PCA scores, including high predicted benthic flux such as in the South China Sea, Arafura Sea (north of Australia), Northern Europe, Persian Gulf, Northeastern coast of Americas, and Argentina, intermediate benthic flux such as in the Arctic, and low predicted benthic flux such as the deep-sea (Figure 1.12).

1.3.4 Discussion

The use of globally available environmental variables and benthic flux measurements from published studies in conjunction with random forests modeling effectively predicted benthic fluxes of O_2, nitrate, nitrite, NOx and silicate ($R^2 > 0.6$), but not ammonium, DIN (which is dominated by ammonium flux) and phosphate ($R^2 < 0.5$). The difference of predictability between models can be explained by the larger amount of flux data available for northern hemisphere continental shelf studies compared to other regions of the world, and the limited availability of flux data for some variables (e.g. ammonium, phosphate) compared to others (e.g. O_2). Therefore, flux models with lower predictability may be biased by data collected in regions that do not closely reflect overall ocean patterns.

Benthic fluxes originate from many factors, including diffusion, that influence the chemical reactions and biological processes that degrade organic matter and add complexity (Schulz 2000). Bacterial enzymatic reactions can increase flux rates by many orders of magnitude (Jorgensen 2006). Moreover, previous studies have shown that infaunal activities (e.g. feeding, irrigation, tube-building) can enhance these fluxes by a factor of 3-4 (Archer & Devol 1992, Devol & Christensen 1993). Although numerous studies have addressed O_2 uptake (Glud 2008), identifying relevant predictive variables (Christensen 1989) for other cycles such as the much more complex marine nitrogen cycle, have proven more difficult (Gruber 2008). Other fluxes, such as phosphate vary greatly over relatively small spatial scales with many influencing factors (Sundby 1992).

Random forests analyses identified biological variables from the surface water (e.g. primary productivity) to the seafloor (e.g. bacterial biomass), sediment characteristics (e.g. depth and slope), and bottom water variables (e.g. O_2 concentration) as the most important predictors of benthic fluxes for the variables included in my model.

Overall, my model predictions agree with previous studies and indicate generally higher organic matter degradation and resulting benthic flux rates on the continental shelf that decrease with increasing water depth (Smith 1987, Jahnke 1996, Christensen 2000). Model predictions also identified bottom water dissolved oxygen concentration, a variable noted for its importance in previous benthic flux studies (Seiter et al. 2005, Middelburg & Levin 2009, Nunnally et al. 2013), and other recognized drivers including surface primary productivity (Christensen 1989, 2000) and resulting particulate organic matter flux to the seafloor (Smith 1987, Jahnke 1996, Seiter et al. 2005, Berelson et al. 2013, Link et al. 2013a). The model also identified potential candidate variables rarely measured or even overlooked in previous studies such as bottom slope and other seafloor characteristics (e.g. topographic position index, terrain ruggedness index, roughness). Although the specific mechanisms by which these variables contribute to benthic fluxes and organic matter degradation remain unknown, they might influence bottom current flow velocity, which in turn, influences ammonium fluxes and possibly infaunal bioturbation activities (Biles et al. 2003). Future studies should investigate these links in greater detail, given their omission from most previous benthic flux studies.

1.4 Significance of study

Increasing human impacts on oceans over the last decades (Halpern et al. 2015) have often resulted in negative effects on marine biodiversity and raise questions regarding effects on marine ecosystem functioning (Kappel 2005, Halpern et al. 2008). Benthic habitats and the organisms that they harbour provide important ecosystem functions such as recycling of organic matter that drives benthic-pelagic coupling and fuels surface waters with nutrients essential for primary production (Snelgrove et al. 2014). Understanding and potentially preserving these essential ecosystem functions requires greater investigation of abiotic and biotic contributions to ecosystem functioning (Godbold 2012, Strong et al. 2015).

The measurement of benthic fluxes at the sediment-water interface offers a reliable strategy for evaluating organic matter degradation, widely recognized as an important ecosystem function of benthic habitats (Giller et al. 2004). Previous studies have recognized multiple biological and environmental influences on benthic fluxes. Important environmental predictors of benthic flux include temperature (Hargrave 1969, Cowan et al. 1996, Alonso-Pérez & Castro 2014) and POC flux to the seafloor (Berelson et al. 1996, Jahnke 1996). Other studies emphasize important biological variables such as bioturbation and bio-irrigation (Aller 1982, Aller & Aller 1998, Aller 2014). More recent studies add species diversity (Godbold & Solan 2009) and functional diversity (Link et al. 2013b) as major contributors to benthic flux. However, the vast majority of these studies investigated biodiversity and environmental effects on benthic fluxes separately.

The few studies that investigated the relative contributions of biological and environmental variables showed important roles for biological and environmental variables in ecosystem functioning (Godbold 2012, Strong et al. 2015). Nonetheless, a need remains for more studies investigating these factors together to validate previous studies and improve understanding of the relationships between biodiversity, environment, and ecosystem functioning.

1.5 Thesis overview

My thesis spans two fields of science, namely marine ecology and biogeochemistry. Specifically, it investigates the ecosystem function of organic matter remineralization along natural environmental gradients and at soft-sedimentary locations varying strongly in functional and species diversity (see Snelgrove et al. 2014). This thesis provides the first benthic flux measurements in continental shelf and slope sediments near British Columbia, and in doing so provides a better understanding of the most important biological and environmental factors influencing benthic flux variation and organic matter degradation. Decision makers can use this information on the importance of biodiversity and environment in developing strategies to maintain essential ecosystem functions of marine ecosystems.

1.6 Thesis format

Within the 5 chapters of this thesis, I use natural biological and environmental gradients to improve my understanding of the importance of diversity and environmental variables to benthic ecosystem functioning. This introductory chapter (Chapter 1) provides a global review and global predictive model to identify potential environmental drivers of seafloor nutrient fluxes. Chapters 2-4 present original data written as stand-alone manuscripts for publication, thus creating some repetition among chapters, particularly in Methods sections. Chapter 2 was published in PLOS ONE (Belley et al. 2016), Chapter 3 was published in Frontiers in Marine Science (Belley & Snelgrove 2016), and Chapter 4 was submitted to the Journal of Experimental Marine Biology and Ecology (currently in revision).

In all chapters I investigated factors influencing benthic flux variation in Northeast Pacific sediments using techniques never or rarely used for these types of studies. Chapter 2 investigates environmental drivers of benthic flux variation using redundancy analysis. I then take advantage of natural gradients in Chapter 3, which addresses a major ecological gap identified by many authors, namely the relative roles that functional diversity of sedimentary fauna and environment play in ecosystem functioning in natural marine communities. In Chapter 4, I add manipulative experiments to examine the effects of functional and species diversity in natural and experimentally enriched sediment core incubations at two locations differing strongly in biodiversity. Finally, Chapter 5 summarizes the key findings of

Chapters 2-4, and the overall significance of this thesis to benthic ecosystem functioning and functional diversity science.

1.7 Tables

Table 1.1 Organic matter oxidation pathways in the seafloor and their standard free energy yields, ΔG^0, per mol of organic carbon. Modified from Jorgensen (2006).

Pathway and stoichiometry of reaction	**ΔG^0 (kJ mol^{-1})**
Oxic respiration:	
$[CH_2O] + O_2 \rightarrow CO_2 + H_2O$	-479
Denitrification:	
$5[CH_2O] + 4NO_3^- \rightarrow 2N_2 + 4HCO_3^- + CO_2 + 3H_2O$	-453
Mn(IV) reduction:	
$[CH_2O] + 3CO_2 + H_2O + 2MnO_2 \rightarrow 2Mn^{2+} + 4HCO_3^-$	-349
Fe(III) reduction:	
$[CH_2O] + 7CO_2 + 4Fe(OH)_3 \rightarrow 4Fe^{2+} + 8HCO_3^- + 3H_2O$	-114
Sulfate reduction:	
$2[CH_2O] + SO_4^{2-} \rightarrow H_2S + 2HCO_3^-$	-77
$4H_2 + SO_4^{2-} + H^+ \rightarrow HS^- + 4H_2O$	-152
$CH_3COO^- + SO_4^{2-} + 2H^+ \rightarrow 2CO_2 + HS^- + 2H_2O$	-41
Methane production:	
$4H_2 + HCO_3^- + H^+ \rightarrow CH_4 + 3H_2O$	-136
$CH_3COO^- + H^+ \rightarrow CH_4 + CO_2$	-28
Acetogenesis:	
$4H_2 + 2CO_3^- + H^+ \rightarrow CH_3COO^- + 4H_2O$	-105
Fermentation:	
$CH_3CH_2OH + H_2O \rightarrow CH_3COO^- + 2H_2 + H^+$	10
$CH_3CH_2COO^- + 3H_2O \rightarrow CH_3COO^- + 2HCO_3^- + 3H_2 + H^+$	77

Table 1.2 Sources for benthic flux measurements listed by region and sampling devices used.

Region	Source	Sampling device
1-Arctic	Link et al. (2013)	Box core
2-Bering Sea	Rowe and Phoel (1992)	Multicore
3-British Columbia	Belley et al. (2016)	ROPOS Push core
4-Washington	Devol and Christensen (1993)	Benthic chambers
5-Oregon-California	Berelson et al. (2013)	Benthic chambers
6-California	Hammond et al (1985)	Benthic chambers
6-California	Berelson et al. (1996)	Benthic chambers
6-California	Berelson et al. (2002)	Benthic chambers
6-California	Berelson et al. (1987)	Benthic chambers (landers)
6-California	Smith et al. (1979)	Grab respirometer
6-California	Bender et al (1989)	Benthic chambers (landers)
7-Pacific equatorial	Berelson et al. (1990)	Benthic chambers (landers)
7-Pacific equatorial	Hammond et al. (1996)	Benthic chambers (landers)
8-North Atlantic	Belley and Snelgrove (unpublished data)	Multicore
8-North Atlantic	Rowe et al. (1975)	Bell jar
8-North Atlantic	Smith et al. (1978)	Grab respirometer
9-Gulf of Mexico	Nullally et al. (2013)	Batch Micro-Incubation Chambers
10-North Sea	Van Raaphorst (1992)	Sediment cores
11-Adriatic Sea	Hammond et al. (1999)	Benthic chambers
11-Adriatic Sea	Tahey et al. (1996)	Benthic chambers and modified box corer
12-Gulf of Lions	Denis and Grenz (2003)	Multicorer
13-Australia	Berelson et al. (1998)	Benthic chambers

Table 1.3 Environmental data and abbreviations for Random Forests analyses.

Abbreviation	Variable	Unit
Bact.biom.mean	Mean bacterial biomass	mg C m^{-2}
Chl_mean	Mean Chlorophyll *a* concentration	mg m^{-3}
Elevation	Water depth	m
Lutz_POC	Particulate organic carbon flux to the seafloor based on Lutz et al. (2007)	mg C m^{-2} d^{-1}
Macro.biom.mean	Mean macrofaunal biomass	mg C m^{-2}
Mega.biom.mean	Mean megafaunal biomass	mg C m^{-2}
Meio.biom.mean	Mean meiofaunal biomass	mg C m^{-2}
Nitrate	Bottom water nitrate concentration	µmol L^{-1}
Oxygen	Bottom water oxygen concentration	mL L^{-1}
Phosphate	Bottom water phosphate concentration	µmol L^{-1}
Roughness	Roughness of the seafloor	m
Salinity	Bottom water salinity	ppm
Silicate	Bottom water silicate concentration	µmol L^{-1}
Slope	Slope of the seafloor	Radian degree
Temperature	Bottom water temperature	° C
TPI	Topographic Position Index	m
TRI	Terrain Ruggedness Index	m
VGPM_mean	Standard vertical general production model mean	mg C m^{-2} d^{-1}
VGPM_svi	Seasonal Variation Index (SVI) of the standard vertical general production model (SVI = sd/mean)	mg C m^{-2} d^{-1}

Table 1.4 List of the three most important variables to Random Forests models for each predicted benthic flux and their associated cross-validated R^2.

Flux	Variable 1	Variable 2	Variable 3	Cross-validated R^2
Oxygen	Elevation	Lutz_POC	VGPM_SVI	0.80
Ammonium	Oxygen	Mega.biom.mean	TPI	0.45
Nitrate	VGPM_mean	Slope	Lutz_POC	0.71
Nitrite	TPI	Slope	TRI	0.61
NOx	Slope	VGPM_mean	VGPM_svi	0.75
DIN	Bact.biom.mean	Silicate	VGPM_mean	0.46
Silicate	Chl_mean	TRI	Lutz_POC	0.82
Phosphate	Oxygen	TPI	Mega.biom.mean	0.39

1.8 Figures

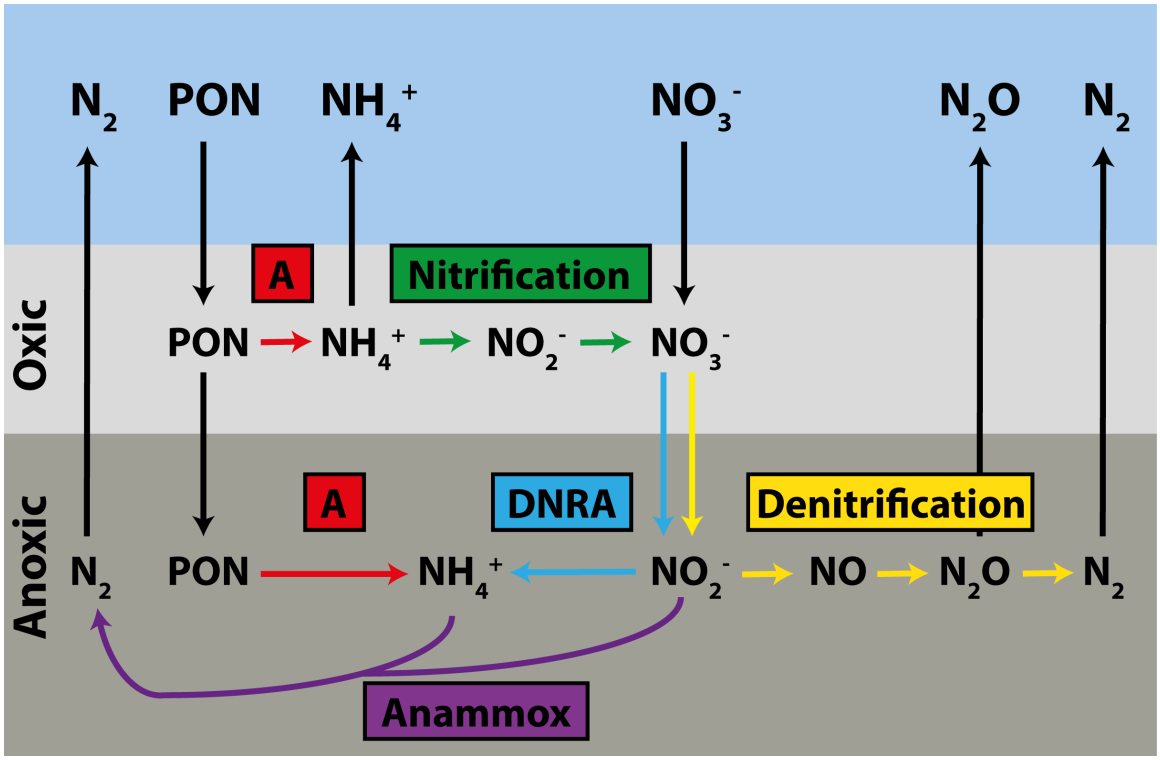

Figure 1.1 Benthic microbial nitrogen cycle between water and sediment. A = ammonification, DNRA = dissimilatory nitrate reduction to ammonium, PON = particulate organic nitrogen. Modified from Stief (2013).

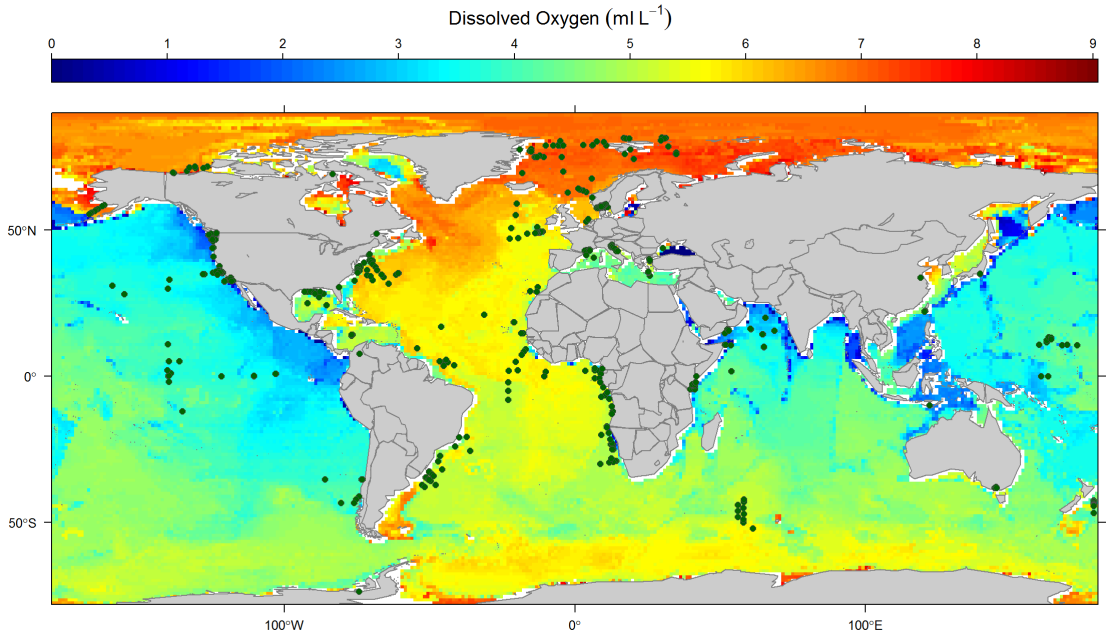

Figure 1.2 Map of bottom water dissolved oxygen concentrations (mL L^{-1}) used to predict benthic fluxes. Green points indicate locations where actual oxygen uptake values were available to perform Random Forests model.

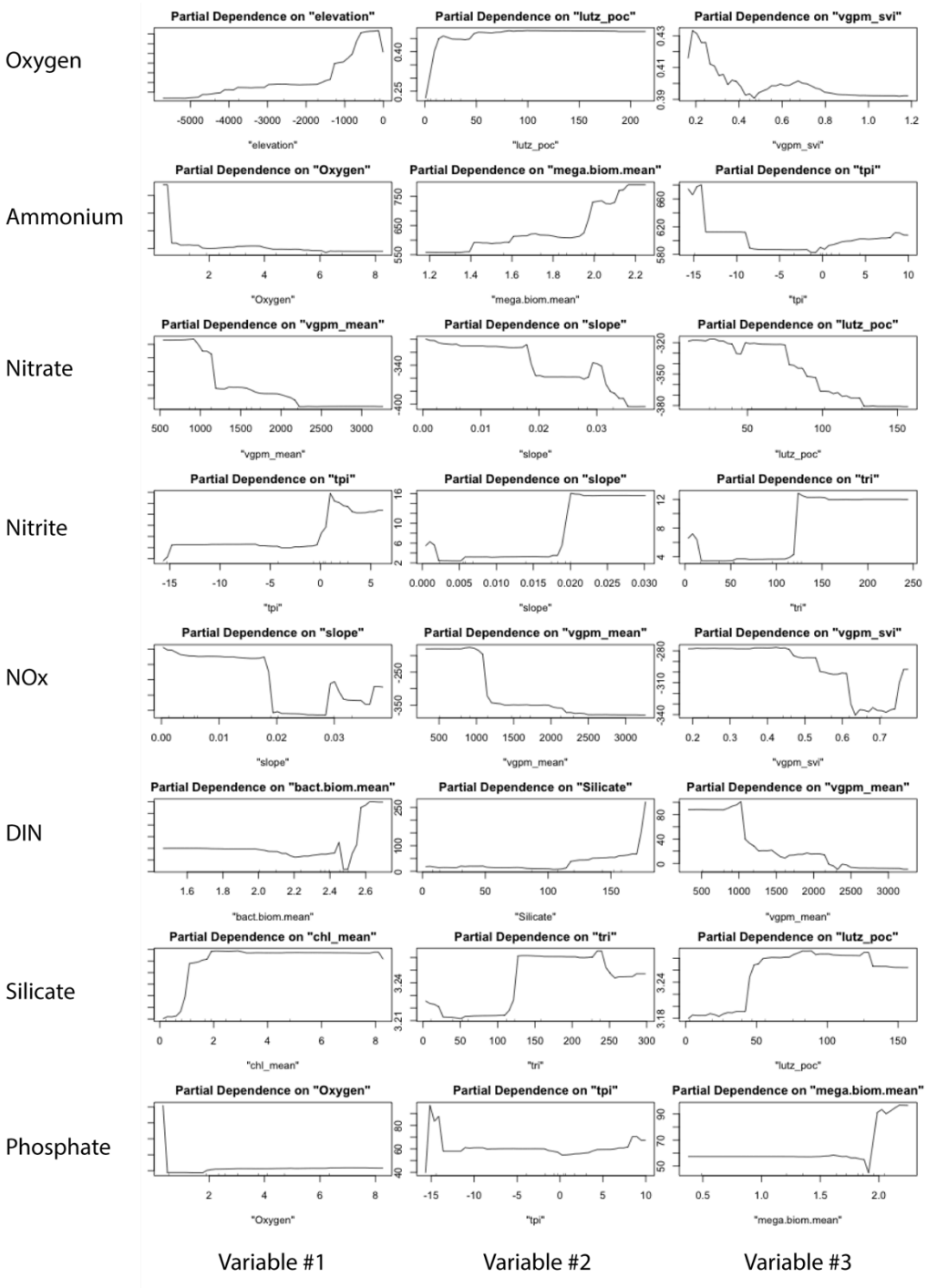

Figure 1.3 Partial dependence and variable importance for each predicted benthic flux.

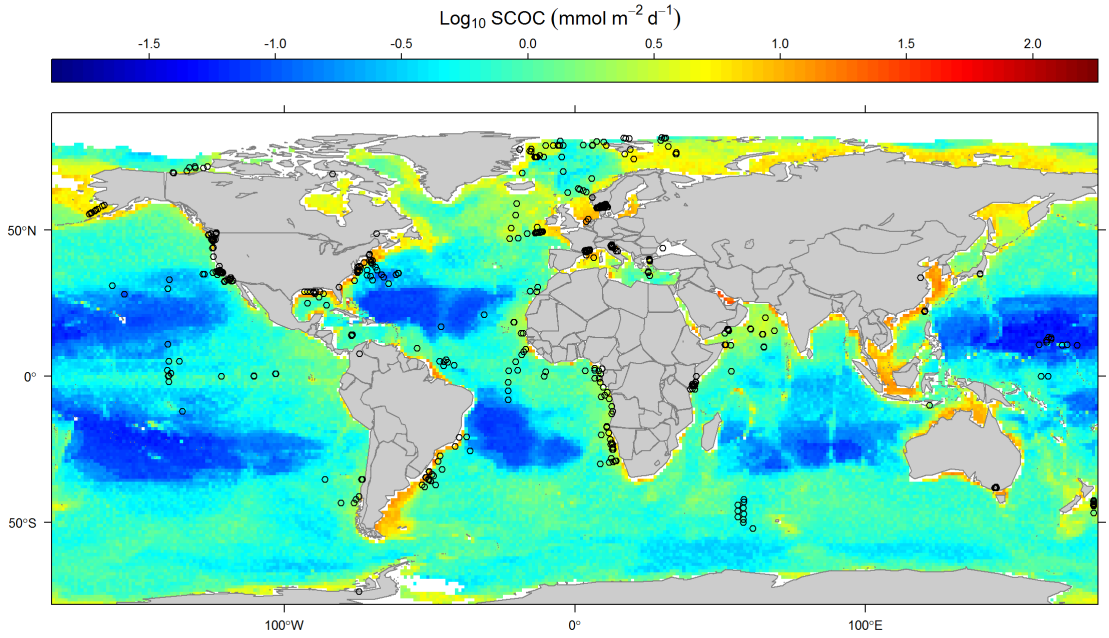

Figure 1.4 Map of predicted sediment oxygen uptake (SCOC, log_{10}) based on Random Forests model. Colder colors indicate regions with lower predicted fluxes whereas warmer colors indicate regions with higher predicted fluxes. Dots denote locations of data used in analysis. Negative values represent areas with very low O_2 uptake rates and reflect the logarithmic scale used.

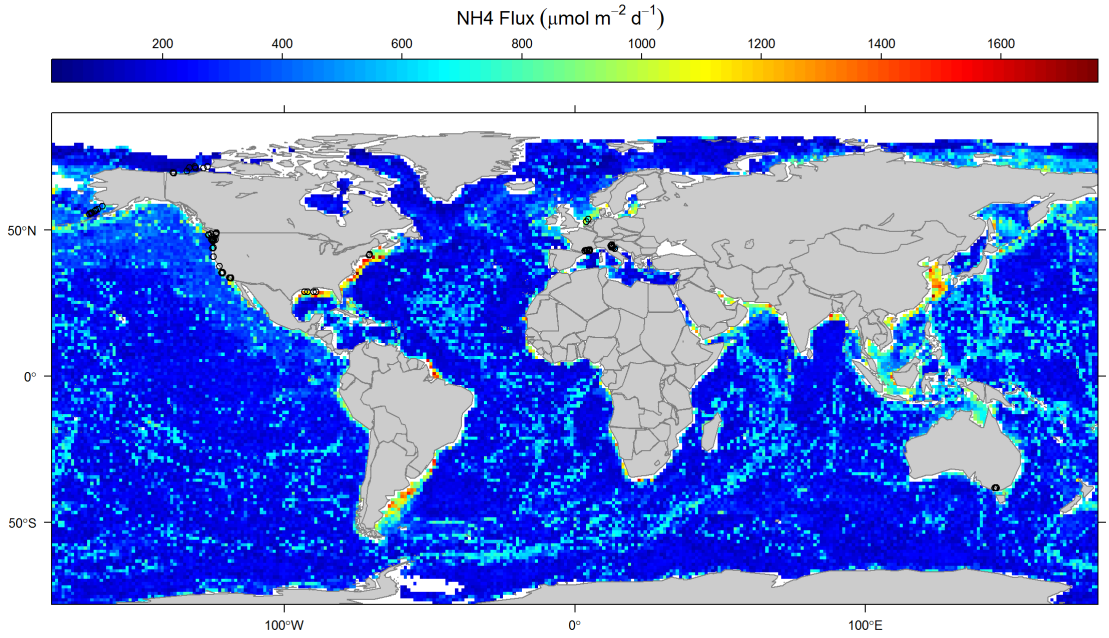

Figure 1.5 Map of predicted ammonium sediment efflux based on Random Forests model. Colder colors indicate regions with lower predicted fluxes whereas warmer colors indicate regions with higher predicted fluxes. Dots denote locations of data used in analysis.

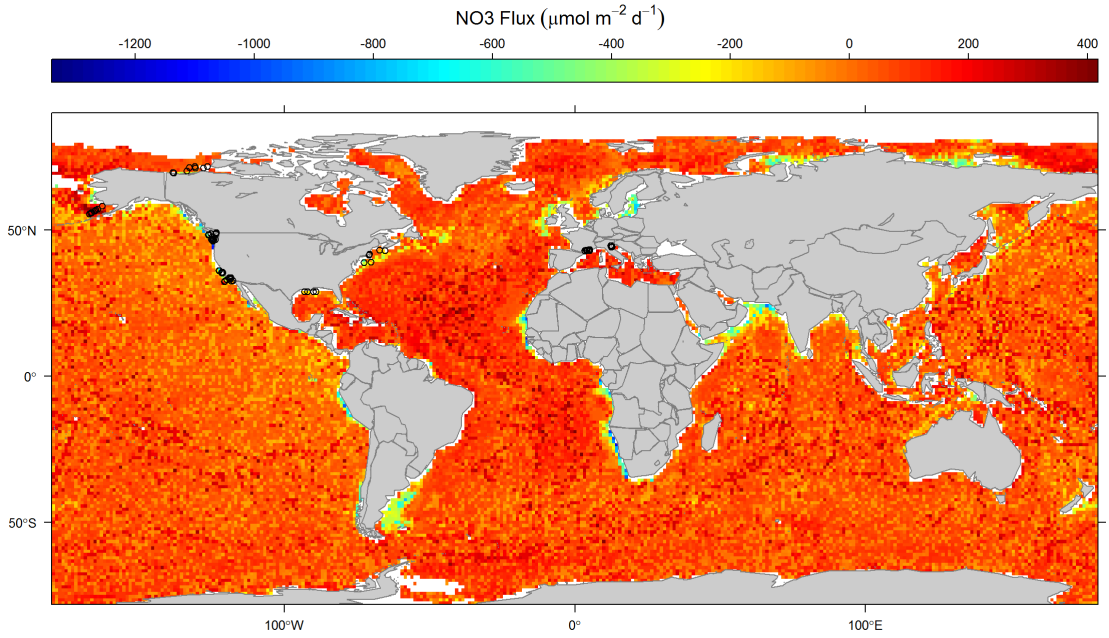

Figure 1.6 Map of predicted nitrate sediment flux based on Random Forests model. Warmer colors indicate regions with lower predicted fluxes whereas colder colors indicate regions with higher predicted sediment uptakes. Dots denote locations of data used in analysis.

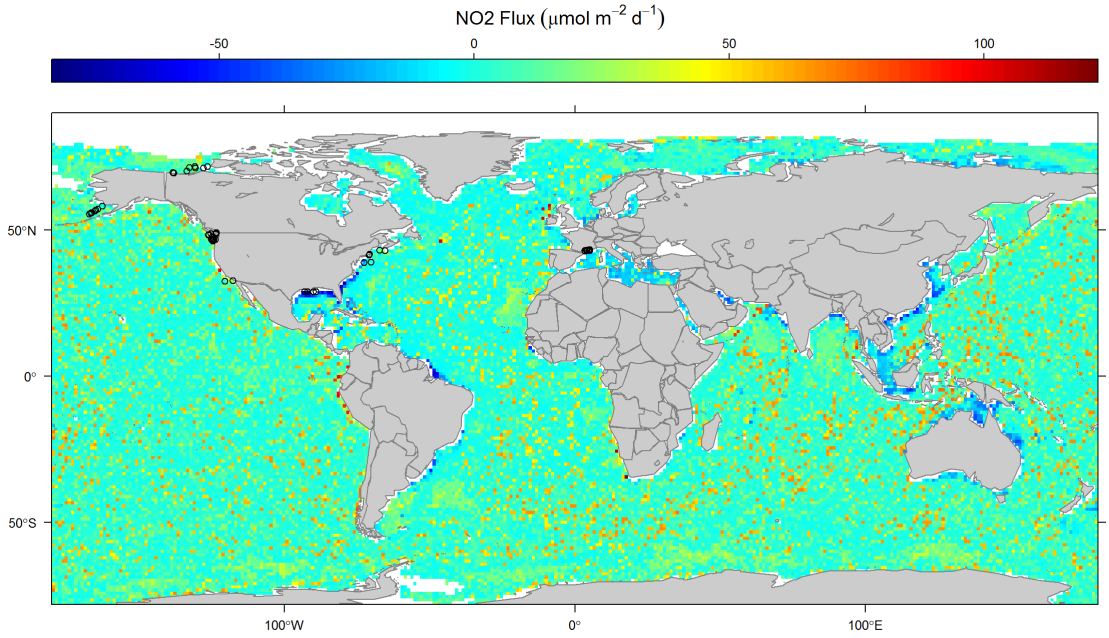

Figure 1.7 Map of predicted nitrite sediment flux based on Random Forests model. Warmer colors indicate regions with lower predicted fluxes whereas colder colors indicate regions with higher predicted sediment uptakes. Dots denote locations of data used in analysis.

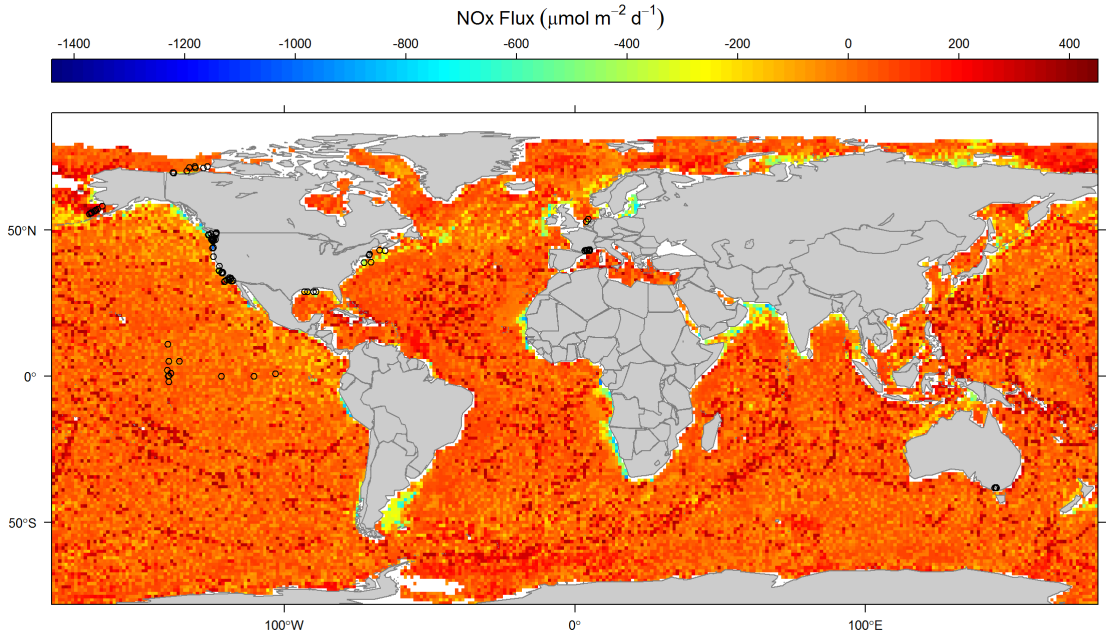

Figure 1.8 Map of predicted NOx sediment uptake based Random Forests model. Warmer colors indicate regions with lower predicted fluxes whereas colder colors indicate regions with higher predicted sediment uptakes. Dots denote locations of data used in analysis.

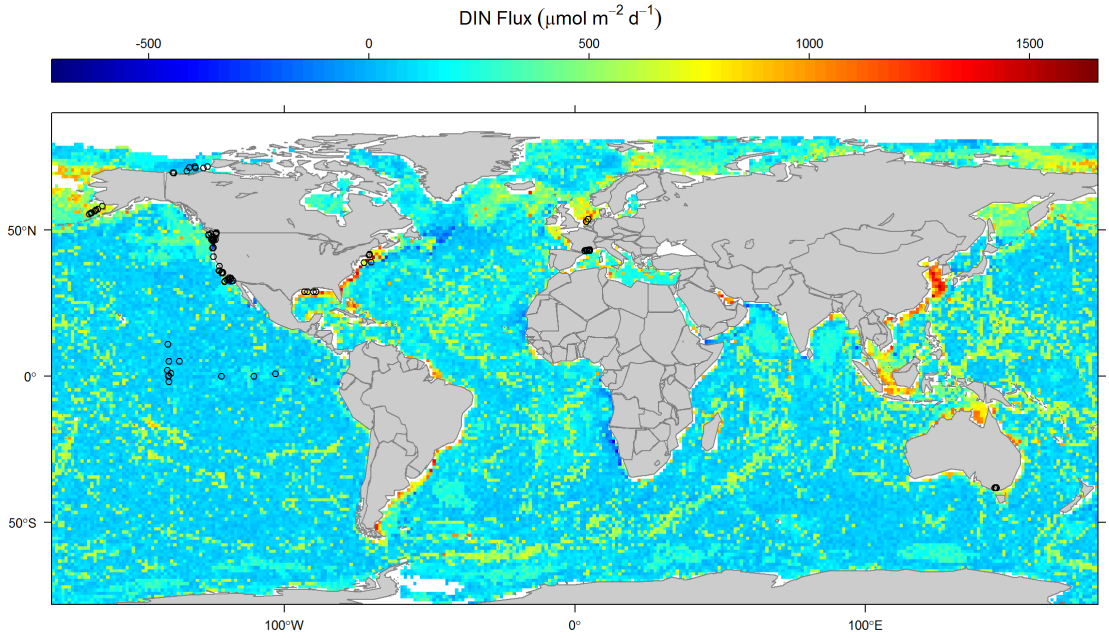

Figure 1.9 Map of predicted DIN sediment flux based on Random Forests model. Colder colors indicate regions with lower predicted fluxes whereas warmer colors indicate regions with higher predicted fluxes. Dots denote locations of data used in analysis.

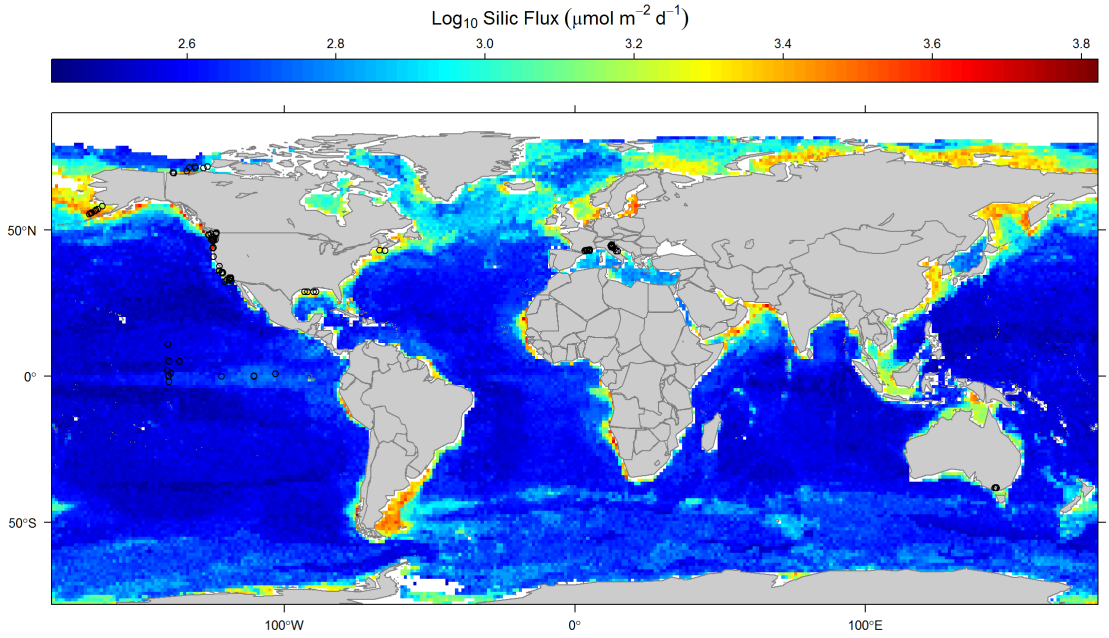

Figure 1.10 Map of predicted silicate sediment efflux (log_{10}) based Random Forests model. Colder colors indicate regions with lower predicted fluxes whereas warmer colors indicate regions with higher predicted fluxes. Dots denote locations of data used in analysis.

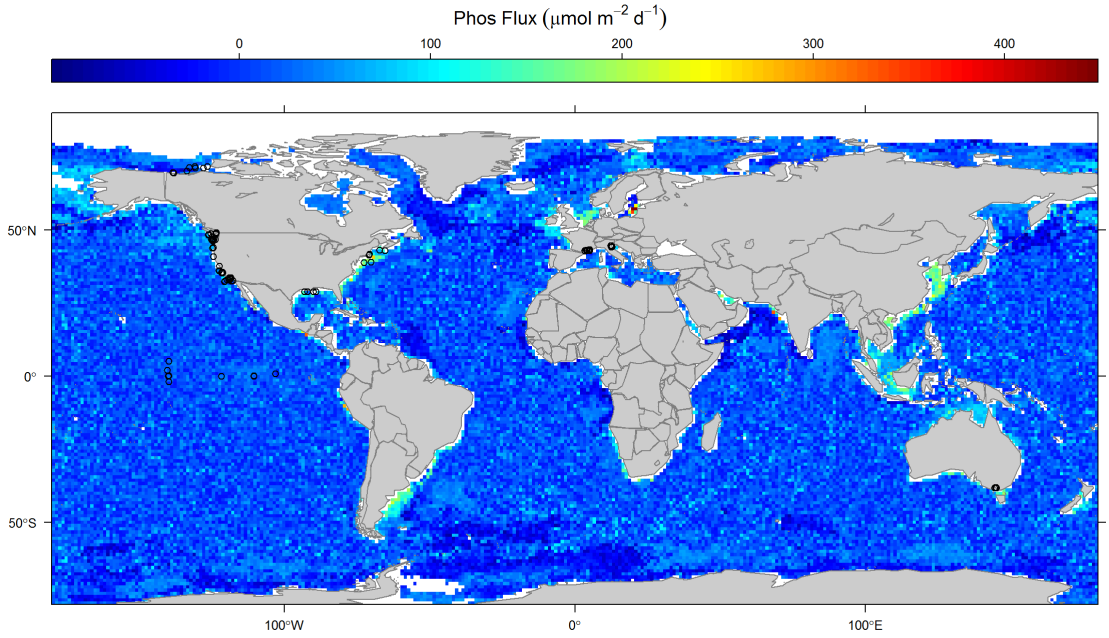

Figure 1.11 Map of predicted phosphate sediment efflux based Random Forests model. Colder colors indicate regions with lower predicted fluxes whereas warmer colors indicate regions with higher predicted fluxes. Dots denote locations of data used in analysis.

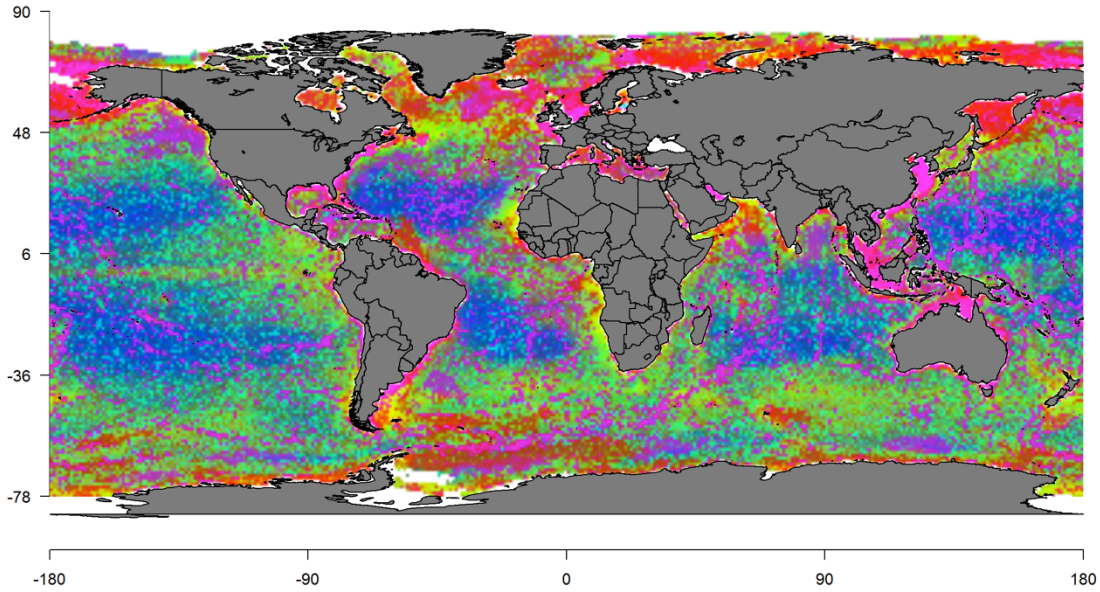

Figure 1.12 Map of multiple ecosystem functions based on O_2 and five main nutrients. Regions with similar color indicate shared multivariate benthic fluxes. Colder colors indicate regions with lower predicted fluxes whereas warmer colors indicate regions with higher predicted fluxes.

Chapter 2 — Environmental drivers of benthic flux variation and ecosystem functioning in Salish Sea and Northeast Pacific sediments*

2.1 Abstract

The upwelling of deep waters from the oxygen minimum zone in the Northeast Pacific from the continental slope to the shelf and into the Salish Sea during spring and summer offers a unique opportunity to study ecosystem functioning in the form of benthic fluxes along natural gradients. Using the ROV ROPOS I collected sediment cores from 10 sites in May and July 2011, and September 2013 to perform shipboard incubations and flux measurements. Specifically, I measured benthic fluxes of oxygen and nutrients to evaluate potential environmental drivers of benthic flux variation and ecosystem functioning along natural gradients of temperature and bottom water dissolved oxygen concentrations. The range of temperature and dissolved oxygen encountered across my study sites allowed me to apply a suite of multivariate analyses rarely used in flux studies to identify bottom water temperature as the primary environmental driver of benthic flux variation and organic matter remineralization. Redundancy analysis revealed that bottom water characteristics (temperature and dissolved oxygen), quality of organic matter (chl *a*:phaeo and C:N ratios) and sediment characteristics (mean grain size and porosity) explained 51.5% of benthic flux

variation. Multivariate analyses identified significant spatial and temporal variation in benthic fluxes, demonstrating key differences between the Northeast Pacific and Salish Sea. Moreover, Northeast Pacific slope fluxes were generally lower than shelf fluxes. Spatial and temporal variation in benthic fluxes in the Salish Sea were driven primarily by differences in temperature and quality of organic matter on the seafloor following phytoplankton blooms. These results demonstrate the utility of multivariate approaches in differentiating among potential drivers of seafloor ecosystem functioning, and indicate that current and future predictive models of organic matter remineralization and ecosystem functioning of soft-muddy shelf and slope seafloor habitats should consider bottom water temperature variation. Bottom temperature has important implications for estimates of seasonal and spatial benthic flux variation, benthic–pelagic coupling, and impacts of predicted ocean warming at high latitudes.

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2.2 Introduction

Marine carbon, nitrogen, and phosphate cycles are linked through their fixation by phytoplankton in surface waters and their remineralization in the water column and on the seafloor (Ruttenberg 2003). The decomposition of organic matter on the seafloor and resulting early diagenetic reactions at the sediment–water interface significantly impact nutrient composition within the water column and associated ecosystem processes, releasing 25–80% of the essential nutrients (e.g., N, P, and Si) that fuel primary production in the photic zone of shallow water (<50 m) systems (Aller 2014). This co-dependence of processes between the water column and sediments, which varies with water depth (Suess 1980), defines benthic–pelagic coupling (Soetaert et al. 2000).

On the continental shelf, close benthic–pelagic coupling typically occurs over time scales of days. The benthic community generally responds rapidly to increased particulate organic carbon (POC) flux to the seafloor, resulting in measurable increases in benthic respiration (Graf 1992). This response to increased food supply may be rapid and limited in duration when food pulses to the seafloor vary seasonally, as seen in the Arctic (Sun et al. 2007, Link et al. 2011) and in some deep-sea regions (Graf 1989, Gooday 2002, Smith et al. 2002). If organic matter (OM) sinks through several hundred meters in the water column before reaching the seafloor, the lag between peak surface primary production and settlement of associated OM particles on the seafloor may span weeks (Wei et al. 2010b). In addition to an increase in oxygen uptake, several studies correlate POC flux reaching

the seafloor with increased abundance and activity in bacteria, foraminifera, and meiofauna (Pfannkuche 1993, Gooday 2002).

Ecosystem functioning of benthic habitats, such as organic matter remineralization, depends strongly on biological (e.g., faunal activities and diversity) and environmental (e.g., particulate organic matter flux to the seafloor) factors (Godbold 2012, Stief 2013). Although many previous studies investigated the effects of biological drivers on ecosystem processes and functions under controlled conditions (see reviews of Duffy (2009), Hooper et al. (2005), Stachowicz et al. (2007)), the few studies that also addressed one or more abiotic drivers have shown that environmental variables also play a key role in controlling ecosystem functioning (Godbold & Solan 2009, Godbold et al. 2011, Godbold 2012, Link et al. 2013b). Among them, most studies identify bottom water temperature (Hargrave 1969, Cowan et al. 1996, Alonso-Pérez & Castro 2014), dissolved oxygen concentration (Cowan et al. 1996) and POC flux to the seafloor (Jahnke 1990, Berelson et al. 1996) as the most important environmental drivers of benthic fluxes and organic matter remineralization. In the field, *in situ* studies that utilize natural variation such as those that occur along environmental gradients could potentially highlight the main environmental drivers of benthic fluxes, organic matter remineralization and ecosystem functioning in natural systems (Snelgrove et al. 2014).

Nutrient regeneration, a central contribution of marine benthic habitats to ecosystem functioning, can be quantified by measuring oxygen and nutrient fluxes at the sediment–water interface (Giller et al. 2004). Many benthic flux studies use

sediment core incubations which, despite some artefacts (Aller 2014), produce reliable estimates of benthic flux in water depths <1000 m (e.g., oxygen measurements (Glud et al. 1994)) and therefore provide a valuable tool for studying spatial and temporal variation in benthic fluxes.

The decomposition of organic matter at the sediment surface releases or takes up multiple dissolved nutrients such as ammonium, nitrate, nitrite, silicate, and phosphate, but the vast majority of published studies used oxygen uptake as a proxy for organic matter remineralization. Even so, oxygen uptake may not necessarily be the best variable to evaluate seafloor organic matter oxidation (Berelson et al. 2003), and a recent study in the Beaufort Sea showed that oxygen flux poorly represented other nutrient dynamics (Link et al. 2013a). Here, I examine multiple flux measures of OM constituents and determine the effectiveness of multivariate analyses in discerning among potential drivers of ecosystem function and providing a more global understanding of benthic remineralization patterns and drivers.

My study focuses specifically on two contrasting seabed environments in the Northeast Pacific. The Salish Sea, a semi-enclosed inland sea between Vancouver Island and mainland British Columbia, Canada, was chosen because past studies indicated strong seasonality in temperature, dissolved oxygen (Masson & Cummins 2007), and primary productivity (Grundle et al. 2009, Johannessen & Macdonald 2009). In contrast, the British Columbia continental slope offers a deep seafloor study site within an oxygen minimum zone (OMZ, dissolved O_2 < 0.5 mL L^{-1}); the OMZ affects the Northeast Pacific continental shelf and Salish Sea bottom waters to

different degrees (see Sect. 2.2). The comparison of two very different environments offers an opportunity to study the drivers of benthic flux along natural gradients of bottom water dissolved oxygen concentration and temperature. Furthermore, recent declines in dissolved oxygen concentrations in both study areas add to the importance of understanding the role of dissolved oxygen in determining benthic fluxes.

The bottom waters off Vancouver Island on the British Columbia continental shelf and slope experienced declining oxygen concentrations from the early 1980s to 2011, declining at rates of 0.019 to 0.025 mL L^{-1} y^{-1} (Crawford & Pena 2013). This phenomenon partly explains the observed 0.02 to 0.03 mL L^{-1} y^{-1} oxygen decrease in the bottom waters of the Salish Sea (Strait of Georgia) between 1970 and 2006 (Masson & Cummins 2007, Johannessen & Macdonald 2009). The oxygen concentration in the deep Strait of Georgia now reaches a minimum of ~ 2 mL L^{-1} (Johannessen et al. 2014). Ongoing climate warming associated with human activities (IPCC 2013) could further change seawater properties (e.g., increase temperature, decrease dissolved oxygen and pH) and thereby affect biogeochemical fluxes in the Salish Sea (Johannessen & Macdonald 2009).

The main objective of this study was to apply a suite of multivariate analyses widely used by ecologists to measurements of ecosystem functioning related to sediment geochemistry. Specifically, I examined benthic oxygen and nutrient fluxes in order to determine environmental drivers of spatial and temporal variation in organic matter remineralization. I addressed my objective by exploring the following research questions: i) do regional flux differences exist between the Salish

Sea and NE Pacific, ii) do Salish Sea sites vary spatially and temporally, iii) do NE Pacific sites vary spatially in remineralization and nutrient flux, and iv) which environmental variables drive benthic fluxes and remineralization at my study sites?

2.3 Materials and Methods

2.3.1 Field sampling

Sampling targeted locations near the VENUS Observatory nodes in the Salish Sea and some NEPTUNE Observatory nodes on the continental shelf and slope off Vancouver Island (Figure 2.1). These observatories are operated by Ocean Networks Canada (www.oceannetworks.ca). I collected push core sediments using the Remotely Operated Vehicle (ROV) ROPOS (www.ropos.com) on board the Canadian Coast Guard Ship John P. Tully (May 7–14, 2011), and the Research Vessels Thomas G. Thompson (June 30–July 3, 2011) and Falkor (September 6–18, 2013). I sampled the VENUS Strait of Georgia Central (SoGC) and the Delta Dynamic Laboratory (DDL) sites in May and July 2011, the Strait of Georgia East (SoGE) in May 2011 and September 2013, and Saanich Inlet (SI) in July 2011 and September 2013 (Table 2.1). NEPTUNE sites were sampled in July 2011 except for BC300 (Barkley Canyon, 300 m depth), which I sampled in September 2013. The ROV collected 3–10 push-cores at each site (i.d. = 6.7 cm, L = 35.6 cm) at random locations. One core per site served to determine prokaryotic cell abundance and sediment properties, and the remaining cores were used for incubations to measure fluxes. A SBE 19plus V2 CTD

mounted on the ROV recorded near-bottom dissolved oxygen (DO), temperature, and salinity. No specific permissions were required for these locations/activities and field studies did not involve endangered or protected species.

2.3.2 Study area hydrographic description

Ocean circulation around my study area results from complex interactions between multiple currents, eddies, and water masses, as well as tides and seasonal wind patterns. An oxygen minimum zone (OMZ) at intermediate depth (400–1000 m) (Keeling et al. 2010) adds complexity to continental slope waters along the west coast of North America, including my Barkley Canyon mid-slope sites (Axis, BMC, and Hydrates) (Juniper et al. 2013). Summertime northerly winds upwell this low-oxygen deep water to the continental shelf (Freeland & Denman 1982, Hsieh et al. 1995, Crawford & Pena 2013). Estuarine circulation, driven by freshwater from the Fraser River at the north in the Strait of Georgia, facilitates subsurface movement of hypoxic water into the Salish Sea through the Strait of Juan de Fuca. Re-oxygenation of this deep water can occur during transport over the sill at the tidal passages of Haro Strait, replenishing oxygen in Strait of Georgia deep waters in late spring and late summer (Johannessen & Macdonald 2009, Khangaonkar et al. 2012, Johannessen et al. 2014). Finally, during fall, these same deep waters enter Saanich Inlet, a seasonally hypoxic fjord, by flowing over the sill from Haro Strait and replenishing oxygen-depleted bottom waters in the basin of the fjord (Thomson 1981).

2.3.3 Incubations

At each sampling site I incubated 2–4 sediment cores by capping the bottom of each core and, where necessary, topping up core tubes with bottom water collected from the same site by the ROV suction sampler. Sediment cores were incubated in a dark cold room at *in situ* temperatures (4–9 ˚C), in May and July 2011, and in a modified chest freezer in September 2013. The high sampling intensity, tight dive schedule, and limited number of incubations that could be run simultaneously meant that core acclimation times to allow sediment particles in suspension in the overlying water to settle back to the sediment surface varied from 4–24 hours, which is within the normal range of acclimation time reported in the literature (Valdemarsen et al. 2012, Link et al. 2013a, Nunnally et al. 2013). Before the end of the acclimation period and just before the onset of incubations, I simultaneously aerated the overlying water in each core for a minimum of one hour using aquarium air pumps to avoid suboxic conditions during incubations; this strategy has no significant effect on flux rates (see below), as reported in previous studies (Link et al. 2013a). At the beginning of the incubations, I hermetically sealed cores with caps equipped with magnetic stirrers and gas-tight sampling ports. This system constantly stirred and homogenised the overlying water gently without resuspending surface sediments. Incubations ran for 12–48 hours until 15–30% of available oxygen was consumed and the volume of the overlying water was 444 ± 90 mL (mean ± SE).

2.3.4 Oxygen uptake

I measured oxygen consumption periodically (4–8 hours intervals) using a 500-µm oxygen microsensor (Unisense, Aarhus, Denmark) inserted through a small resealable hole on the top of the cap in May and July 2011, and with a non-invasive optical oxygen meter used in conjunction with oxygen optode patches (Fibox 4, PreSens, Regensburg, Germany) in September 2013. I then determined oxygen uptake from the slope of the linear regression of oxygen concentration versus time of incubations after correction for the oxygen concentration in the replacement water.

2.3.5 Nutrient fluxes

At the beginning, midpoint, and end of the incubations I collected water samples with 60-mL, acid-rinsed plastic syringes, except in the SI, SoGC, and DDL incubations in July 2011 where high oxygen consumption limited water sampling to the beginning and end of the incubations as a result of the shortened incubation period (12 hours). I immediately replaced withdrawn water with an equivalent volume of bottom water of known oxygen and nutrient concentrations. Syringes and sample containers were initially rinsed with ~5 mL of water sample. At each sampling time I collected and stored two 25-mL water samples in acid-rinsed twist-cap 30-mL HDPE bottles. Upon collection, water samples were immediately placed in an upright position at -20 °C until analysed. Given the numerous nutrients analysed, the risk of contamination, and the absence of suspended particles in water samples, I followed Aminot & Chaussepied (1983) and chose not to filter water

samples prior to storage. In the few instances where suspended particles were present in water samples, I allowed particles to settle and excluded them from the analysis (Aminot et al. 2009). I determined the concentrations of nutrients (NH_4^+, NO_3^-, NO_2^-, $Si(OH)_4$ & PO_4^{3-}) in the water samples using a Technicon Segmented Flow AutoAnalyzer II, following the method recommended by Technicon Industrial Systems (1973, 1977, 1979) with the exception of ammonia (hereafter referred as ammonium) analysis, which followed Kerouel & Aminot (1997). Nutrient fluxes were determined from the slope of the linear regression of nutrient concentrations versus time of incubations after correction for the solute concentration in replacement water.

2.3.6 Effect of overlying water air bubbling on benthic flux rates

I added a complementary experiment at BC300 in September 2013 to determine whether air bubbling before the onset of the incubations affected benthic flux rate measurements. For this experiment, I processed four cores exactly as described above but added a second treatment in which I gently topped up five additional cores with bottom water collected *in situ* and quickly sealed them to maintain oxygen concentrations as close to *in situ* condition as possible but without bubbling. I held replacement water to exchange with withdrawn water in a sealed container equipped with an optical oxygen patch (see above) to measure DO in replacement water. I measured overlying water DO prior to incubations, and performed O_2 uptake and nutrient analyses as described above.

2.3.7 Oxygen penetration depth (OPD)

Immediately after recovery of the ROV I profiled oxygen concentrations as a function of depth in the sediment for one sediment core from each site. In each core, I performed three replicate profiles with Unisense oxygen microsensors (500 µm and 250 µm tip sizes in 2011 and 2013, respectively) in vertical increments of 1000 µm and 500 µm in 2011 and 2013, respectively. I defined the oxygen penetration depth (OPD) in the sediment as the mean depth where oxygen concentration decreased below the suboxic level of 5 µmol L^{-1} (Thibodeau et al. 2010).

2.3.8 Prokaryotic cells

To sample sediment prokaryotes I subcored the sediment cores with a cut off 10-mL sterile plastic syringe at depths of 0–2, 2–5 and 5–10 cm. I placed 1 mL of sediment from each depth in a 20-mL scintillation vial containing 4 mL of a filtered-sterilized 2% seawater-formalin solution. Samples were frozen at -20 ˚C until analysis. Sediment prokaryote abundance and biomass were determined following Danovaro (2010).

2.3.9 Sediment properties

To characterize sediment properties I sectioned the upper 2-cm layer of sediment from one sediment core using inert plastic spatulas. Each sediment layer was carefully placed in a Whirl-Pak bag and stored at -20 °C until analysed. Total organic matter (TOM) was determined by ignition loss, and water content as the

difference between the wet and dry sediment weights divided by the sediment initial weight (Danovaro 2010). Sediment porosity and dry bulk density were calculated using formulas from Avnimelech et al. (2001) with a particle density of 2.65 g cm^{-3}. I determined granulometric properties (sediment mean grain size; MGS) with a HORIBA Partica LA-950 laser diffraction particle size analyzer (Horiba Ltd, Kyoto, Japan). To prepare samples for analyses of total organic carbon (TOC) and total nitrogen (TN), I dried them for 24 h at 80 °C, fumed with 1 M HCl for 24 h, and dried them again for a minimum of 24 h. Finally, approximately 2 mg of sediment samples were weighed into a tin capsule and stored at 80 °C until analysed in a Perkin-Elmer 2400 Series II CHN analyzer. I used the carbon to nitrogen (C:N) ratio as a measure of organic matter nutritional quality on a long time scale (Le Guitton et al. 2015), where lower ratios indicate fresher and higher quality organic matter (Vidal et al. 1997, Godbold & Solan 2009).

2.3.10 Chlorophyll-*a* and Phaeopigments

Concentrations of chlorophyll-*a* (chl *a*) and phaeopigments (phaeo) were quantified fluorimetrically following a modified version of Riaux-Gobin & Klein (1993). I incubated 1–2 g of wet sediment for 24 h in 90% acetone (v/v) at 4 ˚C and then analysed the supernatant prior to and following acidification using a Turner Designs 10-AU-005-CE fluorometer (Turner Designs, Sunnyvale, USA). The remaining sediment was dried at 60 °C for 24 h and weighed in order to standardize pigment concentrations per gram of sediment. The chl *a*:phaeo ratio provides a measure of organic matter quality on a short time scale (Le Guitton et al. 2015),

where higher ratios indicate more recently settled phytoplankton particles and therefore fresher organic matter (Morata et al. 2011, Suykens et al. 2011).

2.3.11 Statistical analyses

I examined spatial and temporal variation in all benthic fluxes using a permutational multivariate analysis of variance (PERMANOVA) performed with 9999 random permutations of appropriate units (Anderson 2001, McArdle & Anderson 2001). Three analyses based on subsets of my data addressed three research questions: 1) a one-way PERMANOVA design using all data collected in July 2011 with the factor "Region" (two levels: Salish Sea, NE Pacific) tested regional variability between the Salish Sea and the NE Pacific shelf and slope, 2) a two-way crossed PERMANOVA design tested spatial and temporal variation in the Salish Sea using all data collected in this region with the factors "Date" (three levels: May 2011, July 2011, September 2013), crossed with "Sites" (four levels: SI, SoGC, SoGE, DDL) and their interactions, and finally 3) a one-way PERMANOVA design using data from this region collected in July 2011 with the factor "Sites" (five levels: Axis, BMC, BUP, Folger, Hydrates) tested spatial variation in the NE Pacific. I calculated the resemblance matrix from Euclidean distances of standardized benthic flux and verified homogeneity of multivariate dispersions using the PERMDISP routine (Anderson et al. 2008). When too few possible permutations were possible to obtain a reasonable test, I calculated a *p*-value based on 9999 Monte Carlo draws from the asymptotic permutation distribution (Terlizzi et al. 2005). I further analysed significant terms within the full models using appropriate pair-wise comparisons. I

completed PERMANOVA and PERMDISP analyses in PRIMER 6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

I determined the model that best explained variation of each benthic flux separately based on environmental drivers using multiple linear regression in the software package R 3.1.1 (R Core Team 2016). Predictor variables containing outliers were transformed, excluding highly correlated ($r > 0.95$) predictor variables from the analyses. I further analysed multi-collinearity of the predictor variables from the full models with a variance inflation factor (VIF) test using the "vif" function from the "car" package (Fox & Weisberg 2011), removing predictor variables with the highest VIF so that the best model selected contained only predictor variables with VIF < 5 (Zuur et al. 2009). Temperature, DO, OPD, chl *a*:phaeo (log_{10}), C:N (log_{10}), porosity, MGS, and prokaryotic cell abundance (log_{10}) were entered into the model as predictor variables. I used Akaike's information criterion (AIC) to determine the environmental variables best explaining each benthic flux (Quinn & Keough 2002), visually verifying residual normality and homogeneity. Because ammonium residual distribution was skewed, I applied a log_{10} transformation to resolve the issue.

I also performed a distance-based redundancy analysis (dbRDA) using the distance-based linear model (distLM) routine from the software PRIMER 6 (Clarke & Gorley 2006) and the PERMANOVA+ add-on (Anderson et al. 2008). This ordination technique provided a global understanding of environmental drivers of organic matter remineralization on the seafloor at study locations by analysing all benthic fluxes simultaneously within the same analysis. I determined the model

with environmental drivers that best explained variation in benthic fluxes using a stepwise routine that employed 9999 permutations based on AICc selection criterion. This criterion is more appropriate to use with a small ($N/v < 40$) ratio of number of samples (N) to number of predictor variables (v)(Anderson et al. 2008). Draftsman's plots of predictor variables indicated high correlation ($r > 0.95$) between five of my predictor variables (surface sediment phaeo, TN, water content, bulk density and prokaryotic cells biomass) and other predictors; I therefore excluded these five variables from the analysis. The optimal model selection included 13 predictor variables: bottom water temperature, salinity, depth, DO, OPD, surface sediment chl *a*, chl *a*:phaeo ratio, TOM, TOC, C:N ratio, porosity, MGS and prokaryotic cell abundance. To correct for data skewness, I applied a natural logarithmic (Ln) transformation to four predictor variables (chl *a*, chl *a*:phaeo, C:N and Prokabun) and to the response variable O_2 uptake; the response variable silicate required square root transformation (Anderson et al. 2008). Prior to distLM, I standardised flux and environmental data using the "normalise" function in PRIMER-E (Clarke & Gorley 2006). After standardisation, I created resemblance matrices based on Euclidean distances. I further analysed the multi-collinearity of the predictor variables from the best model with a VIF test as described above, also in R (R Core Team 2016), removing predictor variables with a VIF > 5 (i.e. Depth, Sal and chl *a*) prior to selection of the best model (Zuur et al. 2009).

I analysed the effect of air bubbling (two levels: with bubbling, without bubbling) on each benthic flux (O_2, NH_4^+, NO_3^-, NO_2^-, $Si(OH)_4$ & PO_4^{3-}) separately using one-way analysis of variance (ANOVA), verifying normality of residuals and

homogeneity of variance visually (Quinn & Keough 2002). I also used PERMANOVA to investigate the effect of air bubbling on all benthic fluxes, following the procedure described above except the PERMANOVA design included only "air bubbling" as a factor (two levels: ambient, oxygenated).

2.4 Results

2.4.1 Variation of individual benthic flux

In general, benthic fluxes in the Salish Sea exceeded those in the NE Pacific (Figure 2.2 a-f, Supplementary Table 2.1). Oxygen uptake varied between -2.0 mmol O_2 m^{-2} d^{-1} in BUP-07 and -17.1 mmol O_2 m^{-2} d^{-1} in SoGC-07, with one extreme measurement of -32.9 mmol O_2 m^{-2} d^{-1} in SI-07 (Figure 2.2 a, Supplementary Table 2.1). The sediment biota generally released rather than consumed ammonium, and fluxes varied between modest sediment uptakes of -65.9 μmol m^{-2} d^{-1} for BUP-07 to releases of 2202.0 μmol m^{-2} d^{-1} in DDL-07 (Figure 2.2 b, Supplementary Table 2.1). The sedimentary biota generally consumed nitrate (except SoGE-09 and BC300-09) with the highest uptake of -1018.6 μmol m^{-2} d^{-1} in SI-07 and highest release of 693.5 μmol m^{-2} d^{-1} in BC300-09 (Figure 2.2 d, Supplementary Table 2.1). I observed no clear difference in nitrate fluxes between the Salish Sea and NE Pacific sites. The sedimentary biota also generally consumed nitrite (except SoGC-07 and BUP-07) and fluxes were generally small relative to nitrate flux. I measured the highest uptake of -80.0 μmol m^{-2} d^{-1} in SoGE-05 (Figure 2.2 f, Supplementary Table 2.1). Silicate releases from the sediment varied between 130.3 and 13,458.7 μmol m^{-2} d^{-1}

in DDL-07 and SoGE-09 respectively (Figure 2.2 c, Supplementary Table 2.1). Sediments generally released phosphate in the Salish Sea (except in SI and DDL-07) in contrast to uptake in the NE Pacific (except BUP-07), with highest uptake (-955.4 μmol m^{-2} d^{-1}) at BC300-09 and highest release (697.0 μmol m^{-2} d^{-1}) at SoGC-05 (Figure 2.2 e, Supplementary Table 2.1).

2.4.2 Regional variation in benthic fluxes

July 2011 offered the only opportunity to compare benthic fluxes directly between the Salish Sea and NE Pacific regions at the same time. PERMANOVA revealed significant differences in multivariate benthic fluxes between the two regions (P (perm) < 0.01, Table 2.2).

2.4.3 NE Pacific spatial variation in multivariate benthic fluxes

All NE Pacific benthic flux measurements occurred in July 2011, except for flux measurements at BC300 in September 2013. Therefore, I limited spatial analysis of benthic fluxes in this region to July 2011 samples (Deep Barkley Canyon: Axis, Hydrates and BMC; Upper Slope and shelf: BUP and Folger). PERMANOVA analysis indicated significant between site differences (P (perm) < 0.01, Table 2.2). Pair-wise comparisons showed significant differences between Axis and Hydrates (P (MC) = 0.026), BUP and Axis (P (MC) < 0.01), BUP and Folger (P (MC) < 0.01), and BUP and Hydrates (P (MC) = 0.042). Folger and Axis (P (MC) < 0.01), and Folger and BMC (P (MC) = 0.018) also differed significantly.

2.4.4 Salish Sea spatial variation in multivariate benthic fluxes

Although PERMANOVA analysis of Salish Sea sites sampled during the same time period indicated significant spatial differences (P (perm) < 0.01, Table 2.2), pair-wise comparison tests of benthic fluxes generally showed weak or no significant differences. The strongest flux difference occurred between SI and SoGE in September 2013 (P (MC) = 0.030). I observed weak, but significant differences in benthic fluxes in May 2011 between SoGE and SoGC (P (MC) = 0.046), and between SoGC and DDL (P (MC) = 0.043). SoGC and DDL (P (MC) = 0.049) also differed significantly, though weakly, in July 2011. However, I observed no significant difference in benthic fluxes between SoGE and DDL in May 2011, or between SI and SoGC and SI and DDL in July 2011.

2.4.5 Temporal variation in multivariate benthic fluxes

PERMANOVA analysis of Salish Sea sites sampled at different times indicated significant within-site temporal differences (P (perm) < 0.01, Table 2.2). Pair-wise comparison tests indicated significant temporal differences at SoGC (May and July 2011; P (MC) = 0.028) and DDL (May and July 2011; P (MC) = 0.026) but no significant temporal differences at SI (July 2011 and Sep 2013; P (MC) = 0.088) or SoGE (May 2011 and Sep 2013; P (MC) = 0.105).

2.4.6 Environmental drivers of multivariate benthic fluxes variation

My best distance-based linear model (distLM) explained 51.5% of total benthic flux variation and included six environmental variables (Table 2.3). Bottom water temperature contributed most to the variation (16.3%), followed by chl *a*:phaeo ratio (11.8%), C:N ratio (7.9%), DO (6.3%), MGS (4.9%) and porosity (3.8%) (Table 2.3). The best model excluded O_2 penetration depth, TOM, C and prokaryotic abundance.

The first and second axes of the distance-based redundancy model accounted for 21.3 and 17.0% of total flux variation respectively. The first axis separated Salish Sea and NE Pacific shelf (i.e., Folger) stations from the deeper NE Pacific slope sites (Figure 2.3). Temp, DO, and MGS contributed primarily to the first axis and explained 41.4% of the fitted fluxes variation (Figure 2.3, Table 2.4). Benthic fluxes from the Salish Sea on the second axis varied more than those from the NE Pacific, explaining 33.0% of the fitted variation in fluxes and correlating most strongly with the chl *a*:phaeo ratio (Figure 2.3, Table 2.4).

2.4.7 Environmental drivers of single benthic flux variation

Combinations of the eight primary environmental predictors explained > 50% of the variation in fluxes of oxygen and the five nutrients, except for nitrate and nitrite models, which nonetheless explained 41 and 30% of variance respectively (Table 2.5). Phosphate flux yielded the best predictive model, increasing with bottom water DO, and decreasing with sediment OPD, chl *a*:phaeo (Figure 2.4 d), porosity, MGS, and prokaryote abundance (Adj. $r^2 = 0.88$, $p < 0.001$). Oxygen uptake,

the second best model, increased with temperature (Figure 2.5 a), OPD, and porosity, and decreased with DO and prokaryote abundance (Adj. $r^2 = 0.75$, $p < 0.001$). Ammonium efflux increased with temperature (Figure 2.5 b), OPD, chl *a*:phaeo (Figure 2.4 a), porosity, and MGS, and decreased with prokaryote abundance (Adj. $r^2 = 0.54$, $p < 0.001$). Silicate efflux increased with DO and C:N, and decreased with chl *a*:phaeo (Figure 2.4 c) and MGS (Adj. $r^2 = 0.51$, $p < 0.001$). Nitrate uptake increased with DO and C:N, and decreased with temperature (Figure 2.5 c), OPD, and prokaryote abundance (Adj. $r^2 = 0.41$, $p < 0.001$). Finally, nitrite uptake increased with OPD and C:N, and decreased with DO, chl *a*:phaeo (Figure 2.4 b) and prokaryote abundance (Adj. $r^2 = 0.30$, $p = 0.003$).

2.4.8 Effect of overlying water air bubbling on benthic flux rates

To document the effect of air bubbling on benthic flux rates, I took great care to avoid reoxygenating overlying water before incubations, however I recorded increases in oxygen concentrations between *in situ* (1.06 mL L^{-1}) and *ex situ* conditions (3.83 to 5.12 mL L^{-1}) at the beginning of the incubations. Still, PERMANOVA on all benthic fluxes and ANOVAs on separate nutrient fluxes each indicated no significant differences in rates between aerated and non-aerated cores (P (MC) = 0.315, O_2 uptake: $P = 0.060$, ammonium: $P = 0.455$, nitrate: $P = 0.635$, nitrite: $P = 0.115$, silicate: $P = 0.248$, phosphate: $P = 0.391$).

2.5 Discussion

My study is the first to analyse oxygen and nutrient benthic fluxes along the seafloor affected by the upwelling OMZ waters from the continental slope and shelf off Vancouver Island, to the Strait of Georgia and Saanich Inlet in the Salish Sea. Results demonstrate significant spatial and temporal variation in benthic fluxes resulting from organic matter remineralization, a widely recognized key ecosystem function of benthic habitats (Giller et al. 2004, Strong et al. 2015). Multivariate statistical analyses (i.e. dbRDA) allowed me to consider environmental drivers of all benthic fluxes simultaneously within the same analysis. Multiple environmental variables drove flux variation, of which, bottom water temperature was most important. Additional major drivers included bottom water DO, quality of organic matter (chl *a*:phaeo and C:N ratios), and sediment characteristics (MGS and porosity).

2.5.1 Spatial variation

I observed significant spatial variation in flux rates both in the Salish Sea and in the NE Pacific. For NE Pacific sites, benthic fluxes from the continental shelf generally exceeded those from the slope, driven by depth-related environmental drivers. For instance, deeper, colder, and less oxygenated sites from Barkley Canyon within the OMZ, were similar to each other but generally differed significantly from shallower, warmer, and more oxygenated upper slope and shelf sites. Other, more localised environmental drivers such as small-scale variation in sediment chl

a:phaeo, C:N, MGS and porosity explained smaller differences within Barkley Canyon sites. Relatively large variation in temperature, DO, C:N, porosity, and MGS between shallower NE Pacific sites (BUP and Folger) contributed to between-site spatial differences, keeping in mind depth differences of ~300 m.

The Salish Sea exhibited weak, but significant spatial variation in May and July 2011, in contrast to stronger spatial variation between SI and SoGE in September 2013. These results demonstrate spatial similarity in benthic flux between sites in this region, driven by smaller variation in major environmental drivers compared to those in the NE Pacific. For instance, temperature, the main driver of benthic fluxes in my study, varied by ± 1.38 °C over all Salish Sea sampling locations and times, but by ± 3.88 °C in the NE Pacific.

2.5.2 Temporal variation

Salish Sea sites differed significantly between May and July 2011 (SoGC and DDL) but not between May 2011 and Sep 2013 (SoGE), and July 2011 and September 2013 (SI). The spring bloom, though variable, generally occurs in April-May in the Strait of Georgia (Johannessen & Macdonald 2009) and in Saanich Inlet (Takahashi et al. 1977). Shorter significant blooms occur intermittently over a few days in summer, in contrast to the typically larger fall bloom (Johannessen & Macdonald 2009). The onset of the spring bloom in the Strait of Georgia occurred around April 6-8 in 2011 (Gower et al. 2013), but settling of the bulk of fresh OM on the seafloor apparently occurred after my measurements in May 2011 and preceded my measurements in July 2011, as shown by increased in chl *a*:phaeo ratios (i.e.

short time scale indicator of OM freshness) at DDL between May and July 2011 (Figure 2.6, Table 2.1). Increased nutrient fluxes associated with microbial and macrofaunal community responses to fresh organic matter (OM) deposition to the seafloor following the spring and/or summer phytoplankton blooms can therefore explain temporal variations in fluxes at SoGC and DDL between May and July 2011. Similarly, several studies have reported significant increases in oxygen and nutrient fluxes after a spring bloom in San Francisco Bay (Hammond et al. 1985, Grenz et al. 2000). Jahnke (1990) also linked seasonal variation in benthic fluxes to the reactivity of deposited OM, where seafloor biota quickly metabolized relatively labile OM. In contrast, my study sites exhibited no clear increase in C:N ratios between May and July 2011, arguably because the C:N ratio indicates OM quality on a long time scale (Le Guitton et al. 2015) and therefore cannot easily indicate fresh OM. The stability of other key environmental drivers such as temperature and DO over the two sampling dates in May and July 2011 points to fresh OM deposition on the seafloor following the spring (and possible ephemeral summer) phytoplankton blooms and explains temporal variability in benthic flux rates, especially at DDL.

2.5.3 Environmental drivers of individual benthic flux variation

2.5.3.1 Oxygen

Oxygen uptake in the NE Pacific and Salish Sea varied widely, with uptake rates consistent with measurements made on the continental slope and shelf between California and Oregon using benthic chambers (Archer & Devol 1992, Devol & Christensen 1993, Berelson et al. 1996, Berelson et al. 2002, Berelson et al.

2003, Berelson et al. 2013) and eddy-correlation (Reimers et al. 2012), as well as shipboard incubations in the southeast Bering Sea (Rowe & Phoel 1992).

Previous studies have identified each of the environmental variables highlighted by my multiple linear regression model as major drivers of oxygen uptake. Temperature (Hancke & Glud 2004), DO (Archer & Devol 1992), OPD (Glud 2008), porosity (Grenz et al. 2000), and prokaryotic cell abundance (Van Duyl et al. 1992, Pfannkuche 1993, Witte et al. 2003) have been found to all influence benthic oxygen uptake. Rowe and Phoel (1992) attributed the lack of correlation between sediment oxygen demand (SOD) and depth, temperature, or dissolved oxygen to the small ranges of environmental variables measured. The spatial coverage of my study, which spanned natural environmental gradients, provided an opportunity to measure benthic fluxes over a range of natural variation but within a relatively limited geographic area. This attribute allowed me to identify key environmental drivers of benthic fluxes that may be overlooked in studies that examine a very limited temperature range variation, for example.

Bio-irrigation may also have influenced oxygen uptake; Archer and Devol (1992) found that oxygen uptake estimates using benthic chambers exceeded those measured by microelectrode techniques by 3–4 times. They argued that greater bio-irrigation on shelf sediments could explain this discrepancy because benthic flux calculations based on microelectrode techniques cannot account for macrofaunal irrigation whereas benthic chambers can. The techniques produce similar results in slope sediments because of reduced macrofaunal abundance and bio-irrigation at these depths. I also observed higher macrofaunal abundances at my shelf sites than

at my deeper NE Pacific slope sites (R. Belley, unpublished data). Moreover, oxygen penetration, which typically increases in bioturbated and bio-irrigated sediments (Aller & Aller 1998), increased in my study as a function of bottom water oxygen concentration (Figure 2.7). This increase suggests higher bio-irrigation at the shallower and more oxygenated shelf sites than in deeper and oxygen-depleted slope sites on the NE Pacific.

2.5.3.2 Nitrogen compounds

Given that the marine nitrogen cycle arguably represents the most complex of all biogeochemical cycles in the ocean (Gruber 2008), a complete study of the nitrogen cycle at my sampling stations exceeds the scope of my study. Nonetheless, my analyses indicate important trends in nitrogen cycling within seafloor sediments. Ammonium effluxes were generally low in the Salish Sea before the settling of OM on the seafloor following the spring and smaller summer blooms in May 2011 relative to those measured after the settling of OM on the seafloor following the blooms in July 2011 and September 2013. Whitledge et al. (1986) reported a similar increase in ammonium production following the spring phytoplankton bloom in the southeast Bering Sea and subsequent phytoplankton decomposition. Results from my multiple linear regression models indicate prokaryotic cell abundance, a proxy for the primary metabolic driver of benthic biogeochemical processes, influenced patterns for all nitrogen compounds. On the one hand, the overall higher release of ammonium compared to nitrate and nitrite uptake suggest ongoing nitrification and associated chemoautotrophy and

ammonium oxidation in the Salish Sea as Whitledge et al. (1986) proposed for the Bering Sea. On the other hand, nitrate uptake dominated the NE Pacific, with low ammonium and nitrite fluxes except for BC 300. This pattern suggests ongoing denitrification in my NE Pacific sites. Previous studies emphasize the importance of denitrification as an organic matter oxidation pathway at low bottom water oxygen concentration (Canfield 1993), such as in the OMZ off the coast of Vancouver Island in the NE Pacific.

2.5.3.3 Silicate

My study shows generally higher silicate effluxes from shallower shelf sites than deeper slope sites, with some seasonal variation. Silicate variation often reflects small-scale differences in sediment properties, bioturbation, and irrigation (Rowe & Phoel 1992). Hammond et al. (1985) reported a 3–10 fold increase in silica effluxes associated with high phytoplankton productivity and bio-irrigation. Accordingly, my multiple linear regression model identified quality of OM (chl *a*:phaeo and C:N), bottom water DO, and sediment MGS as the best predictors of silicate benthic efflux variation. Because I did not measure bio-irrigation, I cannot directly link silicate effluxes with this variable. However, increased oxygen penetration with bottom water oxygen concentration suggests higher bio-irrigation at the shallower and more oxygenated shelf sites than in deeper and oxygen-depleted slope sites on the NE Pacific. Lower oxygen concentration can also change macrobenthic community structure to one that primarily inhabits and reworks the surface of the seafloor and poorly bio-irrigates sediment at depth (Belley et al.

2010). Much higher macrofaunal abundances at the shelf sites than in slope sites (R. Belley, pers. obs.) presumably increased bio-irrigation rates and silicate effluxes (Aller 1982). Moreover, Katz et al. (2009) suggested that groundfish sediment resuspension in Saanich Inlet triples the flux of dissolved silica from the sediment to the water column and therefore plays a major role in the silica cycle. Both megafaunal and macrofaunal abundance generally decrease with decreasing bottom water dissolved oxygen concentrations (Levin et al. 2009). I therefore expect higher silicate effluxes in regions with higher bottom water dissolved oxygen concentrations, given anticipated higher densities of megafauna and macrofauna. My results support this hypothesis, given that my multiple linear regression model identified bottom water DO as one of the strongest explanatory variables for silicate efflux variation.

2.5.3.4. Phosphate

Many factors influence seafloor phosphate fluxes (Sundby 1992), which vary widely from sediment uptake (-955.4 μmol m^{-2} d^{-1} in BC300) to release (697.0 μmol m^{-2} d^{-1} in SoGC-05). Although Nixon et al. (1980) reported increased phosphate fluxes in sediment cores collected before and after the spring bloom in Narragansett Bay, they found no clear seasonal variation. Similarly, Berelson et al. (2003) reported little seasonal variation in phosphate fluxes in Monterey Bay shelf sediments. The lack of a seasonal signal in seafloor phosphate flux suggests many factors act on different time scales that no single variable or few variables can explain. Yet, my results indicate that bottom water DO, sediment OPD, chl *a*:phaeo,

porosity, MGS and prokaryote abundance can explain 88% of the variation in phosphate flux. My study apparently encompassed most of the key drivers for phosphate flux, allowing me to predict benthic phosphate flux at these locations. These results are supported by a recent study that modelled benthic phosphate fluxes using three of the variables that I identified (OPD, bottom water DO, and porosity) along with mineral bound inorganic phosphorous (Almroth-Rosell et al. 2015).

2.5.4 Environmental drivers of multivariate benthic fluxes variation

Multivariate dbRDA allowed me to examine all benthic fluxes simultaneously within the same analysis. Environmental drivers related to bottom water characteristics, quality of organic matter, and sediment characteristics, explained 51.5% of the variability in overall oxygen and nutrient fluxes. Bottom water characteristics explained most of the variability (temperature and DO, 16.3 and 6.8% respectively), followed by quality of organic matter (chl *a*:phaeo and C:N ratios, 11.8 and 7.9% respectively) and sediment characteristics (MGS and porosity, 4.9 and 3.8% respectively). In their Beaufort Sea study, Link et al. (2013a) also reported upper sediment concentrations of chl *a* and phaeopigments, and bottom water dissolved oxygen as key environmental drivers of multivariate benthic flux variation. However, in contrast to my study, where temperatures varied by >5.5 °C across sampling locations and dates, temperatures recorded at the time of sampling varied by <2 °C and therefore contributed little to benthic flux variation, just as Rowe and Phoel (1992) suggested for the Bering Sea. Because temperature increase

promotes bacterial production (Cammen 1991), which in turn influences rates of benthic processes, increased benthic fluxes could reasonably be expected along a natural gradient of increasing temperature.

The dbRDA and multiple linear regression approaches identified some differences in environmental drivers of benthic fluxes. On the one hand, the dbRDA approach combines all benthic fluxes (O_2 uptake, ammonium, nitrate, nitrite, silicate and phosphate) in the same analysis to determine the best combination of environmental drivers for all benthic fluxes, hence of seafloor organic matter remineralization. On the other hand, the multiple linear regression approach analysed each benthic flux separately (e.g., ammonium) to determine the best combination of environmental drivers for each specific benthic flux. Given some commonalities in benthic fluxes but different degrees of influence by some environmental drivers on each benthic flux (e.g., temperature influences O_2 uptake but not phosphate release), the linear regression method identifies the environmental drivers of each benthic flux whereas the dbRDA method identifies the common environmental drivers that influence all benthic fluxes and examines seafloor organic matter remineralization as a whole.

The environmental variables I measured could not explain approximately 48.5% of the variability in benthic fluxes. Therefore, biological and environmental factors not measured in this study could also contribute to benthic flux variation. Additional factors known to influence benthic flux rates include sediment resuspension by megafauna (Yahel et al. 2008), bio-irrigation (Aller 1982, Archer & Devol 1992, Devol & Christensen 1993), bacterial activity (Pfannkuche 1993) and

production (Van Duyl et al. 1992), meiofaunal abundance (Aller & Aller 1992, Piot et al. 2014), macrofaunal abundance (Rowe & Phoel 1992) and species richness (Godbold & Solan 2009), functional diversity (Aller 1982) and particulate organic carbon flux to the seafloor (Jahnke 1990, Berelson et al. 1996). Measurement of some of these parameters in tandem with those reported here would likely increase the capacity of future studies to explain benthic flux variation more fully.

Although correlative and regression analysis do not fully demonstrate causality, which requires manipulative experiments, I believe that mensurative data such as those I present here should inform manipulative experiments (which bring other limitations), in order to guide experimental directions. Admittedly, conversion of flux measurements from sediment cores with relatively small surface areas to values per square meter of sediment can increase variability in benthic flux estimates, comparison of flux rates with similar studies (Archer & Devol 1992, Devol & Christensen 1993, Berelson et al. 1996, Berelson et al. 2003) indicate that the values measured represent realistic estimates of ambient benthic flux rates at my study sites.

2.5.5 Effect of overlying water air bubbling on benthic flux rates

My complementary experiment revealed no significant effect of air bubbling of the overlying water on any of my benthic flux rate measurements. These results corroborate previous incubation studies that found no significant effect of incubation time (i.e., oxygen concentration changes within incubations) on flux rates of oxygen, nitrate, phosphate, silicate and, for the most part, ammonium, where flux

rates changed only after oxygen decreased by 50–80% from ambient values (Devol & Christensen 1993, Berelson et al. 2013). This insensitivity demonstrates the absence of a short-term response in flux of these compounds to changes in oxygen concentration and, therefore, to oxygen concentrations at the onset of incubations. Consequently, I believe my benthic flux measurements represent realistic estimates of ambient benthic flux rates at my study sites.

2.6 Conclusions

My study indicates strong variation in spatial and temporal flux, driven primarily by differences in bottom water characteristics (bottom water DO and temperature), quality of organic matter (chl *a*:phaeo and C:N ratios) following significant deposition of particulate organic matter to the seafloor and, to a lesser extent, sediment characteristics (MGS and porosity). Although multiple biological and environmental factors influence different seafloor flux rates (O_2 and nutrients), my study used a suite of multivariate approaches in tandem to demonstrate that a subset (i.e., 6) of the large number of environmental variables measured (i.e., 18) could explain 51.5% of benthic flux variation. I also found that simultaneous and single flux analyses in tandem provided a more comprehensive understanding of the interplay between OM remineralization and flux of O_2 and individual nutrients.

The large variation in natural gradients (e.g., bottom water temperature and dissolved oxygen concentration) at my study sites allowed me to identify bottom water temperature as the key driver of benthic flux variation. These results indicate

that current and future predictive models of organic matter remineralization and ecosystem functioning of shelf and slope soft-muddy seafloor habitats should consider bottom water temperature variation. Temperature could have important implications for estimates of seasonal and spatial benthic flux variation, benthic-pelagic coupling, and potential impacts of predicted ocean warming, particularly at high latitudes.

2.7 Tables

Table 2.1 Station names, sampling dates, number of incubations performed, locations and environmental variables measured. Bottom DO = Bottom water dissolved oxygen concentration; OPD = Oxygen penetration depth; Chl *a*:Phaeo = Chlorophyll-*a* to phaeopigments ratio; C:N = Carbon-to-nitrogen ratio; MGS = Sediment mean grain size.

Station	Date	Inc (#)	Lat (N)	Long (W)	Depth (m)	Temp (°C)	Bottom DO (mL L^{-1})	OPD (mm)	Chl *a*: Phaeo	C:N	Porosity (%)	MGS (µm)	Prokaryotic abundance (# cells g^{-1})
SI	07-2011	3	48°39.25	123°29.20	97	8.72	1.51	4.7	0.23	8.42	66.28	78.62	3.45E+08
SI	09-2013	4	48°39.25	123°29.17	97	9.24	0.97	3.7	0.23	10.01	73.48	87.76	7.66E+07
SoGE	05-2011	4	49°02.56	123°19.15	173	8.25	4.88	13.0	0.22	9.51	64.31	87.29	1.01E+08
SoGE	09-2013	4	49°02.55	123°18.97	167	9.65	2.42	5.8	0.18	34.89	64.40	112.86	7.57E+07
SoGC	05-2011	4	49°02.16	123°25.68	305	9.14	2.59	9.0	0.18	8.64	64.31	38.28	1.60E+08
SoGC	07-2011	3	49°02.42	123°25.51	301	8.63	2.86	12.0	0.21	8.77	83.64	27.30	9.07E+07
DDL	05-2011	2	49°05.05	123°19.76	109	8.27	4.95	10.0	0.37	11.66	65.52	75.08	1.64E+08
DDL	07-2011	3	49°05.05	123°19.75	107	8.91	3.23	14.7	0.59	16.97	60.79	95.66	1.48E+08
Axis	07-2011	3	48°19.01	126°03.03	987	3.87	0.19	8.0	0.16	10.56	81.10	46.86	9.74E+07
Hydrates	07-2011	3	48°18.71	126°03.95	868	4.26	0.20	7.3	0.18	9.66	80.18	33.12	9.09E+07
BMC	07-2011	3	48°18.88	126°03.49	896	4.22	0.19	7.3	0.19	9.34	85.43	32.21	1.56E+08
BUP	07-2011	3	48°25.66	126°10.48	397	5.56	0.71	7.5	0.17	14.17	51.05	124.53	1.07E+08
Folger	07-2011	3	48°48.83	125°16.85	96	7.75	2.01	11.5	0.18	8.89	81.69	44.26	4.66E+08
BC300	09-2013	3	48°24.17	125°53.89	298	6.62	1.06	5.6	0.14	19.44	60.29	164.82	8.54E+07

Table 2.2 Permutational analysis of variance (PERMANOVA) results testing the effect of sampling date and location on benthic fluxes based on Euclidean similarity matrices performed on normalized data.

Regional variation between Salish Sea and NE Pacific				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Region	1	36.868	7.915	<0.01
Residuals	23	4.658		
Total	24			
Temporal and spatial variation in Salish Sea				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	3	13.395	4.092	<0.01
Date	2	15.854	4.843	<0.01
Site x Date	2	5.564	1.700	0.076
Residuals	19	3.273		
Total	26			
Spatial variation in NE Pacific				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	4	14.319	4.813	<0.01
Residuals	11	2.975		
Total	15			

Table 2.3 Distance-based linear model (DistLM) of benthic fluxes against environmental drivers measured in the Salish Sea and NE Pacific in May/July 2011, and September 2013.

Sequential tests for stepwise model (Adj. r^2 = 0.515)							
Variable	**AICc**	**SS (trace)**	**Pseudo-*F***	***P***	**Prop.**	**Cumul.**	**Res.df**
Temp	77.53	43.89	8.54	<0.01	0.163	0.163	44
Chla:Phaeo	72.82	31.87	7.06	<0.01	0.118	0.281	43
C:N	69.85	21.46	5.22	<0.01	0.079	0.360	42
DO	67.18	18.45	4.90	<0.01	0.68	0.428	41
MGS	65.68	13.33	3.78	<0.01	0.049	0.478	40
Porosity	65.04	10.15	3.03	0.012	0.038	0.515	39

Table 2.4 Percent variation explained by individual axes and relationships between dbRDA coordinate axes and orthonormal variables from Distance-based linear model (DistLM) of benthic fluxes against environmental drivers measured in the Salish Sea and NE Pacific in May/July 2011, and September 2013.

Variation explained by individual axes (%)					Relationships between dbRDA coordinate axes and orthonormal X variables (multiple partial correlations)					
	Explained variation out of fitted model (%)		Explained variation out of total variation (%)		Temp	Chl *a*: Phaeo	C:N	DO	MGS	Porosity
Axis	Ind.	Cumul.	Ind.	Cumul.						
1	41.42	41.42	21.35	21.35	0.732	0.197	-0.091	0.539	-0.355	-0.026
2	33.04	74.47	17.03	38.37	0.098	0.888	0.046	-0.262	0.268	0.244
3	14.47	88.93	7.46	45.83	-0.022	0.069	-0.850	-0.374	-0.349	-0.101
4	7.14	96.07	3.68	49.51	-0.331	0.264	0.415	-0.101	-0.784	-0.152
5	3.87	99.94	2.00	51.50	-0.463	0.313	-0.239	0.580	0.198	-0.506
6	0.06	100	0.03	51.53	0.361	0.008	0.195	-0.394	0.159	-0.807

Table 2.5 Results of the multiple linear regression models based on AIC. Data utilized are from all sampling locations and dates. DO = Bottom water dissolved oxygen concentration; OPD = Oxygen penetration depth; Chl *a*:Phaeo = Chlorophyll-*a* to phaeopigments ratio; C:N = Carbon-to-nitrogen ratio; MGS = Sediment mean grain size; Prokabun = Prokaryotic cell abundance; RSE = Residuals standard error; * Not significant term in the model but still provides best AIC.

Flux	Intercept	Temp	DO	OPD	Chl *a*: Phaeo (log_{10})	C:N (log_{10})	Porosity	MGS	Prokabun (log_{10})	r^2 (Adj r^2)	*p*-values	RSE
O_2	-44.10	-1.68	0.89	-0.89	N/A	N/A	-0.14	NA	8.01	0.78 (0.75)	<0.001	1.91
NH_4^+ (log_{10})	3.76*	0.10	N/A	0.04*	1.76	N/A	0.03	0.01	-0.47*	0.60 (0.54)	<0.001	0.37
NO_3^-	2450.28*	-89.95	90.49*	-33.91*	N/A	703.99	N/A	N/A	-334.13*	0.47 (0.41)	<0.001	253.7
NO_2^-	20.15*	N/A	-3.88	2.79	-26.52	15.46*	N/A	N/A	-9.72*	0.39 (0.30)	0.003	9.07
$Si(OH)_4$	-7450.07	N/A	1086.48	N/A	-9272.87	3066.59*	N/A	-11.27*	N/A	0.55 (0.51)	<0.001	1452
PO_4^{3-}	1901.99	N/A	97.39	-13.60	-897.19	N/A	-17.27	-5.96	-114.90	0.90 (0.88)	<0.001	69.49

2.8 Figures

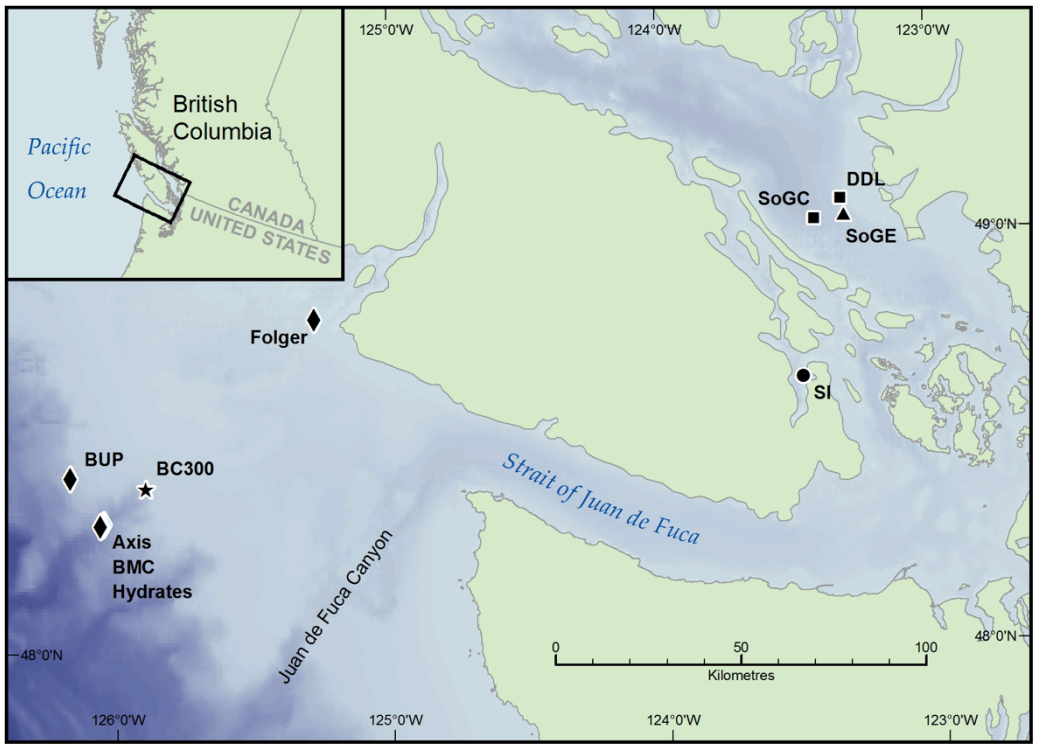

Figure 2.1 Map of stations sampled in the Salish Sea and the North East Pacific in May/July 2011 and September 2013. Label symbols indicate sampling dates. 1) Squares: DDL and SoGC were sampled in May and July 2011; 2) Triangle: SoGE was sampled in May 2011 and September 2013; 3) Circle: SI was sampled in July 2011 and September 2013; 4) Diamonds: Axis, BMC (Barkley Mid-Canyon), Hydrates, BUP (Barkley Upper Slope) and Folger were sampled in July 2011; 5) Star: BC300 (Barkley Canyon at 300 m depth) was sampled in September 2013. Bathymetry data based on the GEBCO_2014 Grid, version 20150318, www.gebco.net.

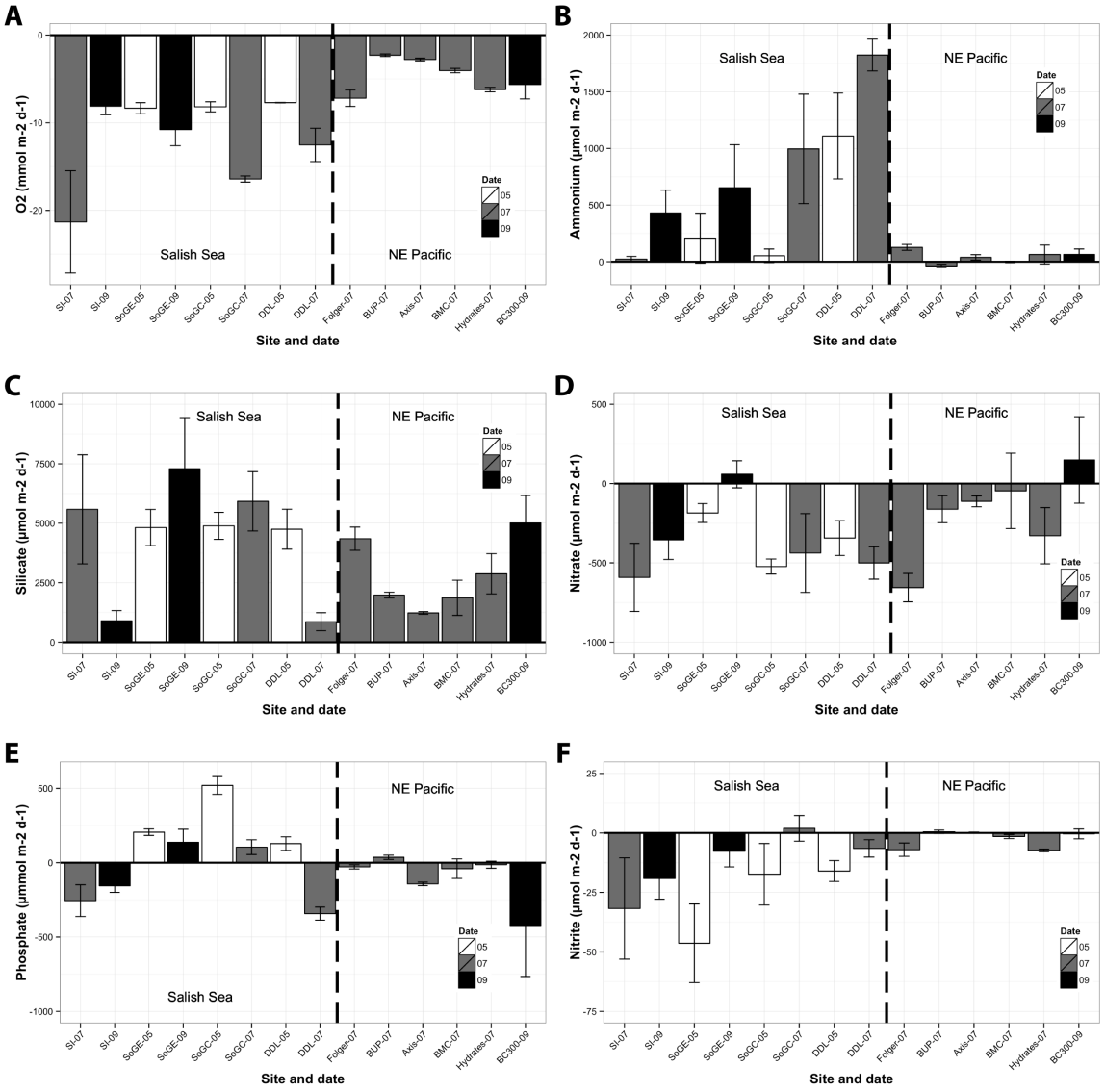

Figure 2.2 Benthic fluxes (±SE) of a) oxygen, b) ammonium, c) silicate, d) nitrate, e) phosphate and f) nitrite measured at each location. Oxygen uptake is reported in mmol m^{-2} d^{-1} whereas other fluxes units are reported in µmol m^{-2} d^{-1}. White bars represent fluxes measured in May 2011, grey bars represent fluxes measured in July 2011, and black bars represent fluxes measured in September 2013. Horizontal lines indicate sediment–water interface where fluxes above the lines represent sediment release and fluxes below the lines represent sediment uptake. Vertical dashed lines separate Salish Sea (left) and NE Pacific (right) stations.

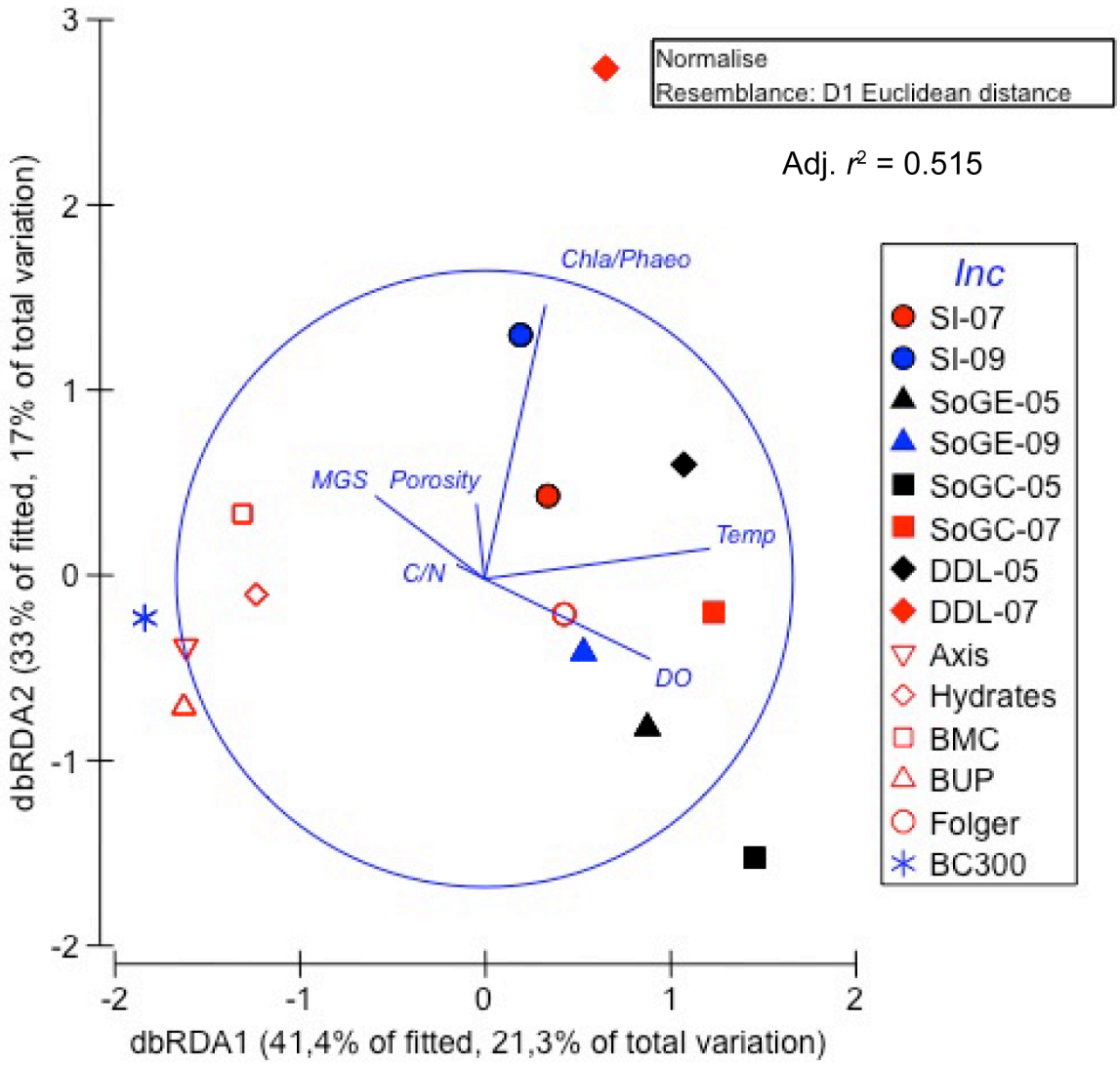

Figure 2.3 Distance-based Redundancy Analysis (dbRDA) plot of the distLM model of the predictor variables best explaining variation in benthic fluxes measured in the Salish Sea and NE Pacific in 2011 and 2013. Color represents sampling date: Black = May 2011; Red = July 2011; Blue = September 2013. Filled symbols denote benthic fluxes from the Salish Sea and open symbols denote NE Pacific benthic fluxes. Chl *a*:phaeo = Ln of sediment chl *a*:phaeo ratio; C:N = Ln of sediment carbon/nitrogen ratio; DO = bottom water dissolved oxygen concentration; MGS = sediment mean grain size.

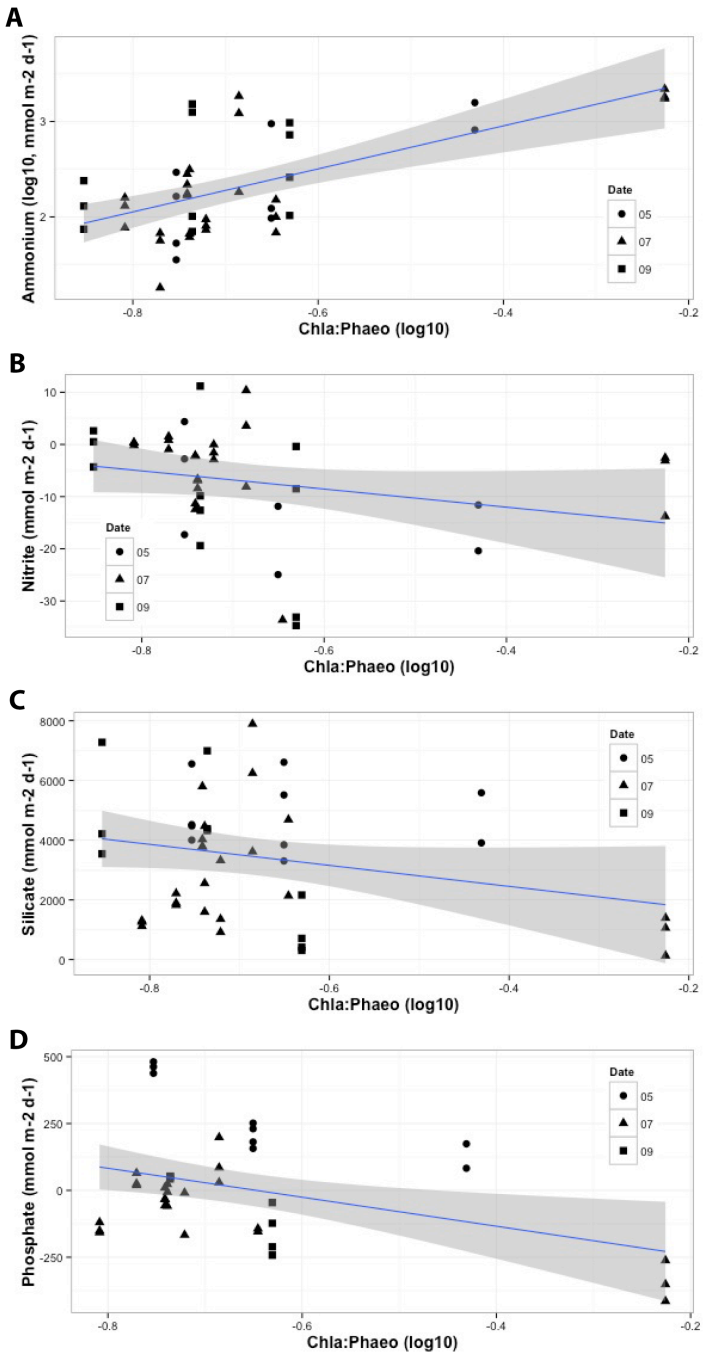

Figure 2.4 Relationships between sediment chlorophyll *a*:phaeopigment ratio and significant benthic flux of a) ammonium, b) nitrite, c) silicate and d) phosphate identified by multiple linear regression models. Grey shaded area around regression line indicates 95% confidence interval. Sample collection date: May 2011 (circle); July 2011 (triangle); September 2013 (square).

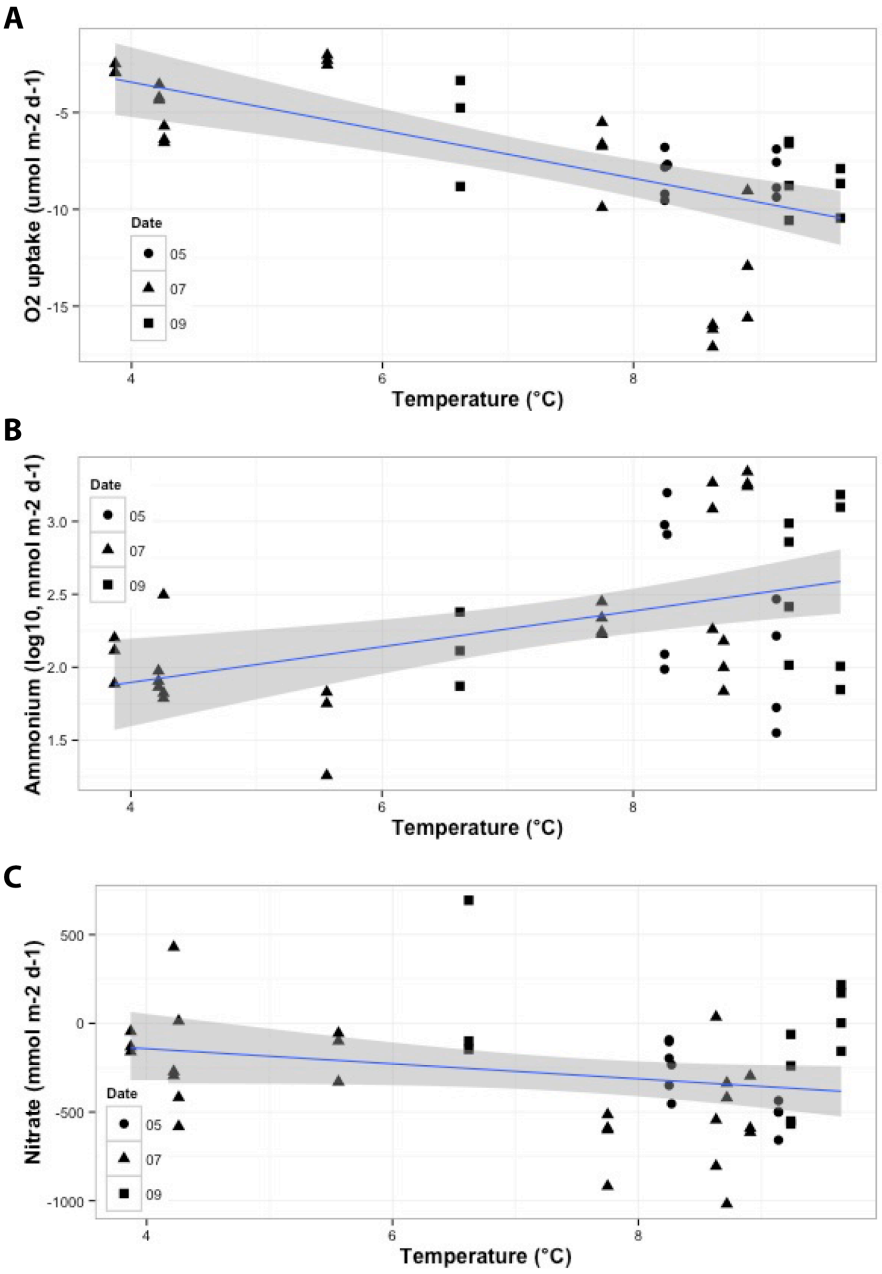

Figure 2.5 Relationships between bottom water temperature and significant benthic flux of a) oxygen, b) ammonium and c) nitrate identified by multiple linear regression models. Grey shaded area around regression line indicates 95% confidence interval. Negative values indicate sediment uptake and positive values indicate sediment release. Sample collection date: May 2011 (circle); July 2011 (triangle); September 2013 (square).

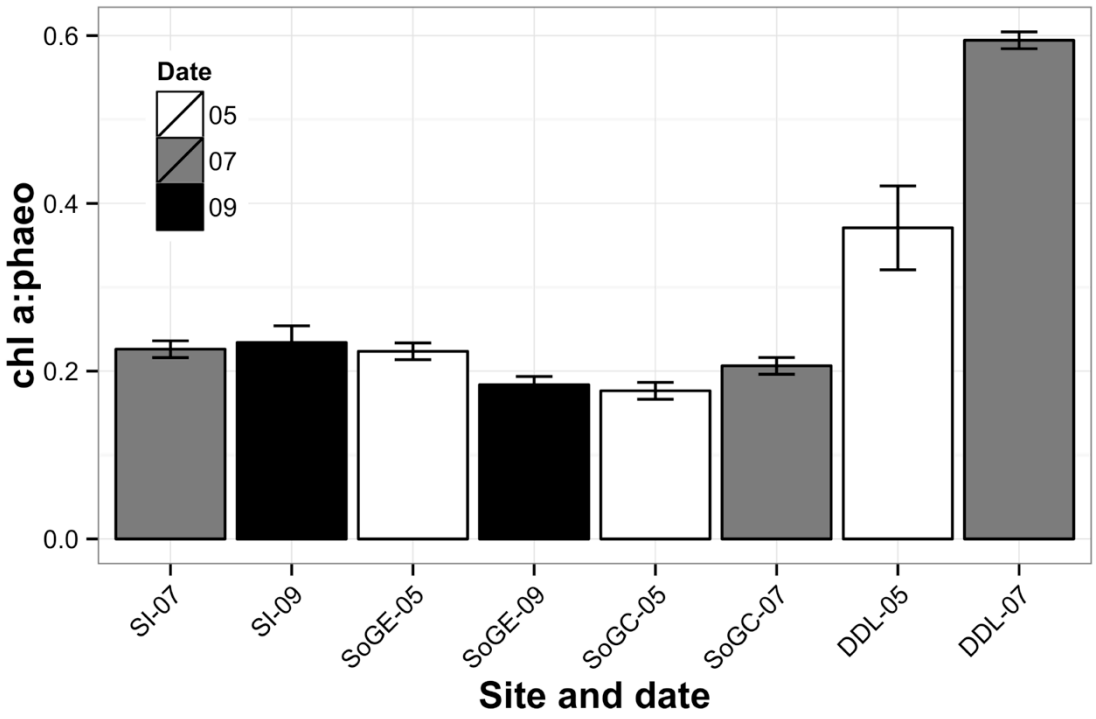

Figure 2.6 Sediment chlorophyll *a*:phaeopigment ratio (±SE) measured at each location in the Salish Sea. White bars represent fluxes measured in May 2011, grey bars represent fluxes measured in July 2011, and black bars represent fluxes measured in September 2013.

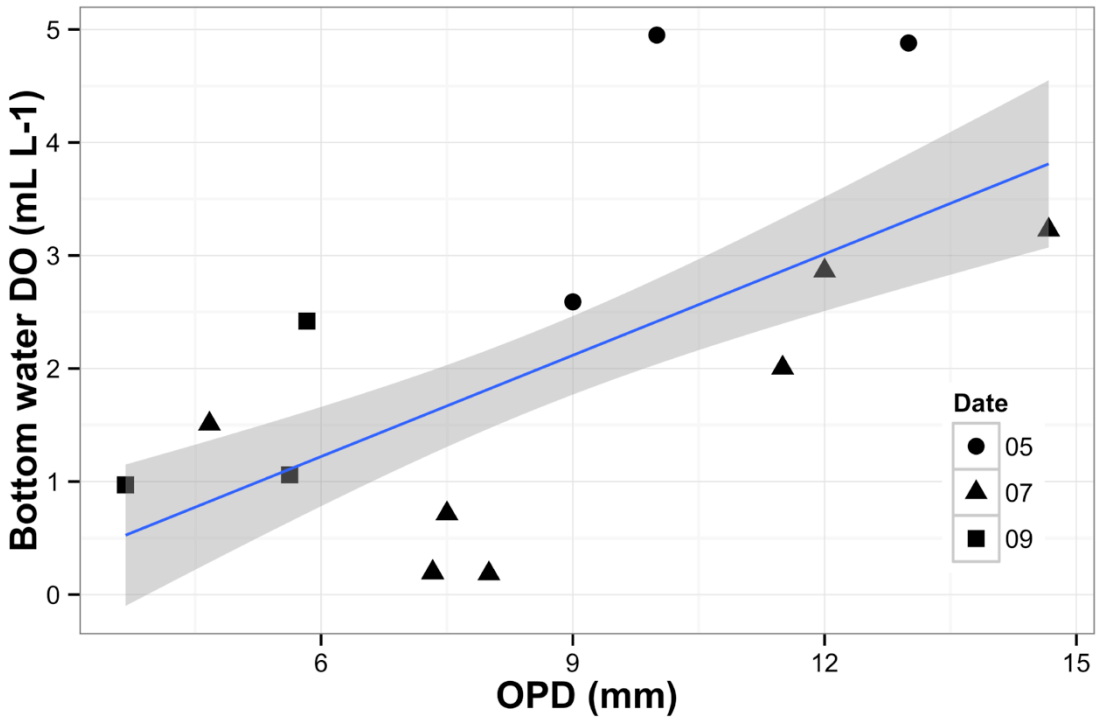

Figure 2.7 Relationship between oxygen penetration depth (OPD) and bottom water dissolved oxygen (Bottom DO). Grey shaded area around regression line indicates 95% confidence interval. Sample collection date: May 2011 (circles); July 2011 (triangles); September 2013 (squares).

Chapter 3 — Relative contributions of biodiversity and environment to benthic ecosystem functioning*

3.1 Abstract

Current concern about biodiversity change associated with human impacts has raised scientific interest in the role of biodiversity in ecosystem functioning. However, studies on this topic face the challenge of evaluating and separating the relative contributions of biodiversity and environment to ecosystem functioning in natural environments. To investigate this problem, I collected sediment cores at different seafloor locations in Saanich Inlet and the Strait of Georgia, British Columbia, Canada, and measured benthic fluxes of oxygen and five nutrients (ammonium, nitrate, nitrite, phosphate and silicate). I also measured 18 environmental variables at each location, identified macrofauna, and calculated a suite of species and functional diversity indices. My results indicated that macrobenthic functional richness (FRic) was a better predictor of benthic flux than species richness, explaining ~ 20% of the benthic flux variation at my sites. Environmental variables and functional diversity indices collectively explained 62.9% of benthic flux variation, with similar explanatory contributions from environmental variables (21.4%) and functional diversity indices (18.5%). The 22.9% shared variation between environmental variables and functional diversity indices demonstrate close linkages between species and environment. Finally, I also identified funnel feeding as a key functional group represented by a small number of

species and individuals of maldanid and pectinariid polychaetes, which disproportionately affected benthic flux rates relative to their abundance. My results indicate the primary importance of environment and functional diversity in controlling ecosystem functioning. Furthermore, these results illustrate the importance of evaluating more fully the consequences of anthropogenic impacts, such as biodiversity loss and environmental changes, for ecosystem functioning.

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3.2 Introduction

The loss of biodiversity and its impact on humanity (Cardinale et al. 2012) have raised considerable interest on potential links between biodiversity and ecosystem functioning in a wide range of ecosystems (Loreau et al. 2001, Loreau et al. 2002, Solan et al. 2004, Loreau 2010). This work points to a strong role for functional groups in the control of ecosystem functions (Hooper et al. 2005, Cardinale et al. 2006) but also a potential role for environment (Yachi & Loreau 1999, Godbold & Solan 2009, Belley et al. 2016). Although most of these studies focus on biodiversity loss by manipulating species in experiments (Cardinale et al. 2012, Naeem et al. 2012) natural gradients in environment offer an alternative "*in situ*" approach to linking function, biodiversity and environment (Snelgrove et al. 2014).

In the world's ocean, seafloor habitats and the organisms that reside in and on marine sediments provide important ecosystem functions that include recycling of organic matter that drives benthic-pelagic coupling and fuels surface waters with nutrients essential for primary production (Snelgrove et al. 2014). Despite a general consensus that biodiversity and environmental factors may both play a role in ecosystem functioning, relatively few studies have attempted to separate abiotic and biotic contributions to ecosystem functioning. Nonetheless, those that have tried generally found that both abiotic and biotic factors played an important role in controlling ecosystem functions (Godbold 2012, Strong et al. 2015).

Measurements of benthic fluxes at the sediment-water interface offer one means of quantifying organic matter remineralization, an important ecosystem

function in seafloor habitats (Giller et al. 2004). Multiple biological and environmental factors influence benthic fluxes. Previous studies point to the importance of environmental variables such as temperature (Hargrave 1969, Cowan et al. 1996, Alonso-Pérez & Castro 2014), and the quality and quantity of organic matter sinking to the seafloor (Berelson et al. 1996, Jahnke 1996). Previous studies also report a strong positive influence of biological factors such as the presence of bio-irrigators and bioturbators on benthic fluxes and organic matter remineralization (Aller 1982, Aller & Aller 1998, Aller 2014), and that focus has expanded to consider the importance of functional diversity on ecosystem functioning (Snelgrove et al. 1997, Raffaelli et al. 2003, Solan et al. 2004, Snelgrove et al. 2014). Indeed, some studies report that functional diversity, defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001), promotes organic matter remineralization and consequently, increases benthic fluxes (Braeckman et al. 2014).

My study focuses on four different sites in the Salish Sea, a semi-enclosed inland sea between Vancouver Island and British Columbia, Canada (Figure 3.1). The large variation in species diversity (Macdonald et al. 2012) and environmental variables (Johannessen et al. 2005, Masson & Cummins 2007) within the Salish Sea over a relatively small spatial scale provides an ideal location for a study that uses natural gradients to identify the influences of biodiversity and environment on ecosystem functioning. Saanich Inlet, a seasonally hypoxic fjord, supports a relatively low diversity benthic community that specialises on low-oxygen environments (Tunnicliffe 1981, Matabos et al. 2012, Chu & Tunnicliffe 2015).

Strong seasonal variation in dissolved oxygen concentrations and temperature also characterizes the Strait of Georgia (Masson & Cummins 2007, Johannessen et al. 2014). Finally, the Delta Dynamic Laboratory site within the Strait of Georgia offers a highly dynamic environment characterised by high organic and inorganic loading resulting from its proximity to the Fraser River outflow (Burd et al. 2008, Macdonald et al. 2012).

The primary objective of this study was to evaluate the contributions of species and functional diversities, and environmental variables to benthic fluxes of oxygen and nutrients (ammonium, nitrate, nitrite, phosphate and silicate) at contrasting sites. I addressed my objective by exploring the following questions at my study sites: i) do benthic fluxes vary spatially, ii) does benthic community composition vary spatially, iii) which environmental variables explain benthic flux variation and remineralization, iv) which species and functional diversity indices, if any, explain benthic flux variation and remineralization, and v) how much benthic flux variation do biodiversity and environmental variables explain, respectively?

3.3 Methods

3.3.1 Field sampling

Samples were collected near the VENUS Observatory nodes in Saanich inlet and the Strait of Georgia, British Columbia, Canada (Figure 3.1). I collected push core sediments using the Remotely Operated Vehicle (ROV) ROPOS (www.ropos.com) on board the Canadian Coast Guard Ship John P. Tully (May 7-14, 2011), and the

Research Vessels Thomas G. Thompson (June 30-July 3, 2011) and Falkor (September 6-18, 2013). Sampling occurred at the VENUS Delta Dynamic Laboratory (DDL) and the Strait of Georgia Central (SoGC) sites in July 2011, Saanich Inlet (SI) in July 2011 and September 2013, and the Strait of Georgia East (SoGE) in May 2011 and September 2013 (Table 3.1). The ROV collected 4-5 push-cores at each site (i.d. = 6.7 cm, L = 35.6 cm) at random locations within a bottom area that spanned ~ 25 x 25 m. One core per site served to determine prokaryotic cell abundance and sediment properties (summarized in Table 3.1), and the remaining cores were used for incubations to measure fluxes. A SBE 19plus V2 CTD mounted on the ROV recorded near-bottom dissolved oxygen (DO), temperature, and salinity. No specific permissions were required for these locations/activities and field studies did not involve endangered or protected species. Below I provide a brief overview of methodologies, but a more detailed description can be found in Belley et al. (2016).

3.3.2 Incubations

At each sampling site, I acclimated 3-4 sediment cores (0.68 L ± 0.10 and 0.42 L ± 0.10, mean volume ± SD of sediment and water, respectively) for 4-24 hours, allowing sufficient time for any sediment particles in suspension to settle back to the sediment surface. The acclimation time varied because of the high sampling intensity, and is within the normal range reported in the literature (Valdemarsen et al. 2012, Link et al. 2013a, Nunnally et al. 2013). I aerated the overlying water in each core for a minimum of 1 hour using aquarium air pumps to avoid suboxic

conditions during incubations. Sediment cores were then sealed with caps equipped with magnetic stirrers and gas-tight sampling ports, prior to incubating in the dark at *in situ* temperatures (8-9 ˚C) for 12-24 hours until 15-30% of available oxygen was consumed.

3.3.3 Oxygen uptake

I measured oxygen consumption periodically (4-8 hours intervals) using a 500-µm diameter oxygen microsensor (Unisense, Aarhus, Denmark) inserted through a small resealable hole on the top of the cap in May and July 2011, and with a non-invasive optical oxygen meter used in conjunction with oxygen optode patches (Fibox 4, PreSens, Regensburg, Germany) in September 2013. I determined oxygen uptake from the slope of the linear regression of oxygen concentration versus time of incubations after correction for oxygen concentration in the replacement water (see example in Supplementary Figure 3.1).

3.3.4 Nutrient fluxes

At the beginning, midpoint, and end of the incubations I collected water samples with 60-mL, acid-rinsed plastic syringes, except in the SI, SoGC, and DDL incubations in July 2011, where high oxygen consumption shortened the incubation period to 12 h and limited water sampling to the beginning and end of the incubations. I immediately replaced withdrawn water with an equivalent volume of bottom water of known oxygen and nutrient concentrations. Syringes and sample

containers were initially rinsed with ~5 mL of water sample. At each sampling time I collected and stored two 25-mL water samples in acid-rinsed, twist-cap 30-mL HDPE bottles. Upon collection, water samples were immediately placed in an upright position at -20 °C until analyzed. I determined the concentrations of nutrients (NH_4^+, NO_3^-, NO_2^-, $Si(OH)_4$, PO_4^{3-}) in the water samples using a Technicon Segmented Flow AutoAnalyzer II, following the method recommended by Technicon Industrial Systems (1973, 1977, 1979) with the exception of ammonia (hereafter referred as ammonium) analysis, which followed Kerouel & Aminot (1997). Nutrient fluxes were determined from the slope of the linear regression of nutrient concentrations versus time of incubations after correction for the solute concentration in replacement water (see example in Supplementary Figure 3.1).

3.3.5 Macrofaunal identification and taxonomic diversity

After incubations, sediment cores were sectioned onto 0-2, 2-5, and 5-10 cm layers and processed over a 300 μm sieve prior to preservation in a 4% seawater-formaldehyde solution and subsequent transfer to 70% ethanol for identification. Specimens were sorted under a dissection microscope in the laboratory and identified to the lowest possible taxonomic level, usually to species. I determined abundance (N) for each taxon and taxonomic richness (S) as the number of taxa present in each sediment core. Biomass was not measured because of time constraints. I also determined diversity indices including Simpson's index (Simp or 1 - *D*), Pielou's evenness (*J*'), Rarefaction (es25) and Shannon-Wiener index (*H*') for

each sediment core. Diversity indices were computed in R (R Core Team 2016) using the package "vegan" (Oksanen et al. 2013).

3.3.6 Biological traits and functional diversity

I selected five biological traits and 24 modalities based on their presumed influence on benthic fluxes and availability for all taxa (Table 3.2). These reflected behaviour (bioturbation mode, feeding type, habitat and mobility) and morphology (size). Biological traits were collected for each taxon from published sources (MarLIN 2006, Macdonald et al. 2010, Link et al. 2013b, Queiros et al. 2013, Jumars et al. 2015, WoRMS Editorial Board 2015). When biological traits information was not available for a specific taxon, I obtained information from one taxonomic rank higher. For example, the absence of species-specific information on the feeding type of the crustacean *Diastylis abboti* required me to use genus-level information. I allowed more than one functional trait for a given taxon for each category, and scored from 0 to 1 based on the extent to which they displayed each trait. For example, the polychaete *Paraprionospio pinnata* can alternate between filter and surface deposit feeding depending on environmental conditions, so these two traits each scored 0.5 for the feeding type category. Trait category scores for each taxon and taxa abundance matrices were used to obtain functional diversity (FD) indices using the "FD" package (Laliberté & Legendre 2010) in R (R Core Team 2016). I then computed the following multidimensional FD indices for use in my analyses: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al. 2008), functional dispersion (FDis) (Laliberté & Legendre 2010),

Rao's quadratic entropy (RaoQ) (Botta-Dukat 2005) and an index of functional composition, the community-level weighted means of trait values (CWM) (Lavorel et al. 2008).

3.3.7 Oxygen penetration depth (OPD)

Immediately after recovery of the ROV I profiled oxygen concentrations as a function of depth in the sediment for one sediment core from each site. In each core, I performed three replicate profiles with Unisense oxygen microsensors (500 µm and 250 µm tip sizes in 2011 and 2013, respectively) in vertical increments of 1000 µm and 500 µm in 2011 and 2013, respectively. I defined the oxygen penetration depth (OPD) in the sediment as the mean depth at which oxygen concentration decreased below the suboxic level of 5 µmol L^{-1} (Thibodeau et al. 2010).

3.3.8 Prokaryotic cells

I subcored the sediment cores with a cut off 10-mL sterile plastic syringe at depths of 0-2, 2-5 and 5-10 cm to sample sediment prokaryote abundances (hereafter abbreviated as prokabun). I placed 1 mL of sediment from each depth in a 20-mL scintillation vial containing 4 mL of a filtered-sterilized 2% seawater-formalin solution. Samples were frozen at -20 ˚C until analysis. Sediment prokaryote abundance and biomass were determined following Danovaro (2010).

3.3.9 Sediment properties

I sectioned the upper 2 cm layer of sediment from one sediment core using inert plastic spatulas to characterize sediment properties. Each sediment layer was carefully placed in a Whirl-Pak bag and stored at -20 °C until analysed. I determined total organic matter (TOM) by ignition loss, and water content as the difference between the wet and dry sediment weights divided by the wet sediment weight (Danovaro 2010). Sediment porosity and dry bulk density were calculated using formulas from Avnimelech et al. (2001) with a particle density of 2.65 g cm^{-3}. I determined granulometric properties (sediment mean grain size; MGS) with a HORIBA Partica LA-950 laser diffraction particle size analyzer (Horiba Ltd. Kyoto. Japan). Samples were prepared for analyses of total organic carbon (TOC) and total nitrogen (TN) by drying for 24 h at 80 °C, fuming with 1 M HCl for 24 h, and drying again for a minimum of 24 h. Finally, approximately 2 mg of sediment samples were weighed into a tin capsule and stored at 80 °C until analysed in a Perkin-Elmer 2400 Series II CHN analyzer. I used the carbon to nitrogen (C:N) mass ratio as a measure of organic matter nutritional quality on a long time scale (Le Guitton et al. 2015), where lower ratios indicate fresher and higher quality organic matter (Vidal et al. 1997, Godbold & Solan 2009).

3.3.10 Chlorophyll-a and Phaeopigments

Concentrations of chlorophyll-*a* (chl *a*) and phaeopigments (phaeo) were quantified fluorimetrically following a modified version of Riaux-Gobin & Klein (1993). I placed 1-2 g of wet sediment in 90% acetone (v/v) at 4 ˚C for 24 h and then

analysed the supernatant prior to and following acidification using a Turner Designs 10-AU-005-CE fluorometer (Turner Designs. Sunnyvale. USA). The remaining sediment was dried at 60 °C for 24 h and weighed in order to standardize pigment concentrations per gram of sediment. The chl *a*:phaeo ratio provides a measure of organic matter quality on a short time scale (Le Guitton et al. 2015), where higher ratios indicate more recently settled phytoplankton particles and therefore fresher organic matter (Morata et al. 2011, Suykens et al. 2011).

3.3.11 Statistical analyses

I examined spatial variation in benthic fluxes and taxonomic community composition using a permutational multivariate analysis of variance (PERMANOVA) performed with 9999 random permutations of appropriate units (Anderson 2001, McArdle & Anderson 2001). Previous benthic flux analyses (Belley et al. 2016) and preliminary analyses of benthic communities indicated no significant temporal variation at SI (July 2011 and September 2013) and SoGE (May 2011 and September 2013). I therefore grouped data from a single site collected on the two different occasions (i.e., SI and SoGE). Two separate analyses addressed two research questions: 1) a one-way PERMANOVA design using all benthic flux data with the factor "Site" (four levels: DDL, SI, SoGC and SoGE) tested for benthic flux spatial variation among sites, and 2) a one-way PERMANOVA design using all macrofaunal taxonomic data with the factor "Site" (four levels: DDL, SI, SoGC and SoGE) tested for spatial variation in macrofaunal community composition among sites. Taxa that appeared only once were removed from the latter analysis (Clarke & Warwick

1994), although this removal had little effect on overall patterns. I calculated the resemblance matrices from Euclidean distances of standardized benthic flux and from Bray-Curtis distances of fourth root transformed benthic community data. This transformation was applied to bring all taxa to a similar relative scale of abundance (Anderson 2001, Anderson et al. 2008). I verified homogeneity of multivariate dispersion using the PERMDISP routine (Anderson et al. 2008). When there were too few possible permutations for a meaningful test, I calculated a *p*-value based on 9999 Monte Carlo draws from the asymptotic permutation distribution (Terlizzi et al. 2005). I further analysed significant terms within the full models using appropriate pair-wise comparisons. Multivariate patterns were visualized using non-metric multidimensional scaling (nMDS) ordinations of similarity matrices; this technique allows visualization of PERMANOVA results, which identified significant differences between sites. I completed nMDS, PERMANOVA and PERMDISP analyses in PRIMER 6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

I used two separate redundancy analyses (RDA) to identify the environmental variables (RDA #1) and functional diversity indices (RDA #2) that best explained benthic flux variation. RDA, a multivariate (i.e. multi-response) analysis, combines regression and principal component analysis (PCA). First, RDA performs a multivariate multiple linear regression followed by a PCA of the fitted values. Therefore, it allows identification of the linear combinations of variables that best explain response matrix variation. Finally, RDA tests the significance of the explained variation using a permutation procedure (Legendre & Legendre 2012). I

used stepwise selection with a significance level of 0.05 and 9999 random permutations to obtain the model with the most parsimonious set of variables. Predictor variables containing outliers were transformed and highly correlated ($r > 0.85$) predictor variables were excluded from the analyses (RDA #1 = chlorophyll-*a*, phaeopigments, total organic matter, nitrogen, water content, bulk density, and prokaryotic biomass; RDA #2 = Shannon-Wiener index, taxonomic richness, Rao's quadratic entropy, community-level weighted mean of epifauna). The optimal environmental model selection included 11 predictor variables: bottom water temperature, salinity, and dissolved O_2 concentration, seafloor depth, sediment O_2 penetration depth, chl *a*:phaeo ratio, Carbon content, Carbon:Nitrogen ratio, porosity, mean grain size, and prokaryotic abundance. To correct for data skewness, I applied a natural logarithmic (Ln) transformation to three predictor variables (chl *a*:phaeo, Carbon:Nitrogen and prokaryotic abundance). The optimal diversity model selection included 25 predictor variables: abundance, Simpson's diversity, Pielou's evenness, Expected Species, functional richness, functional evenness, functional divergence, functional dispersion, community weighted means of carnivores, omnivores, scavengers, grazers, detritivores, filter feeders, surface and sub-surface deposit feeders, funnel feeders, and predators, small, medium, and large-sized organisms, surficial modifiers, organisms with limited and slow movement trough sediment, and infauna. I further analysed multi-collinearity of the predictor variables from the full models with a variance inflation factor (VIF) test using the "vif" function from the "car" package (Fox & Weisberg 2011), removing predictor variables with the highest VIF so that the best model selected contained only

predictor variables with VIF < 5 (Zuur et al. 2009). I verified the homogeneity of multivariate dispersion assumption using the PERMDISP routine (Anderson et al. 2008). Contributions of each predictor variables to benthic fluxes reported here are based on R^2 and not on Adj. R^2 calculations.

Finally, I performed variation partitioning (Legendre & Legendre 2012) to determine relative contributions of environmental variables and functional diversity indices to benthic flux variation. Variation partitioning analysis allowed quantification of portion of benthic flux variation explained by the two subsets of explanatory variables (diversity and environmental subsets) when controlling for the effect of the other subset. This is done by: 1) performing a RDA of the flux by diversity data, 2) performing a RDA of the flux by environmental data, 3) performing a RDA of the flux by diversity and environmental data, 4) computing the adjusted R^2 of the three RDAs, and finally 5) computing fractions of adjusted variation by subtraction (Legendre & Legendre 2012). Variation partitioning analysis is most often used when variables included in each RDA models differ at different scales (see examples in Legendre & Legendre 2012).

I completed RDA and variation partitioning analyses in R (R Core Team 2016) using the package "vegan" (Oksanen et al. 2013) and calculated the contribution of each predictor variable to benthic flux variation in PRIMER 6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

3.4 Results

A total of 21 incubations spanned four different sites and three different time periods (Supplementary Table 3.1). In total, I identified 1942 specimens representing 119 different taxa (Supplementary Table 3.2). The most diverse and abundant animal Class was Polychaeta; the most abundant species, *Mediomastus cf. californiensis* (Capitellidae), occurred in highest densities in SoGE cores. The Spionidae *Prionospio lighti* also occurred in high densities, but mostly in the Strait of Georgia sites (i.e., DDL, SoGC and SoGE). Malacostraca was the second most diverse and abundant animal Class; *Cumella* sp. (Cumacea), the most abundant taxon, occurred only at SoGE (Supplementary Table 3.2).

PERMANOVA indicated significant differences in benthic community assemblages among the four sampling sites (P (perm) < 0.01, Table 3.3). Pair-wise comparisons showed significantly different benthic communities at each of my sampling sites (Figure 3.2A).

PERMANOVA indicated significant differences in benthic fluxes among the sampling sites (P (perm) < 0.01, Table 3.3). Pair-wise comparisons showed that benthic fluxes at SoGE differed significantly from fluxes measured at all the other sites (DDL, P (perm) = 0.0073; SI, P (perm) = 0.0002; SoGC, P (perm) = 0.0345). Pair-wise comparisons also showed that benthic fluxes at DDL differed significantly from fluxes measured at SoGC (P (MC) = 0.0339) (Figure 3.2B). Moreover, nMDS plot showed greater similarity in benthic fluxes within than across sites (Fig. 3.2B).

3.4.1 Environmental variables explaining multivariate benthic flux variation

The best model that emerged from my redundancy analysis between benthic fluxes and environmental variables explained 58.3% (R^2 = 0.583, Adj. R^2 = 0.444) of the total multivariate benthic flux variation and included five environmental variables (Supplementary Table 3.3). Chl *a*:phaeo ratio contributed most to the variation (18.8%), followed by prokaryotic abundance (14.5%), depth (8.8%), temperature (8.8%), and porosity (7.4%) (Supplementary Table 3.3).

The first and second axes of the redundancy model accounted for 27.3% and 14.6% of total flux variation respectively (Supplementary Table 3.4). The first axis mostly separated SoGE and SoGC from DDL and SI fluxes (Figure 3.3A). Chl *a*:phaeo ratio, prokaryotic abundance and depth contributed primarily to the first axis and explained 46.9% of fitted flux variation (Figure 3.3A, Supplementary Table 3.4). In explaining 25.0% of the fitted variation in fluxes, the second axis mostly separated SoGE from DDL, SoGC and SI fluxes (Figure 3.3A) and correlated most strongly with prokaryotic abundance, and to a lesser extent to chl *a*:phaeo ratio and temperature (Figure 3.3A, Supplementary Table 3.4).

3.4.2 Functional diversity indices and multivariate benthic flux variation

The best model that emerged from my redundancy analysis between benthic fluxes and functional diversity indices explained 67.8% (R^2 = 0.678, Adj. R^2 = 0.414) of the total multivariate benthic flux variation and included nine functional diversity indices (Supplementary Table 3.5). Functional richness (FRic) contributed most to the variation (19.7%), while the eight other functional diversity indices contributed

to a lesser extent, with contributions ranging between 4.5%-8.3% (Supplementary Table 3.5).

The first and second axes of the redundancy model accounted for 30.2% and 19.6% of total flux variation respectively (Supplementary Table 3.6A). Again, the first axis mostly separated SoGE and SoGC from DDL and SI fluxes (Figure 3.3B). Functional richness (FRic), community weighted means of sub-surface deposit feeders (CWM.Feed.SSD), abundance (N) and Simpson's diversity (Simp) contributed primarily to the first axis and explained 44.6% of the fitted flux variation (Figure 3.3B. Supplementary Table 3.6A-B). As with the first axis, the second axis mostly separated SoGE and SoGC from DDL and SI fluxes (Figure 3.3B), explaining 28.9% of the fitted variation in fluxes and correlating most strongly with community weighted means of surficial modifiers (CWM.Ri.S.mod), Simpson's diversity (Simp) and functional richness (FRic) (Figure 3.3B. Supplementary Table 3.6A-B).

3.4.3 Benthic flux variation partitioning

Variation partitioning analysis of benthic fluxes between environmental variables and functional diversity indices identified by RDA indicated that environmental variables and functional diversity indices together explained 62.9% of benthic flux variation (R^2 = 0.889, Adj. R^2 = 0.629) (Figure 3.4, Supplementary Table 3.7). Environmental variables alone explained 21.4% of benthic flux variation, whereas functional diversity indices alone explained 18.5%; environmental

variables and functional diversity indices shared 22.9% of the variation (Figure 3.4, Supplementary Table 3.7).

3.5 Discussion

In this study I determined the environmental variables and functional diversity indices influencing benthic flux rates using redundancy analyses and further evaluated their contributions using variation partitioning analysis. My study is the first to use variation partitioning analysis to examine the contribution of environmental variables and functional diversity indices on multivariate flux rates and organic matter remineralization, in my case for soft sedimentary habitats. My results show that environmental variables and functional diversity indices collectively explain the majority of the flux variation in my system and that they play a similar role in the control of flux rates. Furthermore, my results also indicate that environmental variables and functional diversity indices share a large proportion of the flux variation, which demonstrates the close links between the environment and the resident species in delivery of key ecosystem functions.

3.5.1 Benthic fluxes and benthic community spatial variation

Most studies have investigated the effects of abiotic and biotic factors influencing ecosystem processes and functions separately in the laboratory, but relatively few have attempted to separate the contribution of abiotic and biotic factors in the field (Godbold 2012, Strong et al. 2015). My analyses demonstrate that

despite significantly different macrofaunal communities at each of my sampling sites, differences in benthic fluxes were less consistent. On the one hand, SoGE fluxes differed significantly from the three other sites, and DDL fluxes also differed significantly from SoGC. On the other hand, SI fluxes were similar to those at DDL and SoGC. A previous study reported no consistent changes in ecosystem function with changes in functional diversity (Frid & Caswell 2015) and I also found consistent differences in benthic communities at my study sites but not in benthic flux rates. Therefore, the specific attributes of my study system provide an opportunity to evaluate the contribution of environmental variables and functional diversity to benthic flux variation. Because communities consistently varied among all sites whereas functions did not, this might suggests that between-site differences in environmental variables and biodiversity have their own influence on ecosystem functions as reported by Strong et al. (2015).

3.5.2 Functional diversity effects on multivariate benthic flux variation

Based on the functional traits and modalities selected, functional richness (FRic), defined as "the amount of functional space filled by the community" (Villéger et al. 2008), influenced multivariate benthic flux variation more than any other functional diversity index, alone explaining 19.7% of the variation. This result indicates the primary importance of functional trait richness for benthic fluxes as suggested by Braeckman et al. (2014) for fine sandy sediments in the Southern North Sea. My redundancy analysis indicated that, with the exception of ammonium, high fluxes of O_2 and nutrients characterized sediment cores with the highest

functional richness (FRic) (e.g. SoGE, Figure 3.3B). Similarly, I found positive relationships between functional richness and nutrient effluxes, especially phosphate and silicate, where efflux rates increased with increasing functional richness (Supplementary Figure 3.2). The larger influence of functional richness (FRic) on benthic flux variation than measures of species diversity (Simp, 5.0%) and abundance (N, 4.5%), suggests that a community composed of a few species in relatively low abundance could match or enhance benthic flux rates relative to another community comprised of more species in higher abundance if their functional trait diversities are similar (similar FRic). In my study, lower abundance (Mean±SE = 28±9, Figure 3.5) and Simpson's diversity (0.88±0.3, Figure 3.5) at SI compared to DDL (N = 116±44 and Simp = 0.93±0.01, Figure 3.5) but similar functional richness (SI = 21.57±25.50 and DDL = 19.13±6.52, Figure 3.5) corresponded to similar benthic fluxes, as identified by my PERMANOVA. This result could have important implications for future studies and conservation efforts because it suggests greater importance of richness of functional traits (i.e., FRic) than species diversity (i.e., Simpson's diversity index) and species abundance in maintaining benthic ecosystem functioning (i.e., benthic fluxes). Similarly, a recent review of the biodiversity-ecosystem functioning (BEF) literature (Strong et al. 2015) also concluded that measures of functional diversity produced better BEF relationships compared to other measures of biodiversity such as species richness. Finally, a recent study using coastal marine benthic macrofaunal data from the Skagerrak-Baltic Sea region showed that although functional diversity usually decreases with decreasing taxonomic richness, in some cases functional diversity

can still remain high even at low taxonomic richness, suggesting that ecosystem processes and functions could potentially be maintained at lower taxonomic richness but similar functional diversity (Törnroos et al. 2015). This finding led them to suggest the primary importance of functional characteristics of species in maintaining ecosystem functions.

Other functional diversity indices identified in my redundancy analysis demonstrate the important contribution of bioturbation and bio-irrigation of the sediment matrix to benthic flux variation. Functional diversity indices related to reworking of the sediment matrix (i.e., bioturbation), namely the community weighted means of taxa with limited (CWM.Mi.Lmt) and slow (CWM.Mi.Slow) movement through the sediment matrix, and of surficial modifiers (CWM.Ri.S.mod) explained 8.3%, 6.0% and 4.5% of benthic flux variation, respectively. Particle reworking and solute transport caused by infaunal movement through surface sediments are known to increase microbial activities, organic matter degradation rates, and nutrient recycling (Aller et al. 2001). In their study, Lohrer et al. (2004) also showed that bioturbation activities of spatangoid urchins had a large positive impact on benthic-pelagic fluxes. Moreover, the sediment resuspension created by groundfish activities (primarily the flatfish *Lyopsetta exilis*) plays a major role in ammonium, phosphate and silica cycles in Saanich Inlet, with a lesser role for infauna (Yahel et al. 2008, Katz et al. 2009). In my study, many taxa contribute to bioturbation activities and increased benthic fluxes cannot be attributed to a single species. Nonetheless, a small subset of traits related to bioturbation activities clearly exhibited an important positive influence on benthic flux rates. Functional traits

known to be more important for bioturbation (e.g. biodiffusors) (Queiros et al. 2013) did not contribute significantly to benthic flux variation because the species exhibiting such traits occurred in lower abundances. For example, surficial modifiers comprised 69 of the 135 taxa (51.1%) identified in our study (compared to 28.9% for biodiffusors), with particularly high abundances at SoGE and SoGC (Figure 3.5) where I recorded the highest effluxes of phosphate and silicate. My results suggest that, despite their modest effect on bioturbation, the high abundances of surficial modifiers positively affected (though explaining only 4.5% of benthic flux variation) phosphate and silicate effluxes at SoGE and SoGC. Thus, weak bioturbators may contribute significantly (and even more than more bioturbators often reported as important) when present in sufficiently high abundances, in this case at SoGE and SoGC where high functional richness in particular contributed to elevated effluxes of phosphate and silicate. More generally, Godbold and Solan (2009) showed that increased biodiversity (i.e, species richness) increased bioturbation activity (i.e., sediment mixing depth) in sediments near a fish farm in Scotland. Similarly, my results indicate that increased presence of bioturbating taxa led to increases in ecosystem processes measured (i.e., benthic flux rates) (Figure 3.3B).

Functional diversity indices related to biological irrigation of sediment (i.e., bio-irrigation), namely the community weighted mean of funnel feeders (CWM.Feed.Fn) and sub-surface deposit feeders (CWM.Feed.SSD) explained 8.1% and 6.0% of benthic flux variation, respectively. The presence of key taxa and their specific functions apparently disproportionately (relatively to their abundance)

impacted flux rates (Supplementary Tables 3.5 & 3.6). For instance, funnel feeders, a sub-group of deposit feeding animals that feed on surficial sediments but from below the sediment surface (Jumars et al. 2015), comprised only six polychaete taxa spanning two families (Maldanidae: Maldanidae spp., *Maldane* sp., *Maldane sarsi*, *Praxillella* sp. and *Praxillella gracilis*, and Pectiniiridae: *Pectinaria californiensis*) represented by a total of only 12 specimens in my sediment cores (Supplementary Figure 3.3). Yet, these taxa occurred mainly at SoGE (Figure 3.5), where I recorded particularly large silicate and phosphate releases, as well as nitrite intakes. Tube-building maldanids (i.e., *Praxillella* sp.) in particular can rapidly subduct freshly deposited organic matter that becomes available for deep-dwelling microbes and other infauna, and consequently enhance organic matter remineralization (Levin et al. 1997). Maldanids were therefore proposed as geochemical keystone species because of their feeding (Levin et al. 1997) and irrigation (Waldbusser et al. 2004) activities. The analysis of the three-dimensional organization of *M. sarsi* tubes also revealed increased concentrations of Fe, Mn, organic carbon, and bacteria, potentially resulting from tube irrigation, mucous secretion, and feeding activities (Dufour et al. 2008). My results and previous studies point to the primary importance of functional traits related to bio-irrigation of sediments for the biogeochemical cycling of nutrients in sedimentary habitats. Moreover, these results point to the disproportionate importance (relative to their abundance) of some taxa and associated traits in sustaining ecosystem functions. In my study, results suggest a strong identity effect, where a small number of taxa (i.e., six funnel feeder taxa) substantially impact ecosystem functions (Strong et al. 2015).

Taken together, biological sediment reworking and irrigation activities explained 32.9% of variation in benthic flux. These results mirror previous studies indicating that biological mixing of sediments and solute transport during feeding and irrigation stimulates microbial activity and organic matter remineralization (Aller & Aller 1998, Aller 2014).

3.5.3 Environmental variables explaining multivariate benthic flux variation

Of the environmental variables I examined, the chl *a*:phaeo ratio most strongly influenced benthic fluxes (i.e., 18.8%); this ratio reflects organic matter quality on a short time scale of days to weeks (Veuger & van Oevelen 2011, Le Guitton et al. 2015). Prokaryotic cell abundance was the second most important environmental variable, explaining 14.5% of the variation in flux. Redundancy analysis indicated that high fluxes of ammonium (e.g. DDL) and nitrite (e.g. SI) characterized sites with the highest chl *a*:phaeo ratio and abundance of prokaryotic cells (Figure 3.3A). Similarly, most environmental variables explaining benthic flux variation identified in my study (i.e., chl *a*:phaeo ratio, temperature, and porosity) were previously reported as strong predictors for this region (see Chapter 2). However, the redundancy analysis performed in my study identified prokaryotic abundance as an important variable explaining benthic flux variation not identified in my previous study (Chapter 2). The fact that prokaryotic abundance remained an important variable explaining single flux variation (from multiple linear regression results) for all but silicate fluxes over a broad geographic area as reported in my previous study (Chapter 2) (i.e., Salish Sea but also sites in the open waters of the

Northeast Pacific) can explain this discrepancy. I included water depth in my analysis because it often correlates well with other environmental variables known to influence benthic flux rates, such as organic flux to the seafloor (Jahnke 1990, Berelson et al. 1996) and temperature (Hargrave 1969, Cowan et al. 1996, Alonso-Pérez & Castro 2014). My model specifically accounted for differences in water depth, which explained 8.8% of the variation in benthic flux and generally high fluxes of O_2, nitrate, phosphate and silicate (e.g. SoGE) generally characterized deeper sites. Overall, my results align with previous studies that reported increased fluxes of seafloor oxygen and nutrients with increased flux of fresh organic matter following phytoplankton blooms (Whitledge et al. 1986) and increased microbial abundance (Pfannkuche 1993, Gooday 2002).

3.5.4 Benthic flux variation partitioning

Environmental variables and functional diversity indices collectively explained 62.9% of variation in benthic flux at my study sites. Environmental variables alone explained 21.4% of this variation, functional diversity indices alone explained 18.5%, whereas the two variable groups shared 22.9% of the variance. These results indicate that the abiotic and biotic variables measured in my study explained the majority of the variation in benthic flux, and that environment and macrofaunal functional diversity weigh almost equally in contribution. The meta-analysis conducted by Godbold (2012), who reported positive and similar abiotic and biotic (i.e., species identity and species richness) effects on ecosystem functions measured in the majority of experiments included in their analysis, support my

results. However, the many field experiments that manipulated diversity and used species that comprised only a fraction of the natural community usually report higher influence of environmental variables on ecosystem functions. Godbold and Solan (2009) and Duffy (2009) propose that including a low number of species in manipulative experiments reduces the observed effect of biodiversity on ecosystem functions relative to environmental variables. Based on my results, and those from the few similar observational studies, I also advocate for the use of natural communities in future studies to fully appreciate the full effect of biodiversity on ecosystem functioning. Although I acknowledge that correlative and regression analysis do not fully demonstrate causality, which requires manipulative experiments, I believe that mensurative data such as those I present here should inform manipulative experiments (which bring other limitations), in order to focus promising experimental directions. Admittedly, the conversion of flux measurements from small sediment cores to values per square meter of sediment can increase variation in benthic flux measurements, comparison of flux rates with similar studies (Archer & Devol 1992, Devol & Christensen 1993, Berelson et al. 1996, Berelson et al. 2003) indicate that the values measured for my study site yielded realistic estimates of ambient benthic flux rates.

The large proportion (22.9 %) of the explained variation shared between environmental variables and functional diversity indices demonstrates the close interactions between resident species and their environment. Environmental variables greatly impact benthic community composition, however, the community also plays an important role in controlling ecosystem functioning. For example, the

rate of particulate organic matter export to the seafloor strongly impacts benthic community composition (Wei et al. 2010a). Decreases in dissolved oxygen concentration can also modify benthic community composition and can lead to lower sediment bioturbation and bio-irrigation (Levin et al. 2009, Belley et al. 2010, Rabalais et al. 2010) which, in turn, can decrease benthic flux rates (Aller 1982, Link et al. 2013b, Aller 2014). The important proportion of the explained variation shared between the environment and the species inhabiting the sediments point to the need to limit anthropogenic impacts that might change the marine environment and potentially lead to loss of biodiversity and associated ecosystem functions in marine sedimentary habitats.

3.5.5 Effect of other variables on benthic flux variation

The biological and environmental variables I measured could not explain approximately 37.1% of the benthic flux variation. Therefore, other factors not measured in this study presumably contribute to variability in benthic fluxes. Concentration gradients and molecular diffusion in sediment porewater and overlying water result in spatial and temporal variation in oxygen and nutrient fluxes at the seafloor (Schulz 2000). For example, the dissolved oxygen contained in the bottom water penetrates the sediment following a diffusion gradient (i.e. from higher to lower concentration). Microorganisms such as bacteria and archaea (i.e. prokaryotes) utilize oxygen and other electron acceptors to degrade organic material within the sediment and therefore affect local concentrations. These changes in local concentrations generate nutrient fluxes directed either towards the

water column or deeper in the sediment depending on the specific chemical compound (Jorgensen 2006). Moreover, macrobenthic organisms influence the distribution of chemical compounds and reaction rates by: 1) moving particles during feeding, burrowing, and tube construction, 2) disrupting the otherwise vertically stratified distribution of biogeochemical compounds during burrow and fecal pellet formation, 3) introducing new reactive organic substances during mucus secretion, 4) influencing bacterial communities that mediate chemical reactions during feeding and sediment mechanical disturbance, and 5) altering sediment during gut passage (Aller 1982). Through their activities, macrofauna control pore water solute concentration profiles (Aller 1982), increasing benthic fluxes by a factor of 3-4 in continental shelf sediments (Archer & Devol 1992, Devol & Christensen 1993). Although I measured the bottom water dissolved oxygen concentrations at my study sites (environmental variable not retained by my RDA analysis), I did not measure *in situ* bottom water nutrient concentrations. Hence, differences in bottom water nutrient concentrations across my study sites could have influenced benthic flux rates and contributed to the 37.1% unexplained benthic flux variation at my study sites. However, I believe such a scenario unlikely for explaining within-site benthic flux variation because bottom and tidal currents would tend to minimize horizontal variation in bottom water properties within the 25m x 25m sites that I sampled.

3.6 Conclusions

My study indicates that environmental variables and functional diversity indices I measured explain the majority of flux variation in my Salish Sea sedimentary sites. Lability of organic matter, microbial abundance, benthic macrofaunal functional richness, and indices related to bioturbation and bio-irrigation were the most important variables to explain benthic flux variation and organic matter remineralization at my seafloor study sites. Moreover, my results suggest that functional richness better predicts benthic flux rates than species diversity and abundance. I also identified funnel feeding as a key function provided by activities of a small number of species and individuals of maldanids and pectinariids polychaetes, which can affect benthic flux rates disproportionately relative to their abundance. My results indicate that biodiversity and environment play a similar role in the control of organic matter remineralization. However, larger flux rates were recorded at sites with higher functional richness (e.g. SoGE) and funnel feeders, suggesting greater efficiency in organic matter processing with higher biodiversity. Given the increasing negative anthropogenic impacts on natural ecosystems and corresponding changes in biodiversity, my results point to the need to maintain functional richness in order to ensure ecosystem functioning. Results of this and other studies could help to predict the impact of non-random species loss associated with environmental change (e.g. decrease of dissolved oxygen concentrations) on ecosystem functions such as nutrient flux rates and organic matter remineralization.

3.7 Tables

Table 3.1 Station names, sampling dates, number of incubations performed, locations end environmental variables measured. “Inc #” = incubation number,”Lat” = latitude, “Long” = longitude, “Depth” = sample depth, “Temp” = temperature, “Bottom DO” = dissolved oxygen concentration at ~ 1 m above bottom, “OPD” = oxygen penetration depth, “Chla:Phaeo” = chlorophyll a to phaeopigment ratio, “C:N” = carbon to nitrogen ratio, “porosity” = sediment porosity, “MGS” = sediment mean grain size and “Prokabun” = prokaryotic cell abundance.

Station	Date	Inc (#)	Lat (N)	Long (W)	Depth (m)	Temp (°C)	Bottom DO (ml/l)	OPD (mm)	Chl *a*: Phaeo	C:N	Porosity (%)	MGS (µm)	Prok. abun. (cells/g)
SI	07-2011	3	48°39.25	123°29.20	97	8.72	1.51	4.7	0.23	8.42	66.28	78.62	3.45E+08
SI	09-2013	4	48°39.25	123°29.17	97	9.24	0.97	3.7	0.23	10.01	73.48	87.76	7.66E+07
SoGE	05-2011	4	49°02.56	123°19.15	173	8.25	4.88	13.0	0.22	9.51	64.31	87.29	1.01E+08
SoGE	09-2013	4	49°02.55	123°18.97	167	9.65	2.42	5.8	0.18	34.89	64.40	112.86	7.57E+07
SoGC	07-2011	3	49°02.42	123°25.51	301	8.63	2.86	12.0	0.21	8.77	83.64	27.30	9.07E+07
DDL	07-2011	3	49°05.05	123°19.75	107	8.91	3.23	14.7	0.59	16.97	60.79	95.66	1.48E+08

Table 3.2 Biological traits used in the functional diversity analysis. Categories and levels are defined as per sources provided in Section 3.3.6.

Category	Level
Feeding type	C = Carnivore/predator
	Dt = Detritus feeder
	F = Filter/suspension feeder
	Fn = Funnel feeder
	G = Grazer
	O = Omnivore
	P = Parasitic
	Sc = Scavenger
	SD = Surface deposit feeder
	SSD = Sub-surface deposit feeder
Size	S = Small (< 1 cm)
	M = Medium (1-5 cm)
	L = Large (> 5 cm)
Reworking (R_i)	Epifauna
	Surficial modifier
	Up/Down conveyor
	Biodiffusor
Mobility (M_i)	Live in fixed tube
	Limited movement
	Slow movement in sediment matrix
	Free movement in burrow system
Habitat	Epifauna
	Infauna
	Pelagic

Table 3.3 Permutational analysis of variance (PERMANOVA) results testing the effect of site on benthic communities based on Bray-Curtis similarity matrices performed on fourth root-transformed data, and on benthic fluxes based on Euclidean similarity matrices performed on normalized data.

Benthic community taxonomic composition variation				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	3	7815.9	6.921	0.0001
Residuals	17	1129.3		
Total	20			
Benthic flux variation				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	3	16.141	3.8335	0.0001
Residuals	17	4.2104		
Total	20			

3.8 Figures

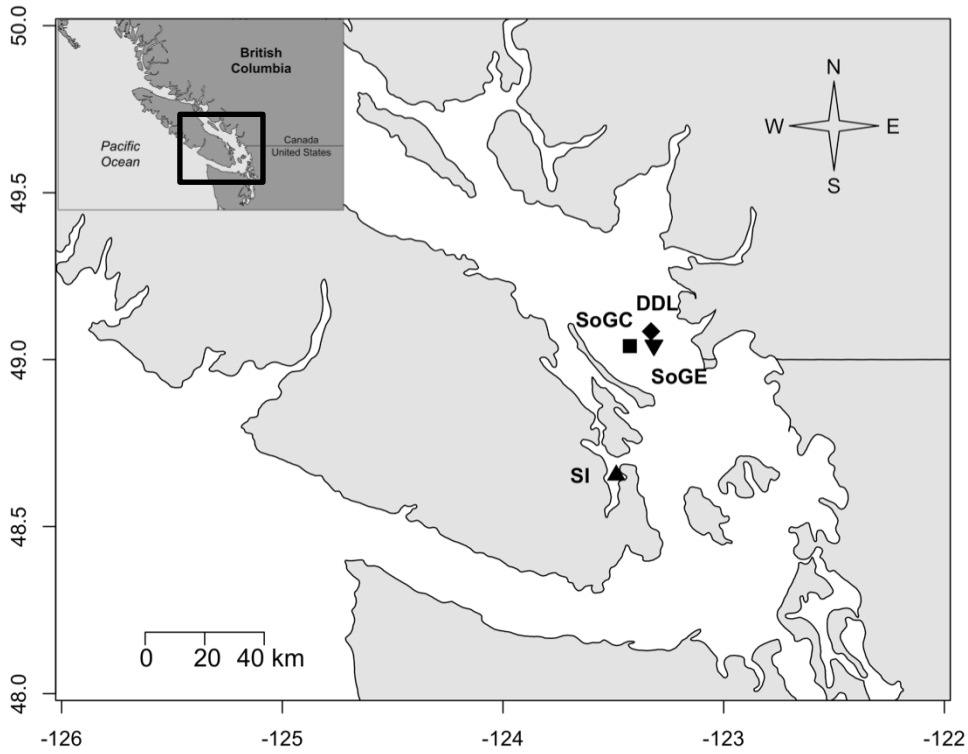

Figure 3.1 Map of stations sampled in Saanich Inlet and in the Strait of Georgia. British Columbia. Canada. Delta Dynamic Laboratory (DDL) and Strait of Georgia Central (SoGC) were sampled in July 2011. Saanich Inlet (SI) sampling occurred in July 2011 and September 2013, and Strait of Georgia East in May 2011 and September 2013.

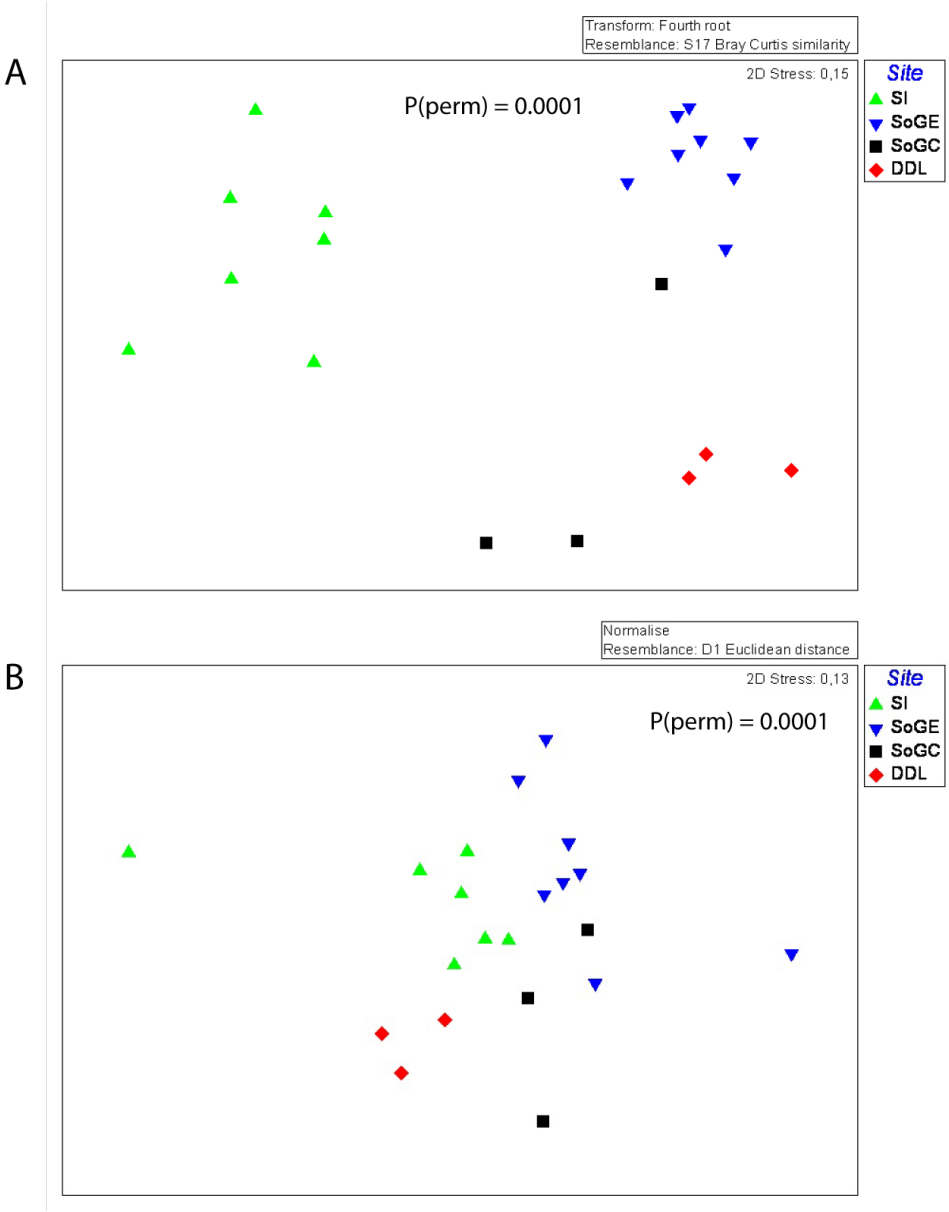

Figure 3.2 Non-metric multi-dimensional scaling (nMDS) plot of a) benthic community taxonomic assemblages at each study site based on Bray-Curtis similarity matrices performed on fourth root-transformed data, and b) benthic fluxes (oxygen, ammonium, nitrate, nitrite, phosphate, and silicate) at each study site based on Euclidean similarity matrices performed on normalized data.

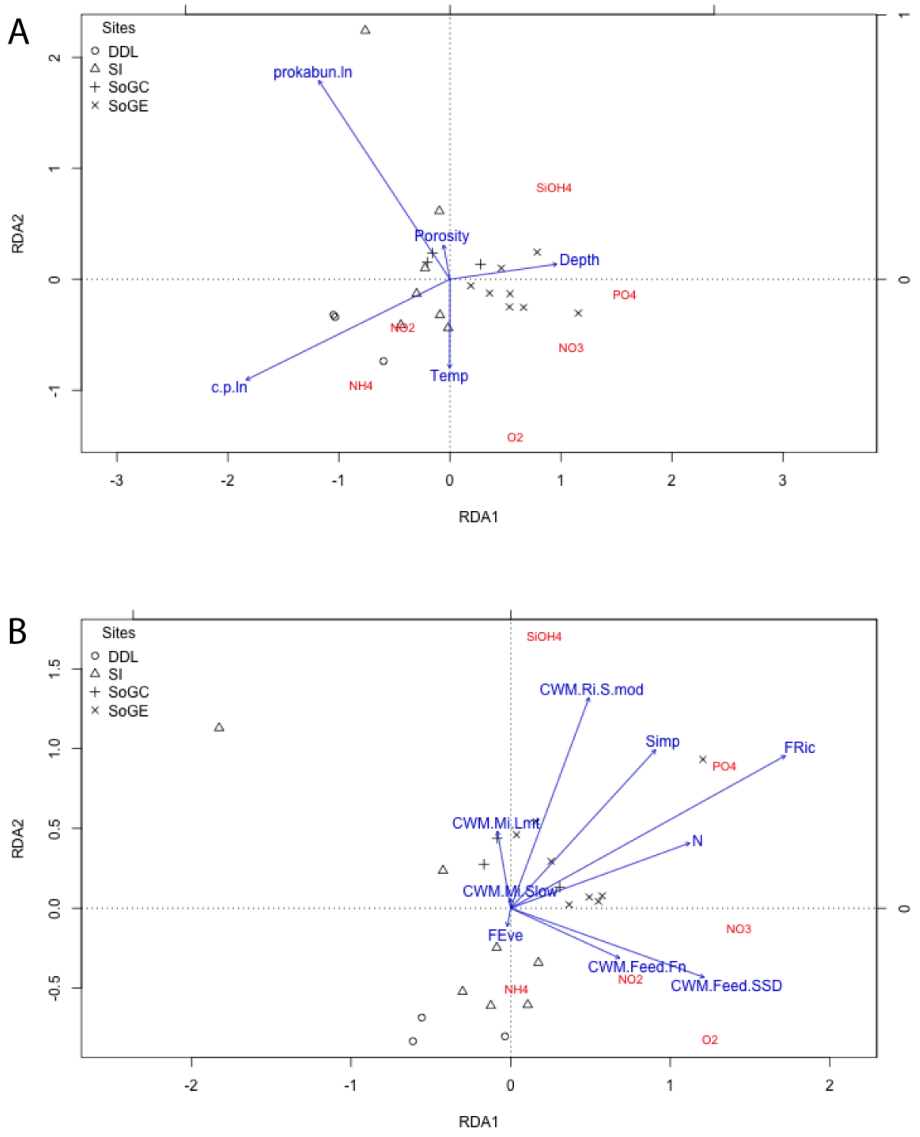

Figure 3.3 Plot of the redundancy analysis (RDA) models of a) environmental variables, and b) functional diversity indices best explaining variation in Salish Sea benthic fluxes measured in May/July 2011, and September 2013.

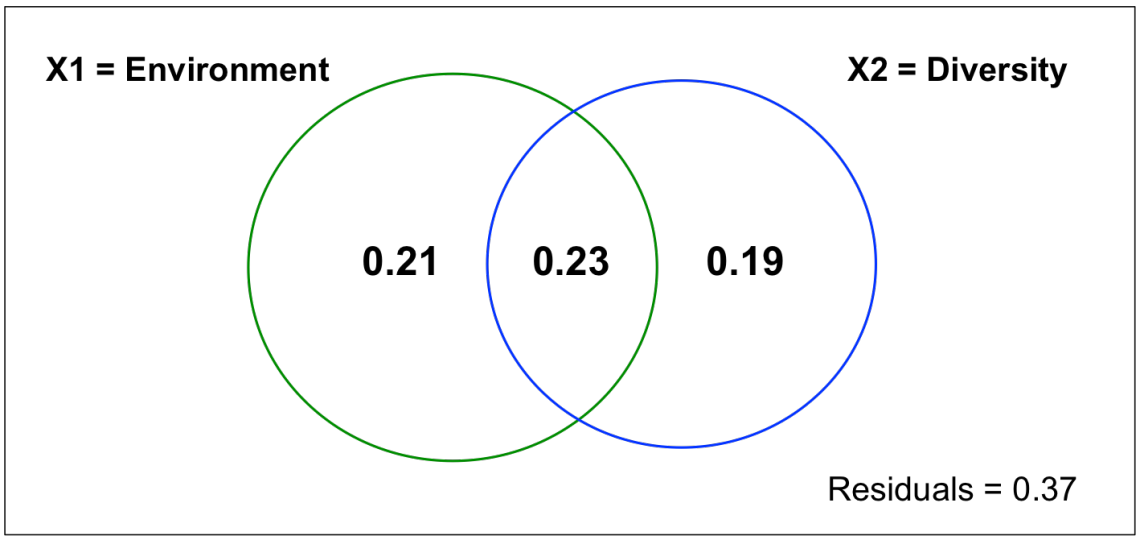

Figure 3.4 Venn diagram illustrating results of variation partitioning of benthic fluxes explained by environmental variables and functional diversity (FD) indices. X1 = environmental variables and X2 = functional diversity indices. Numbers correspond to variation explained by different fractions: environmental variable only = 0.21, FD indices only = 0.19, and intersection of environmental variables and functional diversity indices = 0.23.

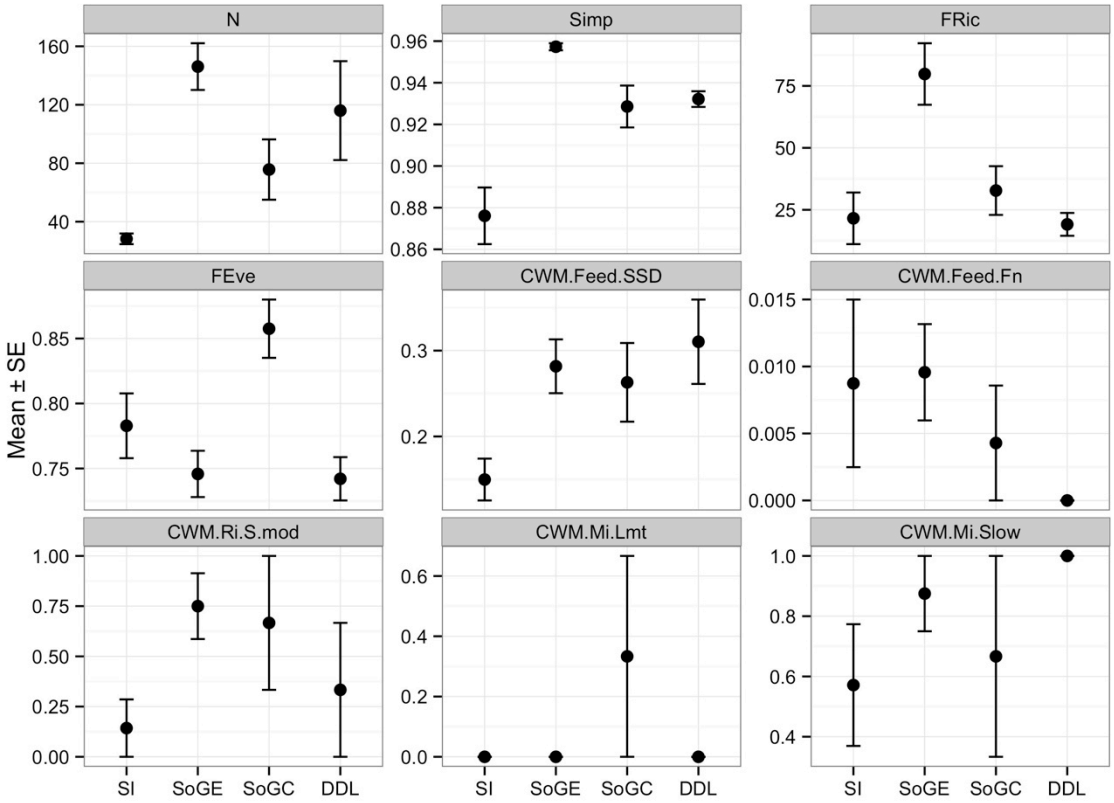

Figure 3.5 Mean (± SE) of each functional diversity (FD) index at the study sites. The nine FD indices presented were identified as significant by the redundancy analysis (RDA) model. N = abundance, Simp = Simpson's diversity index, FRic = functional richness, FEve = functional evenness, CWM = community-level weighted means of trait values, Feed = feeding types, SSD = sub-surface deposit feeders, Fn = funnel feeders, Ri = reworking types, S.mod = surface modifiers, Mi = mobility, Lmt = limited movement, Slow = slow movement through the sediment matrix.

Chapter 4 — The role of infaunal functional and species diversity in short-term response of contrasting benthic communities to an experimental food pulse

4.1 Abstract

Benthic communities play a major role in organic matter remineralization but the role played by macrofauna functional and taxonomic diversity remains elusive. To investigate this topic, I collected sediment cores from two different continental shelf locations near British Columbia, Canada, that differed in diversity to determine how the communities would respond to organic enrichment in the short term (~24 h). I added phytodetritus to half of the cores, measured benthic oxygen and nutrient fluxes in natural and enriched incubations, identified macrofauna, and calculated a suite of functional and taxonomic diversity indices. I found that benthic communities in Saanich Inlet (SI) and the Strait of Georgia East (SoGE) differed significantly in composition and that this difference corresponded to significant differences in benthic flux rates between sites. Multivariate analyses showed that the higher taxonomic (Simpson's diversity) and functional richness (FRic) observed in SoGE explained generally higher benthic flux rates at SoGE compared to SI. In enriched incubations, the higher species richness observed at SoGE explained most of the enhanced benthic flux rates measured in SoGE compared to SI. My results also identify mean densities of detritivores and

omnivores as primary predictors of the higher benthic flux rates measured in enriched incubations in SoGE compared to SI. These results suggest that detritivores and omnivores are the first functional groups of macrofaunal organisms to ingest fresh phytodetritus on the seafloor, and point to their primary importance in short-term remineralization of organic matter following phytoplankton bloom deposition on the seafloor. My results further indicate that sediments with higher functional diversity may process organic matter and regenerate nutrients more quickly than lower diversity sediments, and that diversity loss may have negative consequences for ecosystem functioning of continental shelf sediments.

4.2 Introduction

Benthic communities play an important role in recycling organic matter (OM) that escapes water column remineralization and settles on the seafloor. In addition to direct ingestion of OM, feeding bio-irrigation and bioturbation activities of infaunal organisms typically enhance microbial OM remineralization by oxygenating sediments and physically breaking down organic material (Aller & Aller 1998, Welsh 2003). Organisms that live on and in sediments also experience different amounts of OM deposition seasonally and spatially, and macrofaunal and bacterial populations are known to respond quickly and at various degree to fresh OM deposition on the continental shelf and in the deep-sea (Moodley et al. 2005).

Most previous studies investigating the role of macrofauna on organic matter recycling manipulated species abundance and diversity in laboratory experiments,

whereas other studies highlighted the need to investigate the role of macrofauna in organic matter remineralization following organic matter deposition in natural, mixed communities (Welsh 2003, Snelgrove et al. 2014).

Interestingly, most enrichment experiments on the effects of fresh phytodetritus have focused on deep-sea benthic community respiration rates and followed the fate of this labile food source through different benthic compartments (Levin et al. 1999, Aberle & Witte 2003, Witte et al. 2003, Sweetman & Witte 2008). Using ^{13}C-labelled diatoms, these studies usually showed increased sediment community oxygen consumption (SCOC) rates and carbon remineralization following enrichment, and identified macrofauna as key players in food uptake. They also often attribute ingestion of ^{13}C-labelled phytodetritus to surface and sub-surface deposit feeders (Levin et al. 1999, Aberle & Witte 2003, Witte et al. 2003, Sweetman & Witte 2008). However, few studies have specifically investigated the impact of fresh phytodetritus on oxygen and nutrient flux rates in benthic communities with contrasting diversity to investigate the effect of diversity on benthic flux rates and organic matter recycling (Sweetman et al. 2014), an important benthic ecosystem function (Giller et al. 2004).

In order to gain insight into the effect of benthic community diversity on responses to fresh phytodetritus input, I examined short-term changes in oxygen and nutrient flux rates in natural and enriched incubations at two contrasting sites that differed strongly in benthic community diversity. Low diversity characterizes the Saanich Inlet (SI) infauna (Chapter 3), likely because the large annual influx of OM in spring and fall results in severe hypoxia or anoxia and subsequent mass

mortality of sessile animal species and displacement of motile species (Chu & Tunnicliffe 2015). The adjacent Strait of Georgia (SoG) site harbours a more diverse benthic community (Belley & Snelgrove 2016) and, despite the absence of seasonal anoxia, deep-water renewal by neighbouring shelf waters may transport sporadically hypoxic bottom waters (Johannessen et al. 2014). Indications of more frequent and pronounced hypoxic events in the SoG in recent years may affect benthic community and ecosystem functioning (EF) in the near future (Johannessen & Macdonald 2009).

I addressed my objective of understanding the role of macrofauna in OM remineralization by exploring the following research questions: i) do OM enrichment pulses to the seafloor result in rapid increases in oxygen and nutrient flux rates, ii) do macrofaunal functional and taxonomic diversity influence benthic flux rates in both natural and enriched incubations, iii) what aspects of diversity (functional vs. taxonomic) affect the most benthic flux rates in natural and enriched sediments, and iv) what is the influence of diversity on the capacity of the system to rapidly remineralize organic matter pulses?

4.3 Methods

4.3.1 Field sampling

I collected sediment push cores in the Strait of Georgia East (SoGE) and Saanich Inlet (SI) in the Salish Sea (Figure 4.1) near the VENUS Observatory nodes (http://www.oceannetworks.ca/), using the ROV ROPOS (Remotely Operated

Platform for Ocean Science, www.ropos.com) on board the Research Vessel Falkor (September 6-18, 2013). The ROV collected 9 push-cores at each site (i.d. = 6.7 cm, L = 35.6 cm) at random locations within a bottom area that spanned ~ 25 x 25 m. I used one core per site to determine prokaryotic cell abundance and sediment properties as part of a broader study (results not reported here), and the remaining cores for *ex situ* incubations to measure fluxes and taxonomic identification. A Seabird CTD mounted on the ROV recorded near-bottom dissolved oxygen (DO), temperature, and salinity at each location. Below I provide a brief overview of methodologies, but a more detailed description can be found in Chapter 2 and Chapter 3.

4.3.2 Incubations

I acclimated sediment cores for 1.5-2 hours to allow sediment particles in suspension to settle back to the sediment surface before beginning incubations. I aerated the overlying water in each core for 1 hour using aquarium air pumps to avoid suboxic conditions during incubations. Sediment cores were then sealed with water-tight lids equipped with magnetic stirrers and gas-tight sampling ports prior to incubating in a dark, cold room at *in situ* temperatures (8-9 ˚C) for 16 hours (SoGE) and 25.5 hours (SI) until 15-30% of available oxygen was consumed.

Although the conversion of flux measurements from small sediment cores to values per square meter of sediment can increase variation in benthic flux estimates, comparison of flux rates with similar studies (Archer & Devol 1992, Devol & Christensen 1993, Berelson et al. 1996, Berelson et al. 2003) indicates that the

values measured for my study sites represent realistic estimates of ambient benthic flux rates.

4.3.3 Enrichment experiments

I added algae to four sediment cores per site before the onset of the incubations (SI: Incubations 1, 2, 4 and 5; SoGE: incubations 12, 13, 14, and 15) with no additions to the four other cores per site (SI: Incubations 6, 7, 8 and 10; SoGE: incubations 16, 17, 18, and 20). I selected the diatom *Chaetoceros calcitrans* for enrichment because *Chaetoceros* spp. are dominant components of British Colombia diatom blooms (Grundle et al. 2009, Peterson & Harrison 2012, Villareal et al. 2012). Diatoms provided by Badger Bay Mussel Farms Ltd were grown in tanks under controlled conditions and supplied with filtered sterile seawater at the Dr. Joe Brown Aquatic Research Building (http://www.mun.ca/osc/jbarb/index.php). Harvested phytoplankton was centrifuged to produce an algal paste, which was frozen at -20 °C until needed for the cruise. I injected 2.5 ± 0.1 g (mean ± SE) of wet paste (Carbon weight = 14.6 ± 0.4 % and C:N ratio = 5.6 ± 0.1, n = 8) to each core, equivalent to 737 mg OC m^{-2} day^{-1} over a period of 14 days, which corresponds to the maximum seasonal summer concentration recorded at 110 m at the head of SI (Timothy et al. 2003). Another study estimated the flux of organic carbon as 1036 mg OC m^{-2} day^{-1} at SoGE (Burd et al. 2008). Therefore, the amount of OC added to my sediment cores represents high, but realistic levels of OC carbon reaching the seafloor at these sites.

4.3.4 Oxygen uptake

I measured oxygen consumption periodically (4-8 hour intervals) using a non-invasive optical oxygen meter used in conjunction with oxygen optode patches (Fibox 4, PreSens, Regensburg, Germany). I determined oxygen uptake from the slope of the linear regression of oxygen concentration versus time of incubations after correction for oxygen concentration in the replacement water (water removed for measurements and replaced with bottom water from the same locations).

4.3.5 Nutrient fluxes

At the beginning, midpoint, and end of the incubations I collected water samples with 60-mL, acid-rinsed plastic syringes. I immediately replaced withdrawn water with an equivalent volume of bottom water of known oxygen and nutrient concentrations from the same location. Syringes and sample containers were initially rinsed with ~5 mL of water sample. At each sampling time I collected and stored two 25-mL water samples in acid-rinsed twist-cap 30-mL HDPE bottles. Upon collection, water samples were immediately placed in an upright position at -20 °C until analyzed. I determined the concentrations of nutrients (NH_4^+, NO_3^-, NO_2^-, $Si(OH)_4$ & PO_4^{3-}) in the water samples using a Technicon Segmented Flow AutoAnalyzer II, following the method recommended by Technicon Industrial Systems (1973, 1977, 1979) with the exception of ammonia (hereafter referred as ammonium) analysis, which followed Kerouel & Aminot (1997). Nutrient fluxes

were determined from the slope of the linear regression of nutrient concentrations versus time of incubations after correction for the solute concentration in replacement water.

4.3.6 Macrofaunal identification and taxonomic diversity

After incubations, sediment cores were sectioned into 0-2, 2-5, and 5-10 cm depth layers and processed through a 300 μm sieve prior to preservation in 4% seawater-formaldehyde solution and subsequent transfer to 70% ethanol for identification. Specimens were sorted under a dissection microscope in the laboratory and identified to the lowest possible taxonomic level, usually to species. I determined abundance (N) for each taxon and taxonomic richness (S) as the number of taxa present in each sediment core. I also determined taxonomic diversity indices including Simpson's index (Simp or 1 - *D*), Pielou's evenness (*J'*), Rarefaction (ES(25), i.e., the expected number of species (Expected Species) in a hypothetical random sample of 25 individuals) and Shannon-Wiener index (*H'*) for each sediment core. Taxonomic diversity indices were computed in R (R Core Team 2016) using the package "vegan" (Oksanen et al. 2013).

4.3.7 Biological traits and functional diversity

I selected five biological traits and 24 modalities based on their availability for all taxa and presumed influence on benthic fluxes (see Appendix 1 in Belley & Snelgrove 2016). These traits reflected behaviour (bioturbation mode, feeding type,

habitat, and mobility) and morphology (size). Biological traits were collected for each taxon from published sources (MarLIN 2006, Macdonald et al. 2010, Link et al. 2013b, Queiros et al. 2013, Jumars et al. 2015, WoRMS Editorial Board 2015). When biological traits information was not available for a specific taxon, I obtained information from one taxonomic rank higher. I allowed more than one functional trait for a given taxon for each category, and scored the taxon from 0 to 1 based on the extent to which it displayed each trait. I obtained functional diversity (FD) indices from trait category scores for each taxon and taxa abundance matrices using the "FD" package (Laliberté & Legendre 2010) in R (R Core Team 2016). I then computed the following multidimensional FD indices for use in my analyses: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al. 2008), functional dispersion (FDis) (Laliberté & Legendre 2010), Rao's quadratic entropy (RaoQ) (Botta-Dukat 2005) and an index of functional composition, the community-level weighted means of trait values (CWM) (Lavorel et al. 2008).

4.3.8 Statistical analyses

I examined spatial variation and response to enrichment on benthic fluxes, taxonomic community composition, and diversity indices using permutational multivariate analysis of variance (PERMANOVA) performed with 9999 random permutations of appropriate units (Anderson 2001, McArdle & Anderson 2001). I performed three separate two-way crossed PERMANOVA designs to test benthic flux spatial variation and treatment effect within and among sites with the factor

"Site" (two levels, fixed: SI and SoGE), crossed with "Treatment" (two levels, fixed: natural and enriched), and their interactions. I calculated the resemblance matrices from Euclidean distances of standardized benthic flux and diversity indices, and from Bray-Curtis distances of fourth-root transformed benthic community data. Taxa that appeared only once were removed from this analysis (Clarke & Warwick 1994), although this removal had little effect on overall patterns. I verified homogeneity of multivariate dispersion using the PERMDISP routine (Anderson et al. 2008). When there were too few possible permutations for a meaningful test, I calculated a *p*-value based on 9999 Monte Carlo draws from the asymptotic permutation distribution (Terlizzi et al. 2005).

I further analysed significant terms within the full models using appropriate pair-wise comparisons. Non-metric multidimensional scaling (nMDS) ordinations of similarity matrices were performed to visualize multivariate patterns and I determined taxa that contributed most to within site similarity and dissimilarity between sites using SIMPER (Similarity percentage analyses) (Clarke 1993). I completed nMDS, PERMANOVA, PERMDISP and SIMPER analyses in PRIMER 6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

I used two distinct redundancy analyses (RDA) to identify the functional and taxonomic diversity indices influencing benthic flux variation in natural and enriched incubations. To obtain the model with the most parsimonious set of variables, I used stepwise selection with a significance level of 0.05 and 9999 random permutations. Predictor variables containing outliers were transformed, excluding highly correlated ($r > 0.85$) predictor variables (FDiv, CWM.Feed.C and

CWM.Size.M) from the analyses. I further analysed multi-collinearity of the predictor variables from the full models with a variance inflation factor (VIF) test using the "vif" function from the "car" package (Fox & Weisberg 2011). All predictor variables from the selected best model had a VIF < 10 (Zuur et al. 2009). Note that the software PRIMER 6 base contributions of each diversity index to benthic fluxes reported here on r^2 and not on Adj. r^2 calculations. I completed RDA in R (R Core Team 2016) using the package "vegan" (Oksanen et al. 2013), calculating the contribution of each predictor variable to benthic flux variation in PRIMER 6 (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

4.4 Results

4.4.1 Benthic community assemblages and diversity indices variation

PERMANOVA indicated that benthic community assemblages and diversity indices differed significantly between cores collected from SI and SoGE (P (MC) < 0.01, Table 4.1). However, I found no significant differences in sediment core community assemblages and diversity indices between treatments or treatments between sites (Table 4.1, Figures 4.3 & 4.4).

Lower Simp, ES(25), FRic, and a community weighted mean of omnivores and detritivores characterized the SI benthic community compared to SoGE (Figure 4.5). However FEve, community weighted means of large animals, upward/downward conveyors and animals moving slowly through the sediments were higher at SI than SoGE. On the one hand, higher abundances of the polychaetes

Bipalponephtys cornuta and *Spiophanes berkeleyorum* characterized the SI benthic community (Table 4.2). On the other hand, the less variable benthic community at SoGE was composed primarily of *Mediomastus californiensis*, *Cumella* sp., Tanaidacea, bivalvia, *Bilpalponephtys cornuta* and *Levinsenia gracilis* (Table 4.2). These differences contributed to a high average dissimilarity between sites (77.7%) driven mostly by higher abundances of *Cumella* sp., *M. californiensis*, Tanaidacea, *Galathowenia oculata* and *L. gracilis* at SoGE (Table 4.2).

4.4.2 Multivariate benthic flux variation

PERMANOVA indicated similar rates of benthic flux measurements in SI and SoGE cores when considering all cores (P (MC) = 0.29, Table 4.1). However, PERMANOVA revealed significant differences in benthic flux between natural and enriched incubations (P (perm) < 0.01, Table 4.1). Furthermore, PERMANOVA indicated that benthic fluxes differed significantly between sites and treatments (P (perm) = 0.03). Pair-wise comparison tests revealed that benthic flux from SI (P (MC) =0.02) and SoGE (P (MC) < 0.01) differed significantly between enriched and natural incubations (Figure 4.2). Finally, pair-wise comparison tests also revealed that benthic fluxes in natural (P (MC) = 0.04) and enriched (P (MC) = 0.01) incubations differed between sites (Figure 4.2).

4.4.3 Individual benthic flux variation

The addition of OM to incubations resulted in a small though non-significant increase in oxygen uptake for both sites ($P = 0.42$, Table 4.3, Figure 4.6A). However, ANOVA indicated a significant difference between SI and SoGE when considering all measured fluxes (i.e., natural versus enriched cores) ($P = 0.02$, Table 4.3, Figure 4.6A). I observed a marked increase in ammonium effluxes after OM addition at both sites ($P < 0.01$, Table 4.3, Figure 4.6B) but no significant difference between sites (Table 4.3, Figure 4.6B). Silicate efflux increased, although not significantly, between natural and enriched incubations both in SI and SoGE (Figure 4.6C). ANOVA indicated a significant site level difference between SI and SoGE when considering all silicate fluxes ($P < 0.01$, Table 4.3, Figure 4.6C). A Tukey's HSD test also indicated a larger silicate efflux at SoGE than SI irrespective of treatment (Figure 4.6C). Benthic fluxes of nitrate did not differ significantly between SI and SoGE ($P = 0.55$, Table 4.3, Figure 4.6D), however, a Tukey's HSD test indicated a significant difference between natural and enriched incubations at SoGE (Figure 4.6D). Of the nutrients examined, phosphate flux increased most between natural and enriched incubations for both sites ($P < 0.01$, Table 4.3, Figure 4.6E). The Tukey HSD test also indicated significantly larger increase in phosphate flux at SoGE than SI (Figure 4.6E). Finally, ANOVA indicated a weak but significant treatment effect on nitrite fluxes ($P = 0.03$, Table 4.3), however, a Tukey's HSD test found no significant differences between sites or treatments (Figure 4.6F). Of the comparisons, only the SI comparison between natural and enriched incubations was near the selected significance level ($P = 0.05$, Figure 4.6F).

4.4.4 Diversity effects on benthic flux variation

My redundancy analysis (RDA) of fluxes in natural incubations explained 56% (r^2 = 0.87, Adj. r^2 = 0.56) of total benthic flux variation and included five diversity indices (Table 4.4). Simpson's diversity index (Simp) contributed most to this variation (38.1%, contribution hereafter based on R^2), followed by FRic (23.9%), CWM.Mi.Slow (9.4%), FEve (8.6%) and CWM.Ri.UD.conv (7.4%) (Table 4.4). The first and second axes of the RDA model accounted for 60.6% and 12.2% of total flux variation, respectively (Table 4.5). The first axis separated SI from SoGE natural incubations (Figure 4.7). Simp, FEve, FRic and to a lesser extent CWM.Mi.Slow contributed most to the first axis and explained 69.4% of the fitted flux variation (Table 4.5, Figure 4.7). The second axis separated incubations with higher fluxes of oxygen, silicate, nitrate, and phosphate from those with higher fluxes of ammonium and nitrite (Figure 4.7). CWM.Mi.Slow, FEve and CWM.Ri.UD.conv contributed most to the second axis and explained 13.9% of the fitted flux variation (Table 4.5, Figure 4.7). Moreover, the second axis mostly explained within-site differences. I therefore focus on between-site differences (RDA axis 1).

My redundancy analysis (RDA) performed on fluxes measured in enriched incubations explained 54% (r^2 = 0.80, Adj. r^2 = 0.54) of total benthic flux variation and included four diversity indices (Table 4.6). Expected Species (ES(25)) contributed most to total flux variation (29.8%), followed by CWM.Size.L (18.4%), CWM.Feed.O (16.1%) and CWM.Feed.Dt (15.8%) (Table 4.6). The first and second

axes of the RDA model accounted for 43.2% and 23.1% of total flux variation, respectively (Table 4.7). The first axis again separated SI from SoGE enriched incubations (Figure 4.8). All diversity indices (but ES(25) in particular) correlated well with the first axis and explained 54.0% of the fitted flux variation (Table 4.7, Figure 4.8). As noted above, the second axis separated incubations with higher fluxes of oxygen, silicate, nitrate and phosphate from those with higher ammonium and nitrite fluxes (Figure 4.8). CWM.Size.L and to a lesser extent CWM.Feed.Dt and CWM.Feed.O contributed most to the second axis and explained 28.9% of the fitted flux variation (Table 4.7, Figure 4.8). Again, because the second axis explained primarily within-site differences, I focus on across-site differences explained by RDA axis 1.

4.5 Discussion

My experiment investigated the short-term (~24 hours) response of two benthic communities varying in functional and taxonomic diversity to organic enrichment by measuring benthic flux rates in enriched and non-enriched incubations of intact (unaltered) benthic cores. The enrichment was designed to mimic sedimentary community response following a spring phytoplankton bloom. Because my multivariate analyses indicated high similarity of benthic communities in cores within each site but differences between my two study sites, this contrast created an excellent opportunity to evaluate the effect of diversity on benthic fluxes, and on the capacity of the communities to respond to organic matter pulses. My

analysis demonstrated significant differences between the two benthic communities in composition and diversity, which explained a significant component of their different responses to increased organic matter. Specifically, I observed a stronger increase in silicate and phosphate effluxes, and an overall higher O_2 uptake (although not significantly) at my higher diversity SoGE site than my lower diversity SI site. Moreover, the higher Expected Species measured at SoGE and the higher proportion of detritivores and omnivores explained increased benthic flux rates experienced in enriched incubations at SoGE.

4.5.1 Diversity effects on benthic flux variation in natural incubations

Results from my redundancy analysis indicate clearly that the first axis separates benthic fluxes measured in natural incubations at SoGE from those measured at SI. Species richness (Simp) and functional richness (FRic) explained 38.1% and 23.9% of the multivariate benthic flux variation, respectively. Higher Simp and FRic generally led to larger fluxes of ammonium, nitrate, nitrite, phosphate, and silicate at SoGE. In contrast, lower Simp and FRic contributed to higher functional evenness (FEve) and lower benthic flux rates at SI.

Previous studies have linked species richness to increased benthic flux rates and organic matter remineralization in different marine benthic ecosystems (Waldbusser et al. 2004, Godbold & Solan 2009, Link et al. 2013b). Yet, a previous study in my system identified functional richness as the primary diversity index controlling benthic flux rates (Chapter 3). More precisely, my previous study showed that macrobenthic functional richness (FRic) explained ~ 20% of benthic

nutrient flux variation in the Salish Sea. Other studies also usually report that FRic predicts benthic flux variation better than species richness, although species richness can be more important in controlling ecosystem functions in environments characterized by low functional richness (Wahl et al. 2011), as occurs in SI. Nonetheless, my results and those from previous studies point to the importance of both species and functional richness in the control of benthic flux rates and organic matter remineralization (Godbold & Solan 2009, Godbold 2012, Link et al. 2013b, Belley & Snelgrove 2016).

Although correlative and regression analysis do not fully demonstrate causality, which requires manipulative experiments, mensurative data such as those presented here can inform manipulative experiments (which bring other limitations), in identifying potential drivers and promising directions for experimental studies.

4.5.2 Diversity effects on benthic flux variation in enriched incubations

I observed a significant increase in ammonium and phosphate effluxes at both sites with the addition of phytodetritus, as well as a significant increase of nitrate uptake at SoGE. These results indicate a moderate short-term response of the benthic community to the addition of fresh, labile phytodetritus.

The first axis of my redundancy analysis once again separated benthic fluxes in enriched incubations at SoGE from those at SI. Expected Species (ES(25)), a rarefaction method ideal for comparison of diversity datasets (Gotelli & Colwell 2001), explained 29.8% of the multivariate benthic flux variation in enriched

incubations. This result indicates that more species per number of individuals (25 in this instance), explained a significant portion of the larger phosphate and silicate fluxes measured in SoGE enriched incubations compared to SI. Many studies performed in soft-sediment ecosystems report a positive effect of species richness on benthic flux rates and various ecosystem functions (Stachowicz et al. 2007, Godbold 2012). For example, Danovaro et al. (2008) reported increasing ecosystem functioning (i.e., prokaryote carbon production) with increasing Expected Species of nematodes in deep-sea samples from different oceans. My results and those from previous studies demonstrate the primary importance of species richness to efficient recycling of fresh phytodetritus on the seafloor.

Although species richness influences ecosystem functions, previous studies emphasize the importance of species-specific traits (e.g. feeding and bioturbation modes) in controlling benthic fluxes (Waldbusser et al. 2004, Mermillod-Blondin et al. 2005). My study also identified indices related to functional diversity as important drivers of enhanced benthic flux rates at SoGE. The community-weighted means of omnivores and detritivores explained 16.1% and 15.8% of benthic flux variation in enriched incubations, respectively. Although a tracer technique (i.e., using isotope labeled algae) would have allowed me to identify the species and functional groups ingesting the added algae (Sweetman & Witte 2008), my results suggest that omnivores and detritivores are the first groups feeding on fresh, labile phytodetritus. As noted by Jumars et al. (2015), few species classify exclusively as omnivores but instead most occupy multiple feeding groups such as carnivores/predators and surface deposit feeders. In my study, 10 taxa comprised

the omnivores, including the polychaetes Dorvilleidae spp., Hesionidae spp. A, Hesionidae spp. B, *Nereimyra* sp., *Exogone (Parexogone) molesta*, the crustaceans Brachyura spp., *Pinnixa occidentalis*, the *Caprella* sp., the gastropods Buccinidae, and finally the mollusks Caudofoveata. With the exception of *E. molesta* (classified as omnivores only) and Caudofoveata (classified as omnivores and carnivores/ predators), the eight other taxa were also classified as carnivores/predators and scavengers. These multiple categories illustrate the capacity of these taxa to adapt their feeding strategy to available food. Therefore, these omnivore taxa represent opportunistic taxa taking advantage of their mixed dietary preferences to forage on different types of food sinking, including algal detritus sinking from the water column to the sediment surface. Some omnivores increase benthic fluxes through their bioturbation activities. For example, the intertidal burrowing crab *Neohelice (Chasmagnathus) granulata* influenced the direction and rate of nutrient benthic fluxes (Fanjul et al. 2011) and the polychaete *Alitta virens* increased O_2 uptake by respiration and bio-irrigation of galleries in sediments (Piot et al. 2014). Therefore, omnivores were likely among the first macrofaunal taxa to feed on the fresh phytodetritus and their respective activities (e.g. biodiffusors and surficial modifiers) increased phosphate and silicate benthic effluxes.

Similarly, detritivores can feed on a variety of food types, including phytoplankton detritus (Jumars et al. 2015). Polychaetes from the family Onuphidae (Onuphidae spp., *Mooreonuphis exigua* and *Onuphis iridescens*) and isopods (Isopoda spp., *Munna* sp. and *Munnogonium tillerae*) dominated the detritivores in my study. Again, most taxa classified as detritivores also belonged to other feeding groups. I

also classified the onupid polychaetes as scavengers and carnivores/predators, and the isopod *M. tillerae* as a grazer, whereas the other isopod species were solely classified as omnivores. Again, these mixed classifications indicate opportunistic taxa that can adapt their feeding strategy to available food. In their study on incubated cores collected at 688 m depth in Korsfjorden, Norway, Sweetman and Witte (2008) showed a rapid uptake of fresh labeled phytodetritus by one of three sampled onuphids. Laboratory studies showed that ammonium effluxes approximately doubled in the presence of the amphipod, *Corophium volutator*, classified as detritivore, grazer, and suspension feeder, compared to treatments with sedentary filter feeders (Biles et al. 2002). Moreover, van Nugteren et al. (2009) also showed that facultative detritivores incorporate more OM when fresh phytodetritus was concentrated in patches, as in my experiment, rather than homogenised in sediments where microbial uptake dominated. Detritivores also vary in bioturbation modes, which can affect benthic flux rates (Mermillod-Blondin et al. 2002). In my study detritivores were all surficial modifiers, and differences in bioturbation mode therefore cannot explain increased flux rates at SoGE. Still, Braeckman et al. (2014) showed that increased densities and biomass of surficial modifiers explained the higher bioturbation potential in Southern North Sea fine sandy sediments and hence, higher benthic fluxes. In my study, I also observed higher densities of surficial modifiers at SoGE than at SI (results not presented).

Interestingly, sediment cores from SI contained a higher community-weighted mean of large-sized individuals (CWM.Size.L) than SoGE. For instance, the low-oxygen tolerant polychaetes *Paraprionospio pinnata* (Supplementary Figure

3.3), which could be more than 10 cm long, comprised some of the largest specimens collected in my study. This species occurred in six of the eight cores collected in SI but in only one SoGE core. Previous studies showed that large individuals usually enhance ecosystem functioning (Norkko et al. 2013, Séguin et al. 2014). My results indicate that large animals strongly influence benthic fluxes in SI enriched incubations. Given the higher functional and species richness, and community weighted mean of detritivores and omnivores at SoGE than SI, I expected larger differences in benthic fluxes between sites than those I observed. The higher abundance of large-size individuals in SI may have partially compensated for the lower diversity at SI and therefore, buffered anticipated differences in fluxes at SI compared to SoGE, as previous studies suggest (Norkko et al. 2013, Séguin et al. 2014).

4.5.3 Effect of environmental variables on benthic flux variation

Analysis from my locations showed that environmental variables also play an important role in controlling benthic flux rates and organic matter remineralization. Bottom water characteristics (i.e., temperature and dissolved oxygen concentration), quality of organic matter (i.e., chl *a*:phaeopigments and C:N ratios) and sediment characteristics (i.e., mean grain size and porosity) were identified as key environmental variables explaining benthic flux variation in the Salish Sea and Northeast Pacific shelf and slope sediments (Chapter 2). However, I observed smaller spatial variation in benthic fluxes associated with these environmental variables in the Salish Sea compared to the Northeast Pacific shelf and slope

sediments (Chapter 2). Also, environmental variables and functional diversity indices explained similar levels of benthic flux variation at my Salish Sea study sites (Chapter 3). I found that 62.9% of variation in benthic flux could be attributed to environmental variables and functional diversity indices (Chapter 3). Because the manipulative experimental design of the present study precluded the inclusion of environmental variables, I cannot exclude a potential role for variation in environmental variables between my study sites. However, the strong fit of my redundancy models in natural (r^2 = 0.874, Adj. r^2= 0.560) and enriched (r^2 = 0.801, Adj. r^2= 0.536) incubations indicates an important role for benthic communities in explaining benthic flux variation and in the recycling of fresh phytodetritus.

4.5.4 Potential effect of prokaryotes and meiofauna on benthic flux variation

Whereas O_2 and nutrients diffuse at the sediment-water interface based on gradient differences, prokaryotes (i.e. bacteria and archaea) catalyze OM degradation on the sediment surface (Jorgensen 2006) and are therefore considered the primary driver of benthic fluxes. However, previous studies showed that the presence of macrofauna correlated strongly with the uptake of fresh phytodetritus. In a series of short-term experiments (24 h), Moodley et al. (2005) showed that up to 30% of the added ^{13}C-labeled phytodetritus was processed by benthic fauna when biomass was high compared to only 5% at sites with low faunal biomass. Considering that macrofaunal abundances were relatively high at my two study sites and given the short time scale of my experiment (~24 h), I believe that the generation time for prokaryotes was probably insufficient to allow large increases

in number and that prokaryotes were probably not primarily responsible for the changes in flux I measured. Still, I acknowledge that prokaryote metabolism may have increased in response to the phytodetritus input, which represents a limitation of the present study given that I did not specifically measure prokaryote metabolism. Meiofauna can also affect benthic fluxes (Piot et al. 2014) but were not quantified in my study; if meiofaunal differences influenced benthic fluxes, the unexplained variation of the RDA models likely included those contributions.

4.6 Conclusions

My study showed that differences in Saanich Inlet and Strait of Georgia East communities contribute to significant between-site differences in benthic flux rates. The higher taxonomic (Simpson's diversity) and functional richness (FRic) in SoGE natural incubations explained generally higher benthic flux rates in SoGE compared to SI. The higher species richness observed at SoGE, demonstrated by higher rarefaction values (i.e., ES(25)), explained most of the enhanced benthic flux rates measured in enriched incubations. My results also identify detritivores and omnivores as primary functional groups explaining the larger benthic flux rates measured in enriched incubations in SoGE compared to SI. Therefore, this result suggests that detritivores and omnivores are the first functional groups of macrofaunal organisms to ingest fresh phytodetritus on the Salish Sea seafloor, pointing to their primary importance in short-term remineralization of organic matter following phytoplankton bloom deposition.

Accelerating human impacts on marine ecosystems (Halpern et al. 2008, Halpern et al. 2015) increase the risk of species change or loss (Kappel 2005), and my study indicates that loss or alteration of biodiversity (i.e., taxonomic diversity, functional richness, species richness, and diversity of detritivores and omnivores) on the seafloor could alter short-term organic matter recycling and nutrient regeneration, with potentially negative consequences for ecosystem functioning of continental shelf sediments. My results further suggest effects may vary with types of human impact. Warming oceans might be expected to decrease seasonal amplitude of primary production (Henson et al. 2013), which my experiment suggest would result in lower organic matter remineralization. Bottom water hypoxia, which continues to expand world-wide (Rabalais et al. 2010), would presumably reduce benthic biodiversity, such as in Saanich Inlet (SI) in my study, with an anticipated result of slowing down benthic-pelagic coupling and thus potentially limiting nutrient supply for surface water primary productivity. Bottom trawling, which typically alters the functional composition of benthic communities by decreasing the biomass of filter feeders, permanently attached, long-lived, and large animals (Tillin et al. 2006), would result in lower organic matter remineralization as suggested by my experiment and by previous studies (Olsgard et al. 2008). I fully acknowledge the speculative nature of these predictions and also question how these different changes might act in concert. Nonetheless, they punctuate the need to consider seabed functioning within the context of sustainable oceans and ecosystem-based management.

4.7 Tables

Table 4.1 Permutational analysis of variance (PERMANOVA) results testing the effect of location and organic matter enrichment on benthic fluxes based on Euclidean similarity matrices performed on normalized data, benthic community assemblages based on Bray-Curtis similarity matrices performed on $\log_{(x+1)}$ transformed data and benthic community diversity indices based on Euclidean similarity matrices performed on normalized data. Asterisk (*) = *P*(MC). Bold font indicates significant differences.

Benthic fluxes				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	1	16.58	1.89	0.29*
Treatment	1	33.23	12.69	**<0.01**
Site x Treatment	1	8.77	3.35	**0.03**
Residuals	12	2.62		
Total	15			
Benthic community assemblages				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	1	16941.00	29.87	**<0.01***
Treatment	1	1332.70	1.26	0.20
Site x Treatment	1	567.10	0.54	0.74
Residuals	12	1056.10		
Total	15			
Benthic community diversity indices				
Source of variation	**df**	**MS**	**Pseudo-*F***	***P* (perm)**
Site	1	97.01	9.33	**<0.01***
Treatment	1	21.19	1.63	0.15
Site x Treatment	1	10.40	0.80	0.55
Residuals	12	13.03		
Total	15			

Table 4.2 Results of similarity percentage analyses (SIMPER) showing the contribution (%) of the taxa to the average Bray-Curtis similarity within site and dissimilarity across sites (SI and SoGE).

Taxa	Ave. abun SI	Ave. abun. SoGE	Contr. (%)	Cum. (%)
SI (Ave. similarity = 45.61)				
Bipalponephtys cornuta	2.06	NA	40.29	40.29
Spiophanes berkeleyorum	0.92	NA	14.22	54.52
SoGE (Ave. similarity = 67.03)				
Mediomastus californiensis	NA	3.41	12.78	12.78
***Cumella* sp.**	NA	2.72	9.07	21.84
Tanaidacea	NA	2.46	8.46	30.30
Bivalvia	NA	2.20	7.95	38.25
Bipalponephtys cornuta	NA	2.15	7.81	46.07
Levinsenia gracilis	NA	2.02	7.13	53.20
SI & SoGE (Ave. dissim. = 77.70)				
***Cumella* sp.**	0	2.72	7.31	7.31
Mediomastus californiensis	0.85	3.41	6.98	14.30
Tanaidacea	0	2.46	6.60	20.89
Galathowenia oculata	0	2.12	5.65	26.54
Levinsenia gracilis	0	2.02	5.46	32.00
Bivalvia	0.53	2.20	4.50	36.50
***Eteone* sp.**	0	1.22	3.27	39.77
***Leucon* sp.**	0	1.14	3.11	42.88
Ophelina acuminata	0	1.12	3.09	45.97
Dexaminidae	0.09	1.13	2.88	48.84
Prionospio lighti	0.42	0.99	2.59	51.43

Table 4.3 Summary of crossed ANOVAs for individual benthic flux to test the effect of site (SI and SoGE) and treatment (natural or enriched incubations). Bold font indicates significant differences.

Source of variation	df	MS	F	*P*
O_2 uptake				
Site	1	57.68	7.91	**0.016**
Treatment	1	13.08	1.79	0.205
Si x Tr	1	5.16	0.71	0.417
Residuals	12	7.29		
Ammonium (√)				
Site	1	39	0.18	0.678
Treatment	1	18370	84.31	**<0.001**
Si x Tr	1	20	0.09	0.766
Residuals	12	218		
Nitrate				
Site	1	22064	0.38	0.552
Treatment	1	550060	9.35	**0.010**
Si x Tr	1	460415	7.82	**0.016**
Residuals	12	58854		
Nitrite (√)				
Site	1	0.14	0.03	0.856
Treatment	1	25.59	6.19	**0.029**
Si x Tr	1	11.48	2.77	0.122
Residuals	12	4.14		
Silicate (√)				
Site	1	12123	29.10	**<0.001**
Treatment	1	4068	9.76	**0.009**
Si x Tr	1	0	0	0.993
Residuals	12	417		
Phosphate (√√)				
Site	1	15.57	19.43	**<0.001**
Treatment	1	57.93	72.30	**<0.001**
Si x Tr	1	0.16	0.20	0.663
Residuals	12	0.80		

Table 4.4 Redundancy analysis of benthic fluxes in natural incubations against functional and taxonomic diversity indices measured in Saanich Inlet and the Strait of Georgia in September 2013.

Sequential tests for stepwise model (r^2 = 0.874, Adj. r^2 = 0.560)					
Variable	**AIC**	***F***	***P***	**Prop.**	**Cumul.**
FEve	13.40	2.64	0.090	0.086	0.086
Simp	15.03	3.68	0.055	0.381	0.467
FRic	15.19	3.80	0.040	0.239	0.706
CWM.Mi.Slow	16.53	4.86	0.030	0.094	0.800
CWM.Ri.UD.conv	16.87	5.16	0.020	0.074	0.874

Table 4.5 Percent variation explained by individual axes and relationships between RDA coordinate axes and orthonormal variables from redundancy analysis of benthic fluxes in natural incubations against functional and taxonomic diversity indices measured in Saanich Inlet and the Strait of Georgia in September 2013.

Variation explained by individual axes (%)					Relationships between RDA coordinate axes and orthonormal X variables (multiple partial correlations)				
	Explained variation out of fitted model (%)		Explained variation out of total variation (%)		FEve	Simp	FRic	CWM. Ri. UD.conv	CWM. Mi. Slow
Axis	Ind.	Cumul.	Ind.	Cumul.					
1	69.36	69.36	60.64	60.64	-0.691	0.737	0.593	0.018	-0.258
2	13.89	83.25	12.15	72.79	-0.452	0.108	0.028	-0.357	0.488
3	13.30	96.56	11.63	84.42	-0.439	0.658	0.444	-0.270	-0.523
4	3.08	99.63	2.69	87.11	-0.356	0.044	0.373	0.479	-0.649
5	0.37	100	0.32	87.43	0.001	-0.103	-0.558	0.755	-0.039

Table 4.6 Redundancy analysis of benthic fluxes in enriched incubations against functional and taxonomic diversity indices measured in Saanich Inlet and the Strait of Georgia in September 2013.

Sequential tests for stepwise model (r^2 = 0.801, Adj. r^2 = 0.536)					
Variable	**AIC**	***F***	***P***	**Prop.**	**Cumul.**
CWM.Feed.O	13.09	2.43	0.090	0.161	0.161
CWM.Feed.Dt	13.45	2.67	0.075	0.158	0.319
CWM.Size.L	13.90	3.00	0.040	0.184	0.503
ES(25)	14.60	3.44	0.010	0.298	0.801

Table 4.7 Percent variation explained by individual axes and relationships between RDA coordinate axes and orthonormal variables from redundancy analysis of benthic fluxes in enriched incubations against functional and taxonomic diversity indices measured in Saanich Inlet and the Strait of Georgia in September 2013.

Variation explained by individual axes (%)					Relationships between RDA coordinate axes and orthonormal X variables (multiple partial correlations)			
	Explained variation out of fitted model (%)		Explained variation out of total variation (%)		CWM. Feed.O	CWM. Feed.Dt	CWM. Size.L	ES(25)
Axis	Ind.	Cumul.	Ind.	Cumul.				
1	53.96	53.96	43.23	43.23	0.451	0.593	-0.425	0.813
2	28.88	82.84	23.13	66.36	0.237	0.239	-0.626	-0.023
3	12.68	95.52	10.16	76.52	-0.640	0.467	-0.544	0.090
4	4.48	100	3.59	80.11	0.576	-0.611	-0.363	0.575

4.8 Figures

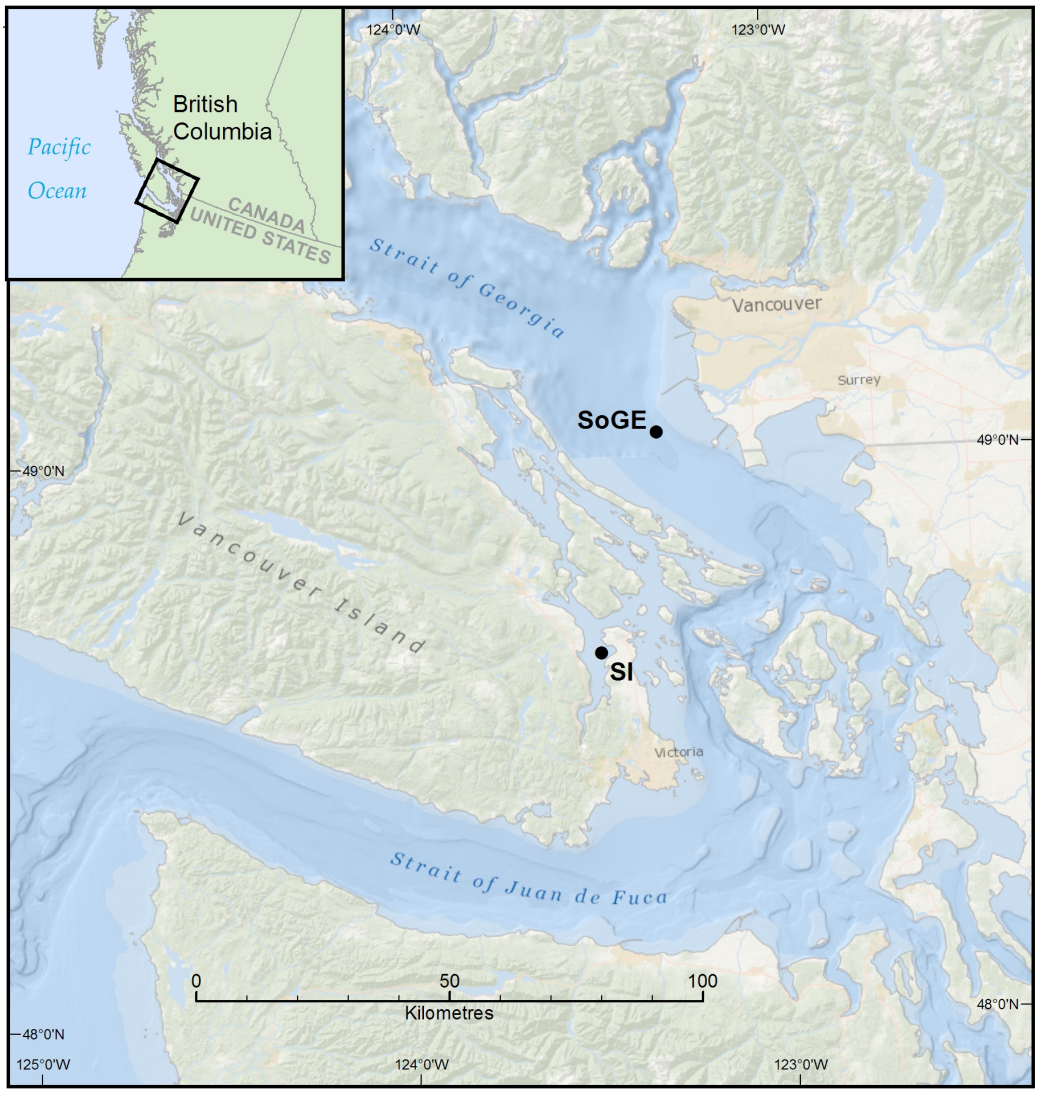

Figure 4.1 Sampling locations in Saanich Inlet (SI) and the Strait of Georgia (SoGE) in September 2013.

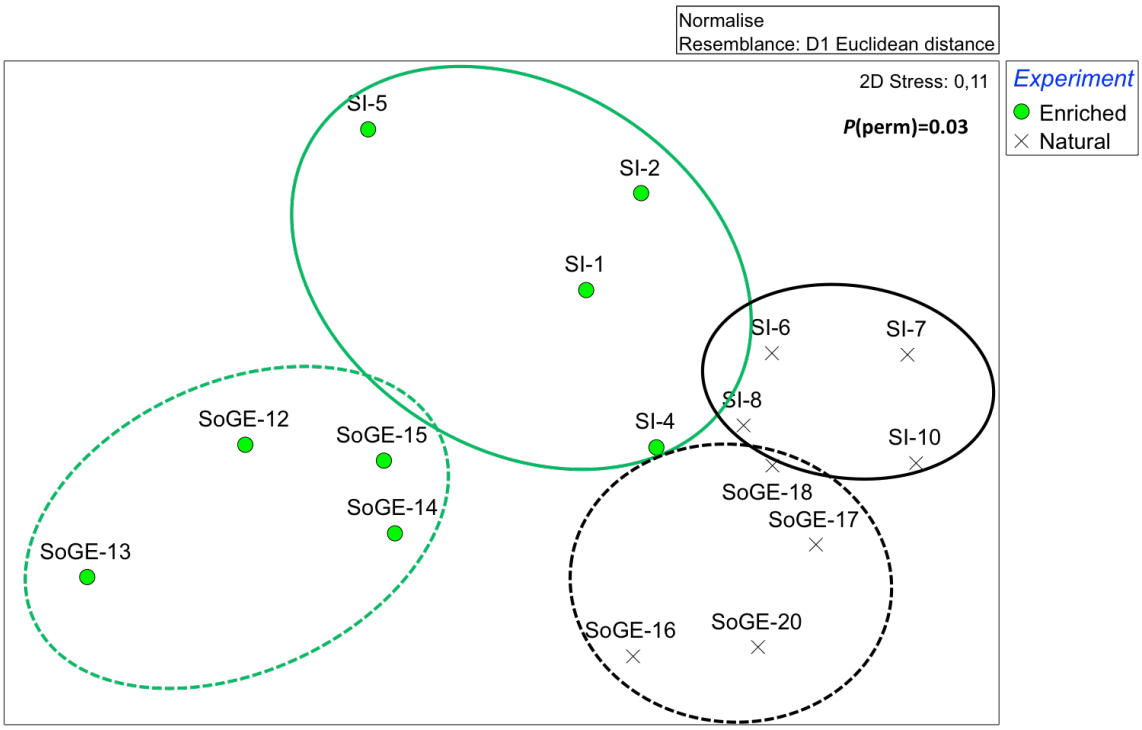

Figure 4.2 Non-metric multi-dimensional scaling (nMDS) plot of benthic flux per incubation. Circles indicate significantly different groups identified by PERMANOVA. Treatment: Enriched (O); Natural (X). Contour lines: SoGE (-); SI (...).

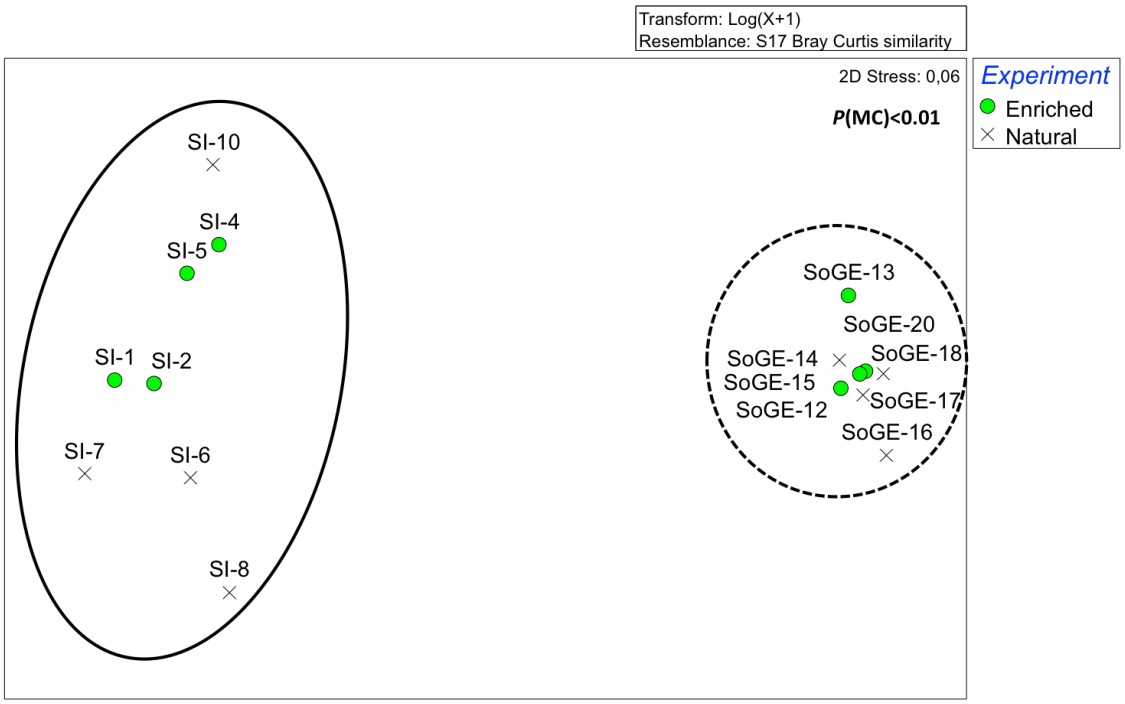

Figure 4.3 Non-metric multi-dimensional scaling (nMDS) plot of species density per incubation. Circles indicate significantly different groups identified by PERMANOVA. Treatment: Enriched (O); Natural (X). Contour lines: SoGE (-); SI (…).

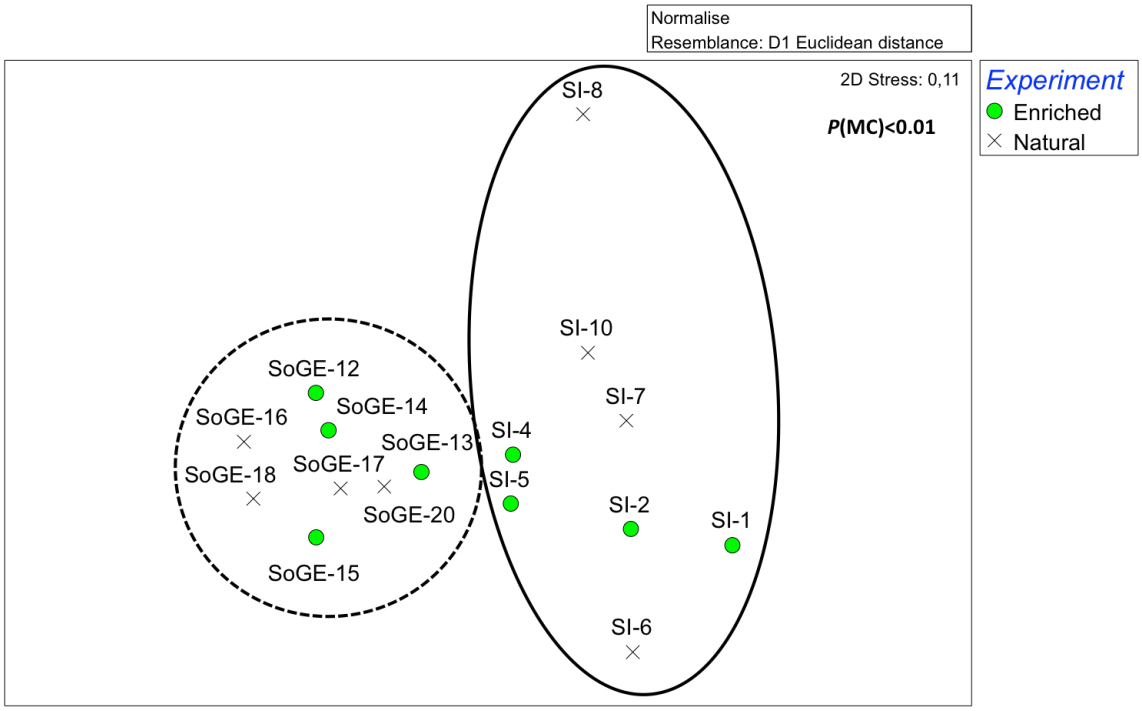

Figure 4. 4 Non-metric multi-dimensional scaling (nMDS) plot of functional and taxonomic diversity indices per incubation. Circles indicate significantly different groups identified by PERMANOVA. Treatment: Enriched (O); Natural (X) Contour lines: SoGE (-); SI (…).

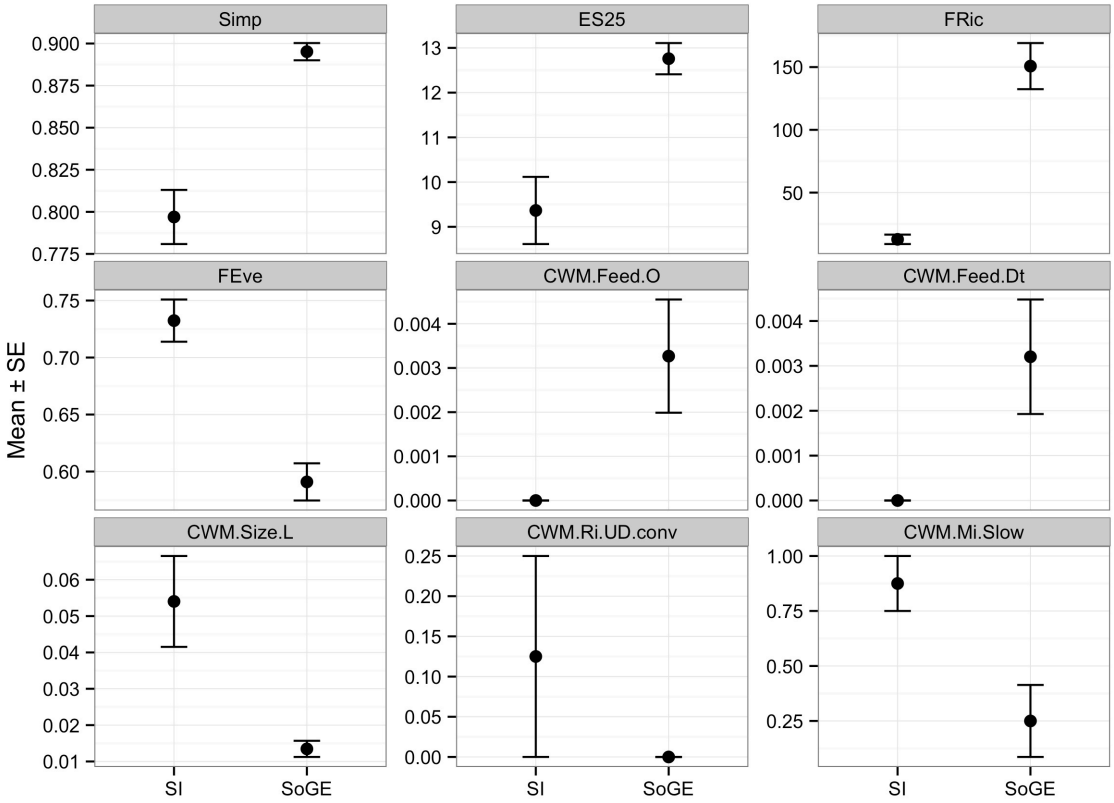

Figure 4.5 Functional and taxonomic diversity indices (mean ± SE) in Saanich Inlet (SI) and the Strait of Georgia (SoGE). Diversity indices presented are those significant as identified by redundancy analysis (RDA) models. Simp = Simpson's diversity index; ES(25) = rarefaction index, expected number of species; FRic = functional richness; FEve = functional evenness; CWM.Feed.O = community weighted mean of omnivores; CWM.Feed.Dt = community weighted mean of detritivores; CWM.Size.L = community weighted mean of large macrofaunal organisms; CWM.Ri.UD.conv = community weighted mean of upward/downward conveyors; CWM.Mi.Slow = community weighted mean of macrofauna moving slowly through the sediment.

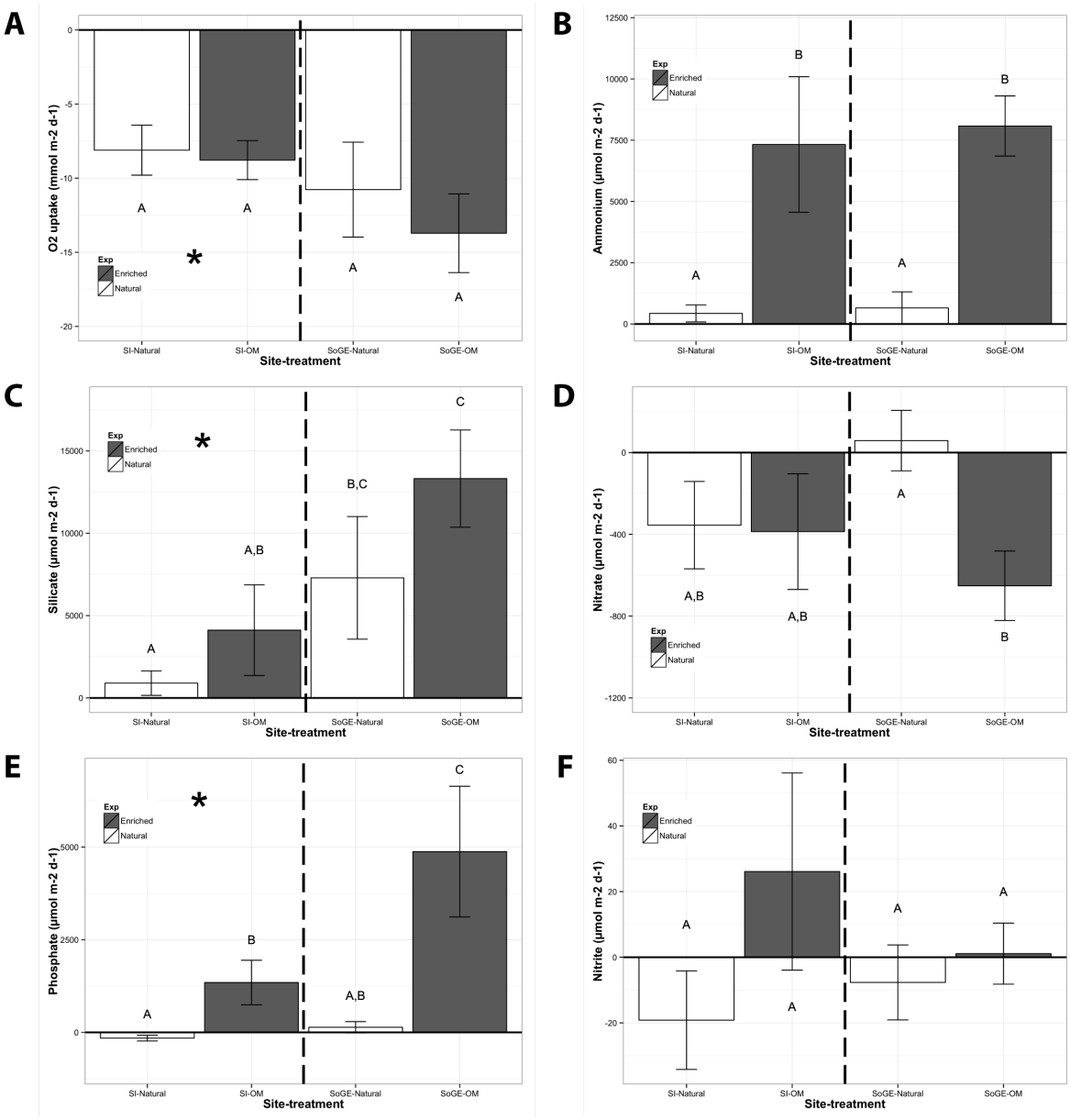

Figure 4.6 Mean (±SE) flux of: (A) O_2, (B) ammonium, (C) silicate, (D) nitrate, (E) phosphate, and (F) nitrite per site (SI = Saanich Inlet; SoGE = Strait of Georgia East) and treatment level (natural or organic matter enrichment (OM)). Units are in µmol m^{-2} d^{-1} except for O_2 which is in mmol m^{-2} d^{-1}. Asterisk (*) indicates significant differences across sites. Letters above bars indicate between site and treatment results of Tukey HSD test, where site and treatment with the same letter did not differ significantly.

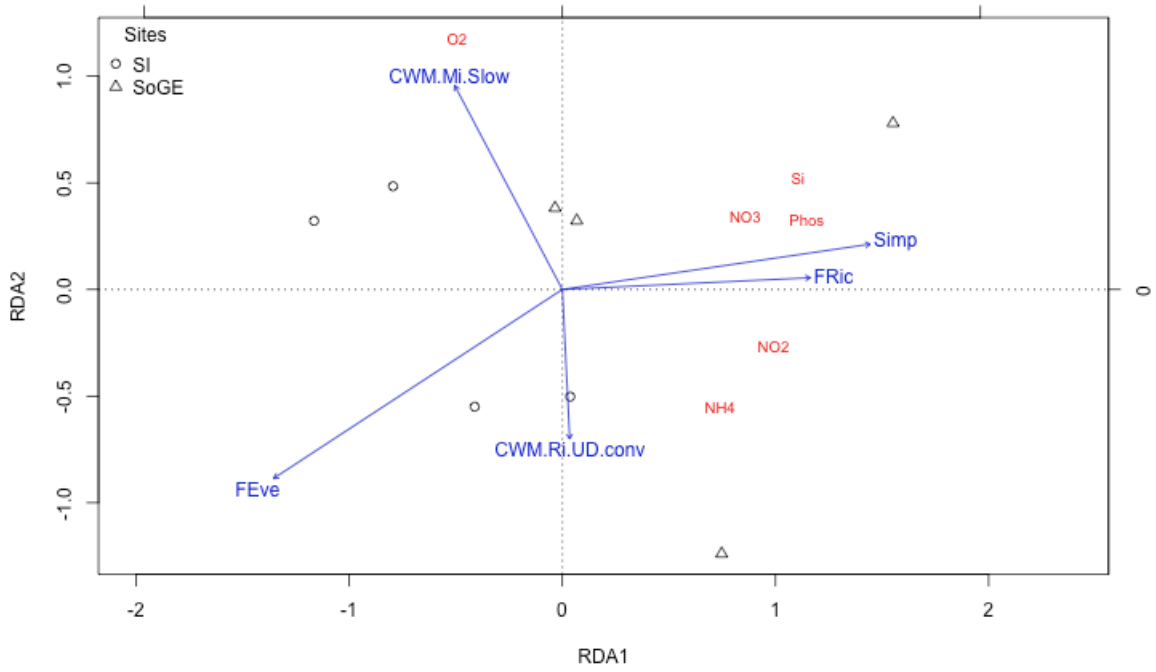

Figure 4.7 Redundancy analysis (RDA) model plot of functional and taxonomic diversity indices best explaining variation in benthic fluxes measured in natural incubations collected from Saanich Inlet (SI) and the Strait of Georgia East (SoGE) in September 2013. CWM.Mi.Slow = community weighted mean of macrofauna moving slowly through the sediment; Simp = Simpson's diversity index; FRic = functional richness; CWM.Ri.UD.conv = community weighted mean of upward/downward conveyors; FEve = functional evenness.

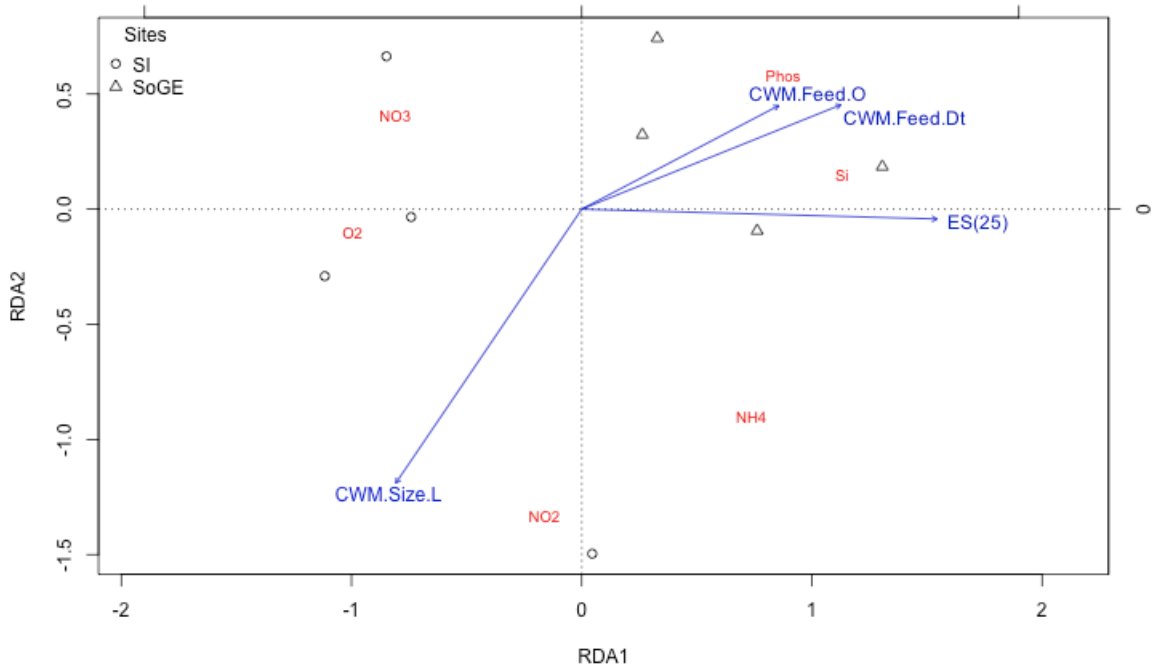

Figure 4.8 Redundancy analysis (RDA) model plot of functional and taxonomic diversity indices best explaining variation in benthic fluxes measured in enriched incubations collected from Saanich Inlet (SI) and the Strait of Georgia East (SoGE) in September 2013. CWM.Feed.O = community weighted mean of omnivores; CWM.Feed.Dt = community weighted mean of detritivores; ES(25) = rarefaction, expected number of species; CWM.Size.L = community weighted mean of large-sized macrofaunal organisms.

Chapter 5 – Conclusions and future directions

5.1 General conclusions

Organic matter recycling on the seafloor drives benthic-pelagic coupling and fuels surface waters with essential nutrients for primary production, thus representing an important core function of benthic ecosystems (Snelgrove et al. 2014). Multiple chemical, biological, and environmental factors influence these complex benthic fluxes (Schulz 2000, Jorgensen 2006, Aller 2014). The comparative field studies that quantify multiple benthic fluxes and related environmental and biological variables through multivariate (i.e., multi-response) analysis (e.g. redundancy analysis) offer the opportunity to gain valuable understanding of the biological and environmental variables contributing to variation in individual fluxes and organic matter degradation as a whole. Although the comparative field study of benthic fluxes through multivariate analysis offers an appropriate approach to investigate the factors influencing these processes, only a single study to date has adopted this method (Link et al. 2013a). A better understanding of these questions can enable decision-makers to evaluate more fully the potential consequences of anthropogenic impacts such as biodiversity loss on ecosystem functioning, and perhaps develop mitigation solutions. This principle formed the core of my doctoral research. Specifically, I utilized field measurements and laboratory experiments to investigate these topics.

5.1.1 Environmental variables explaining benthic flux variation

In Chapter 1, I presented an overview of oxygen and essential nutrient cycles on the seafloor but also proposed a Random Forests modelling approach to create predictive maps of global oxygen and essential nutrient flux on the seafloor. The prediction models and maps supported the idea of higher benthic flux rates on productive, shallow-water continental shelves that are strongly influenced by biological variables from surface waters (e.g. primary production) to the seafloor (e.g. biomass), by bottom water conditions such as dissolved oxygen concentration, and by other environmental variables such as bottom depth. However, the models identified seafloor characteristics, such as bottom slope and the terrain ruggedness index, as important variables for explaining benthic flux variation. Previous benthic flux studies did not consider these seafloor characteristics, perhaps because most focused on relatively local spatial scales where such measures may be relatively invariant and thus perceived as unimportant. These variables may not influence benthic fluxes directly but rather indirectly through influences on current flow velocity, which in turn can influence benthic fluxes and infaunal bioturbation activities (Biles et al. 2003). Future studies should at least consider the potential influence of these seafloor characteristics in order to better understand their global influence on benthic fluxes.

In Chapter 2, I demonstrated that bottom water characteristics (temperature and dissolved oxygen), quality of organic matter (chlorophyll *a* to phaeopigments and carbon to nitrogen ratios) and sediment characteristics (mean grain size and porosity) could explain substantial spatial and temporal variation in benthic fluxes

and organic matter degradation. These results reinforce knowledge gained from previous studies on the contributions of environmental variables to benthic flux variation, and identify particularly strong environmental predictors. The importance of some variables, such as temperature, in explaining benthic flux variation can vary from one study location to another (e.g. more important in Chapter 2 than in Chapter 1). This difference may reflect the fine-scale measurements used in Chapter 2 in contrast to the yearly averages used in Chapter 1. The use of actual temperature measurements from published studies used to create the Random Forests models in Chapter 1 could potentially increase the importance of temperature in explaining and predicting benthic flux variation. However, some studies do not report bottom water temperature measurements at sampling time, requiring the use of yearly averages as an alternative. Finally, this study is the first to report benthic flux measurements in British Columbia shelf and slope sediments and, in doing so, identifies key explanatory environmental variables.

5.1.2 Contributions of biodiversity and environment to benthic flux variation

Chapter 3 focused on: 1) determining the importance of functional and taxonomic diversity in explaining benthic flux variation, 2) determining the environmental variables that best explain benthic flux variation, and 3) using variance partitioning to combine these two analyses in order to determine their relative contributions to variation in benthic flux and organic matter degradation. This study contributes to closing a major ecological gap identified by many authors

by determining the relative roles biodiversity and environment play in ecosystem functioning in natural marine communities and along natural environmental gradients (Godbold 2012, Snelgrove et al. 2014, Strong et al. 2015).

My study demonstrated that biodiversity and environment explained 62.9% of the variation in benthic flux and organic matter degradation. I also demonstrated that biodiversity (18.5%) and environment (21.4%) contribute similarly to benthic flux variation, and that they shared 22.9% of this variation, thus demonstrating the close linkage between species and environment. Moreover, my analyses showed that functional richness explained more of the variation in benthic flux than taxonomic richness (19.7% and 5.0%, respectively). Finally, my study also identified a key functional group, the funnel feeders (including maldanid and pectinariid polychaetes), which affected benthic flux rates disproportionately relative to their low abundance and few species. My study points to the need to evaluate more fully the consequences of anthropogenic disturbances in marine ecosystems, such as loss or alteration of biodiversity, for the long-term maintenance of marine benthic ecosystem functioning.

5.1.3 Biodiversity and short-term response to phytodetritus deposition

In Chapter 4, I simulated a phytodetritus deposition event expected to follow a typical spring phytoplankton bloom. Specifically, I enriched half of the sediment cores collected from two locations of strongly contrasting macrofaunal diversity, and then tested the importance of these functional and taxonomic diversity differences for benthic fluxes in natural and enriched incubations. My study

demonstrated that taxonomic diversity and functional richness were the most important explanatory biological factors for benthic flux variation and organic matter degradation in natural incubations. However, in enriched incubations, species richness and densities of detritivores and omnivores explained the higher benthic flux rates in the high diversity habitat incubations. My study suggests the detritivores and omnivores as the first functional groups of macrofaunal organisms to ingest fresh phytodetritus on the seafloor. Moreover, my study indicates that soft-sediment habitats with higher functional diversity may regenerate nutrients and process organic matter faster than habitats with lower functional diversity, and that biodiversity loss could negatively influence organic matter recycling on the seafloor and weaken benthic-pelagic coupling.

5.1.4 Relationships between benthic fluxes

The chapters comprising my thesis showed that elevated flux of nutrients (e.g. high phosphate and silicate effluxes at SoGE and SoGC, Chapter 3) often characterizes sites with high oxygen uptake. This pattern results from organic matter degradation where high organic matter degradation releases or utilizes oxygen and nutrients. Therefore, the benthic fluxes studied in my thesis link to one other to different degrees, especially for fluxes of nitrogen compounds discussed in detail in Section 1.2.3.

5.1.5 Summary

In conclusion, my thesis spans the disciplines of marine biology and biogeochemistry and bridges field and laboratory approaches to close the knowledge gap regarding the contribution of biodiversity and environment to the functioning of natural ecosystems. By improving understanding of important biological and environmental factors influencing overall benthic flux variation and organic matter recycling in natural and/or experimentally enriched sediments, each chapter provides evidence that decision-makers should strive to minimize the negative effects of anthropogenic impacts, such as climate warming and biodiversity loss, in order to maintain essential functions of benthic ecosystems.

5.2 Future directions

Benthic fluxes vary spatially and temporally as a result of diffusion processes, chemical reactions accelerated by bacterial enzymatic reactions, bioturbation, bio-irrigation, and environmental factors (Schulz 2000, Jorgensen 2006, Aller 2014). Chapter 3 showed that biodiversity and environmental factors could explain 62.9% of benthic flux variation but left 37.1% of this variation unexplained, despite the large number of known important explanatory variables used. This shortfall points to the need to characterize fully the contribution of all factors contributing to benthic fluxes and organic matter recycling, whether related to diffusion processes, biological factors, or environmental factors (Figure 5.1). This need represents the most important knowledge gap to improve global flux models and their ability to

predict how they might be altered by climate change and biodiversity loss. Whereas Chapter 1 utilized meta-analyses of environmental factors and Chapters 2 and 3 used direct measurements, pore water techniques (Berelson et al. 1990, Schulz 2000) or micro-sensor techniques (Archer & Devol 1992, Glud 2008) can be used to specifically measure diffusion processes in sediments. Incubations of intact sediment cores treated with selective metabolic inhibitors (i.e., antibiotics) can assess bacterial contributions by selectively removing bacteria (Smith 1974). Meiofaunal contribution can be eliminated by freezing sediment cores prior to incubations (Piot et al. 2014). Mobile epifaunal contributions could be assessed using cages that exclude large bioturbators (e.g. Katz et al. 2009, 2012). The combination of these different techniques could allow evaluation of the contribution of each compartment of the biota to benthic flux variation using a variation partitioning technique such as that presented in Chapter 3.

Most studies on carbon and nutrient cycling focus on soft sediments (Devol & Christensen 1993, Berelson et al. 2013, Link et al. 2013b) but the contribution of benthic communities on hard substrates could also be important, despite few published studies. The use of modified benthic chambers as in Welch et al. (1997), using a thick rubber seal and a weight to isolate the chamber from the surrounding environment, offers a strategy to evaluate more fully the contribution of different benthic communities to carbon and nutrient cycling on hard seafloor and therefore improve global carbon and nutrient models. Moreover, using a tracer technique with isotope labeled algae could allow identification of the species and functional groups ingesting the fresh phytodetritus (Sweetman & Witte 2008).

Past research suggests that functional richness may equal or even surpass species richness in terms of its importance to ecosystem functioning (Danovaro et al. 2008, Strong et al. 2015). In particular, Danovaro et al. (2008) suggest an exponential increase in ecosystem functioning (prokaryote carbon production) with increasing diversity (deep-sea nematode Expected Species and trophic diversity traits). Results presented in Chapter 3 support this assertion, however, more studies are needed to assess the applicability of these results to other ecosystem functions such as bioturbation, using techniques such as sediment profile imagery (Solan et al. 2004).

Another interesting study avenue would be to assess the potential of using functional diversity as a metric of Marine Protected Area (MPA) efficacy. Although comparisons of species diversity inside and outside MPAs may sometimes demonstrate higher species diversity outside than inside MPAs (potentially because of functionally redundant species) (Serpetti et al. 2013), Chapters 3 and 4, and previous researchers (Snelgrove 1999, Danovaro et al. 2008, Snelgrove et al. 2014, Strong et al. 2015) suggest that functional diversity can provide a better metric of ecosystem processes, functions, and services. The assessment of functional diversity could therefore prove to be a valuable tool in assessing MPA effectiveness, including in Newfoundland and Labrador, Canada.

5.3 Figures

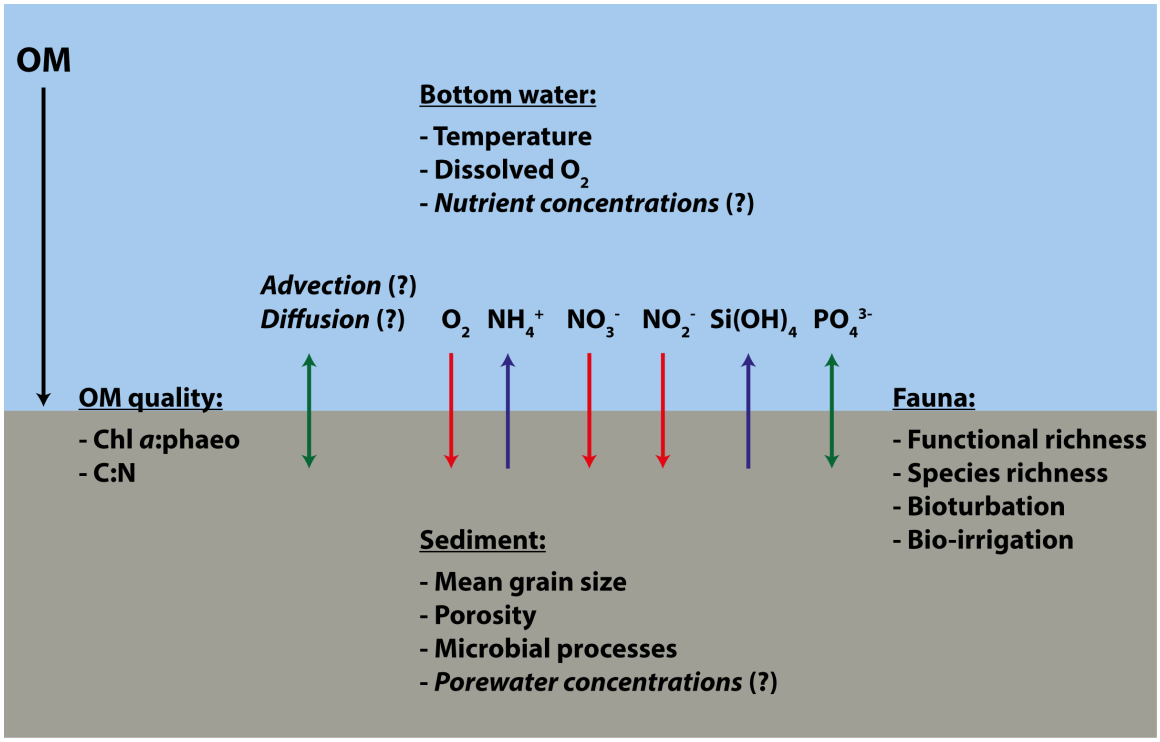

Figure 5.1 Conceptual model of the most important factors influencing benthic flux rates at the sediment-seawater interface and general direction of fluxes. Arrows in red indicate general sediment uptake, arrows in blue indicate general sediment release and arrows in green indicate flux can alternate between sediment uptake and release. Factors in italic followed by question marks (?) are known to influence benthic flux rates but were not measured in this thesis.

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Appendices

Supplementary Table 2.1 Benthic fluxes measured in the Salish Sea and NE Pacific in May/July 2011, and September 2013.

Station/ label	O_2 uptake (mmol/m²/d)	Ammonium (µmol/m²/d)	Nitrite (µmol/m²/d)	Nitrate (µmol/m²/d)	Silicate (µmol/m²/d)	Phosphate (µmol/m²/d)
SI-1-07-11	-14.10	15.78	6.02	-336.43	2138.52	-142.78
SI-2-07-11	-16.97	-15.54	-33.62	-419.61	4688.91	-154.09
SI-3-07-11	-32.86	67.08	-67.65	-1018.62	9924.88	-468.45
SI-6-09-13	-8.78	885.46	-8.50	-550.91	413.41	-122.91
SI-7-09-13	-6.49	19.54	-34.70	-567.28	710.14	-242.30
SI-8-09-13	-10.57	639.34	-0.39	-239.79	2162.96	-45.51
SI-10-09-13	-6.61	176.10	-33.08	-61.88	307.42	-210.98
SoGE-3-05-11	-9.54	863.11	-68.70	-349.43	6610.73	156.72
SoGE-4-05-11	-7.82	38.87	-11.85	-92.38	3844.44	181.41
SoGE-5-05-11	-6.80	-83.22	-24.95	-103.73	3302.75	251.75
SoGE-6-05-11	-9.21	12.91	-79.96	-196.79	5515.63	230.41
SoGE-16-09-13	-16.08	1440.86	-12.62	2.69	6995.57	51.93
SoGE-17-09-13	-10.45	-13.68	-19.39	170.92	4322.76	42.63
SoGE-18-09-13	-8.66	17.64	-9.86	-157.02	4381.93	53.20
SoGE-20-09-13	-7.90	1167.56	11.17	217.72	13458.67	400.82
SoGC-7-05-11	-8.89	209.37	-2.78	-658.15	6556.52	438.03
SoGC-8-05-11	-7.56	-31.04	-17.28	-497.88	4002.87	481.13
SoGC-9-05-11	-9.37	80.12	4.36	-500.60	4521.22	696.98
SoGC-10-05-11	-6.89	-48.46	-53.70	-435.92	4473.27	462.30
SoGC-4-07-11	-16.19	1134.08	-8.10	-543.99	6247.31	29.88
SoGC-5-07-11	-17.11	98.11	3.56	35.63	3617.25	85.26
SoGC-6-07-11	-15.97	1755.44	10.36	-804.99	7895.01	198.26
DDL-11-05-11	-7.73	730.64	-20.40	-233.74	3908.53	82.82
DDL-12-05-11	-7.68	1488.70	-11.60	-453.33	5588.30	174.08
DDL-7-07-11	-15.60	2102.01	-2.56	-590.94	1394.34	-351.40
DDL-8-07-11	-12.94	1649.75	-13.78	-614.12	130.33	-414.38
DDL-9-07-11	-9.03	1720.78	-3.13	-296.81	1059.78	-262.00
Axis-15-07-11	-2.94	46.42	0.32	-158.99	1120.08	-119.46
Axis-16-07-11	-2.48	-6.90	0.36	-45.32	1260.36	-151.10
Axis-17-07-11	-2.92	74.92	-0.18	-131.82	1306.47	-157.52
Hydrates-29-07-11	-6.54	-22.60	-6.90	-417.79	2557.70	-6.07
Hydrates-30-07-11	-5.70	-17.31	-6.66	13.09	4470.22	23.43
Hydrates-31-07-11	-6.39	229.95	-8.42	-581.40	1597.47	-58.38

BMC-18-07-11	-4.36	-3.54	-0.02	-294.73	918.12	-166.59
BMC-19-07-11	-4.23	10.36	-1.58	429.28	3322.99	54.61
BMC-20-07-11	-3.55	-10.81	-2.89	-272.19	1357.28	-9.01
BUP-21-07-11	-2.03	-65.87	-0.93	-99.57	1825.42	19.01
BUP-22-07-11	-2.55	-27.61	0.84	-329.61	1895.60	25.09
BUP-23-07-11	-2.30	-16.43	1.51	-55.88	2217.23	64.86
Folger-24-07-11	-5.51	84.54	-2.12	-591.16	3779.39	-31.81
Folger-25-07-11	-6.63	91.27	-2.23	-600.24	5801.80	-33.45
Folger-26-07-11	-6.74	133.86	-11.33	-918.16	4028.47	-56.87
Folger-27-07-11	-9.90	197.34	-12.42	-514.60	3790.46	10.17
BC300-11-09-13	-4.76	155.33	0.51	693.46	7280.37	217.00
BC300-12-09-13	-8.82	45.80	2.62	-146.79	3542.03	-955.35
BC300-13-09-13	-3.34	-9.68	-4.32	-99.64	4212.73	-529.36

Supplementary Table 3.1 Benthic fluxes measured in sediment core incubations.

All units are in μmol m^{-2} d^{-1}, except for O_2 which is in mmol m^{-2} d^{-1}.

Core	O_2	NH_4^+	NO_2^-	NO_3^-	$Si(OH)_4$	PO_4^{3-}
SI-07-1	-14.10	15.78	6.02	-336.43	2138.52	-142.78
SI-07-2	-16.97	-15.54	-33.62	-419.61	4688.91	-154.09
SI-07-3	-32.86	67.08	-67.65	-1018.62	9924.88	-468.45
SI-09-6	-8.78	885.46	-8.50	-550.91	413.41	-122.91
SI-09-7	-6.49	19.54	-34.70	-567.28	710.14	-242.30
SI-09-8	-10.57	639.34	-0.39	-239.79	2162.96	-45.51
SI-09-10	-6.61	176.10	-33.08	-61.88	307.42	-210.98
SI Ave.	-13.77	255.40	-24.56	-456.36	2906.61	-198.15
SE	8.57	332.22	23.58	281.74	3193.12	124.87
SoGE-05-3	-9.54	863.11	-68.70	-349.43	6610.73	156.72
SoGE-05-4	-7.82	38.87	-11.85	-92.38	3844.44	181.41
SoGE-05-5	-6.80	-83.22	-24.95	-103.73	3302.75	251.75
SoGE-05-6	-9.21	12.91	-79.96	-196.79	5515.63	230.41
SoGE-09-16	-16.08	1440.86	-12.62	2.69	6995.57	51.93
SoGE-09-17	-10.45	-13.68	-19.39	170.92	4322.76	42.63
SoGE-09-18	-8.66	17.64	-9.86	-157.02	4381.93	53.20
SoGE-09-20	-7.90	1167.56	11.17	217.72	13458.67	400.82
SoGE Ave.	-9.56	430.51	-27.02	-63.50	6054.06	171.11
SE	2.68	582.09	29.14	176.47	3052.87	116.03
SoGC-07-4	-16.19	1134.08	-8.10	-543.99	6247.31	29.88
SoGC-07-5	-17.11	98.11	3.56	35.63	3617.25	85.26
SoGC-07-6	-15.97	1755.44	10.36	-804.99	7895.01	198.26
SoGC Ave.	-16.42	995.88	1.94	-437.79	5919.86	104.47
SE	0.49	683.62	7.63	351.31	1761.67	70.07
DDL-07-7	-15.60	2102.01	-2.56	-590.94	1394.34	-351.40
DDL-07-8	-12.94	1649.75	-13.78	-614.12	130.33	-414.38
DDL-07-9	-9.03	1720.78	-3.13	-296.81	1059.78	-262.00
DDL Ave.	-12.52	1824.18	-6.49	-500.62	861.48	-342.59
SE	2.70	198.58	5.16	144.43	534.74	62.52

Supplementary Table 3.2 List of taxa identified in each sediment core.

Class	Family/order	AphiaID	Taxa	SI-07-1	SI-07-2	SI-07-3	SI-09-6	SI-09-7	SI-09-8	SI-09-10	SoGE-05-3	SoGE-05-4	SoGE-05-5	SoGE-05-6	SoGE-09-16	SoGE-09-17	SoGE-09-18	SoGE-09-20	SoGC-07-4	SoGC-07-5	SoGC-07-6	DDL-07-7	DDL-07-8	DDL-9
Bivalvia	Bivalvia	105	Bivalvia	0	0	2	2	1	2	0	8	7	8	10	4	11	10	8	1	0	0	0	1	13
Bivalvia	Lucinidae	464250	Parvilucina tenuisculpta	0	0	0	0	0	0	0	1	0	0	0	0	1	3	0	0	0	0	0	0	0
Bivalvia	Lucinoida	489106	Lucinoida	0	0	0	0	0	0	0	1	1	1	2	3	3	0	3	0	0	0	0	0	0
Bivalvia	Nuculanoidea	14657	Nuculanoidea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Bivalvia	Nuculidae	204	Nuculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia	Nuculidae	140584	Ennucula tenuis	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Bivalvia	Thyasiridae	246819	Axinopsida serricata	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	1	1	4
Bivalvia	Ungulinidae	423334	Diplodonta aleutica	0	0	0	0	0	0	0	3	0	1	0	0	1	1	0	0	0	0	0	0	0
Bivalvia	Ungulinidae	582538	Diplodonta impolita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	0
Bivalvia	Veneroida	217	Veneroida sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	6	2
Bivalvia	Yoldiidae	138669	Megayoldia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0
Caudofoveata	Caudofoveata	151365	Caudofoveata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0
Echinoidea	Spatangoida	123106	Spatangoida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Echinoidea	Schizasteridae	513143	Brisaster latifrons	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Gastropoda	Gastropoda	101	Gastropoda spp. (Juv.)	0	0	0	0	0	0	2	0	0	5	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	Buccinidae	149	Buccinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Malacostraca	Aoridae	101368	Aoridae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Malacostraca	Calliopiidae	146744	Calliopiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Malacostraca	Caprellinae	101430	Caprella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Corophiidae	101376	Corophiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Crustaceans	106673	Brachyura spp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Dexaminidae	101378	Dexaminidae	0	0	0	0	0	0	0	2	2	1	2	4	3	2	2	1	0	0	1	0	0
Malacostraca	Diastylidae	110398	Diastylis sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Malacostraca	Diastylidae	181921	Diastylis abboti	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Malacostraca	Diastylidae	181974	Diastylis pellucida	1	0	0	0	1	0	4	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Gammaridea	1207	Gammaridea spp.	0	0	0	0	0	1	0	1	3	0	0	0	0	0	0	0	0	0	1	0	0
Malacostraca	Harpacticoida	1102	Harpacticoida spp.	6	0	1	0	0	0	6	0	1	1	1	0	1	1	3	1	0	0	1	4	3
Malacostraca	Isaeidae	101388	Isaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Malacostraca	Ischyroceridae	101389	Ischyroceridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Isopoda	1131	Isopoda spp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Malacostraca	Isopoda	1131	Isopoda spp. (?)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Leuconidae	110414	Leucon sp.	1	0	0	0	0	0	0	0	0	0	0	3	1	2	3	0	0	1	0	0	0
Malacostraca	Leucothoidae	101393	Leucothoidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Malacostraca	Lysianassidae	101395	Lysianassidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Malacostraca	Munnidae	118374	Munna sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Malacostraca	Mysida	149668	Mysida spp.	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Malacostraca	Nannastacidae	110416	Cumella sp.	0	0	0	0	0	0	0	25	44	20	17	3	8	19	24	0	0	0	0	0	0
Malacostraca	Oedicerotidae	101400	Oedicerotidae	0	0	0	0	0	0	0	0	0	1	1	0	3	0	2	0	0	0	1	0	0
Malacostraca	Pachynidae	547890	Pachynus cf. barnardi (?)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Paramunnidae	261333	Munnogonium tillerae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Paramunnidae	118801	Pleurogonium rubicundum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Malacostraca	Phoxocephalidae	176848	Heterophoxus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Malacostraca	Phoxocephalidae	101403	Phoxocephalidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	5
Malacostraca	Pinnotheridae	445050	Pinnixa occidentalis	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Malacostraca	Pleustidae	101404	Pleustidae	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Malacostraca	Pontogeneiidae	176946	Pontogeneiidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Malacostraca	Tanaidacea	1133	Tanaidacea	0	0	0	0	0	0	0	7	8	6	6	4	17	8	11	9	1	1	0	0	0
Oligochaeta	Oligochaeta	2036	Oligochaeta	0	6	0	0	0	0	0	1	0	13	0	0	1	3	0	0	0	0	1	0	0
Ophiuroidea	Ophiuroidea	123084	Ophiuroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ophiuroidea	Ophiuridae	123117	Ophiurida (Juv.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophiuroidea	Amphiuridae	123206	Amphiuridae spp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Polychaeta	Ampharetidae	129155	Ampharete sp.	0	0	0	0	0	0	0	0	0	0	0	3	0	1	2	0	0	0	0	0	0
Polychaeta	Aphroditiformia	927	Aphroditiformia (scale worms)	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Capitellidae	921	Capitellidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polychaeta	Capitellidae	326885	Decamastus gracilis	0	0	0	0	0	0	0	0	0	0	0	1	2	4	1	0	0	0	0	1	2
Polychaeta	Capitellidae	129884	Heteromastus cf. filiformis	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Polychaeta	Capitellidae	157483	Mediomastus cf. californiensis	1	3	4	1	0	1	8	40	30	94	19	20	27	46	21	36	15	9	7	3	53
Polychaeta	Cirratulidae	919	Cirratulidae spp.	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0
Polychaeta	Cirratulidae	129240	Aphelochaeta sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Polychaeta	Cirratulidae	326478	Aphelochaeta cf. glandaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Cirratulidae	129242	Chaetozone sp.	0	0	0	0	0	0	0	3	0	0	0	1	0	0	1	0	0	0	0	0	0
Polychaeta	Cirratulidae	327416	Chaetozone commonalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0
Polychaeta	Cirratulidae	129955	Chaetozone setosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	9	3	0	0	0	0
Polychaeta	Cossuridae	129251	Cossura sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0
Polychaeta	Cossuridae	129251	Cossura sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Cossuridae	326845	Cossura bansei	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Polychaeta	Cossuridae	326847	Cossura candida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Cossuridae	326855	Cossura modica	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	4	5	2	2
Polychaeta	Cossuridae	129985	Cossura pygodactylata	0	0	0	0	0	0	0	5	1	0	0	1	1	2	1	5	0	0	0	0	0
Polychaeta	Dorvilleidae	971	Dorvilleidae spp.	0	0	0	0	0	0	0	0	0	3	1	0	0	2	0	0	0	0	0	0	0
Polychaeta	Glyceroidea	328132	Glycera nana	1	0	0	1	2	0	0	1	1	1	0	0	1	0	2	3	1	2	0	1	0
Polychaeta	Goniadidae	953	Goniadidae spp A	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Goniadidae	240625	Glycinde picta	2	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Goniadidae	240564	Goniada brunnea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Hesionidae	946	Hesionidae spp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Polychaeta	Hesionidae	946	Hesionidae spp. B	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Hesionidae	129314	Nereimyra sp. (?)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Polychaeta	Lumbrineridae	967	Lumbrineridae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Lumbrineridae	327174	Lumbrineris limicola	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Polychaeta	Lumbrineridae	333929	Lumbrineris zonata	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0
Polychaeta	Lumbrineridae	329948	Ninoe gemmea	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polychaeta	Maldanidae	923	Maldanidae spp.	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0
Polychaeta	Maldanidae	129352	Maldane sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Polychaeta	Maldanidae	130305	Maldane sarsi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Polychaeta	Maldanidae	129360	Praxillella sp. (?)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Polychaeta	Maldanidae	130324	Praxillella gracilis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Polychaeta	Nephtyidae	558190	Bipalponephtys cf. cornuta	3	4	3	11	3	4	6	2	3	7	5	5	6	7	6	8	8	9	5	6	0
Polychaeta	Onuphidae	965	Onuphidae spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Polychaeta	Onuphidae	334032	Mooreonuphis cf. exigua	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Polychaeta	Onuphidae	334275	Onuphis iridescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Polychaeta	Opheliidae	130500	Ophelina acuminata	0	0	0	0	0	0	0	2	0	5	2	2	1	2	3	0	0	0	3	2	5
Polychaeta	Owenniidae	129426	Myriochele sp.	0	0	1	0	0	0	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0
Polychaeta	Owenniidae	329073	Myriochele olgae	0	0	0	0	0	0	0	0	0	2	2	2	0	1	1	0	0	0	0	0	0
Polychaeta	Owenniidae	329080	Myriochele striolata	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Polychaeta	Owenniidae	146950	Galathowenia oculata	2	0	2	0	0	0	0	3	3	8	0	5	6	13	5	3	0	0	0	0	0
Polychaeta	Paraonidae	130578	Levinsenia gracilis	0	0	0	0	0	0	0	9	10	15	5	6	11	5	8	10	3	3	1	2	2
Polychaeta	Pectinariidae	337505	Pectinaria californiensis	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Polychaeta	Pholoidae	330542	Pholoe glabra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Phyllodocidae	931	Phyllodocidae spp. (Juv.)	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Phyllodocidae	334506	Phyllodoce cf. groenlandica	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Phyllodocidae	730040	Phyllodoce cf. multiseriata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Phyllodocidae	129443	Eteone sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Phyllodocidae	327523	Eteone californica	0	0	0	0	0	0	0	0	0	0	0	4	1	1	0	0	2	0	0	0	0
Polychaeta	Phyllodocidae	327528	Eteone cf. dilatae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	1	1	1	1
Polychaeta	Phyllodocidae	327530	Eteone legtotes	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polychaeta	Phyllodocidae	254735	Eteone cf. pacifica	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Polychaeta	Pilargidae	334520	Pilargis berkeleyae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Polychaeta	Polynoidae	939	Polynoidae spp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Polynoidae	130763	Harmothoe fragilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Polychaeta	Polynoidae	333959	Malmgreniella nigralba	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Polychaeta	Sabellidae	985	Sabellidae spp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Sabellidae	155202	Euchone incolor	0	0	0	0	0	0	0	1	0	2	0	0	0	0	2	0	0	0	0	0	0
Polychaeta	Sabellidae	334322	Oriopsis minuta	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Sigalionidae	943	Sigalionidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Polychaeta	Sphaerodoridae	254759	Sphaerodoropsis cf. sphaerulifer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Polychaeta	Spionidae	131140	Paraprionospio pinnata	2	1	2	1	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Polychaeta	Spionidae	129620	Prionospio sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Polychaeta	Spionidae	331112	Prionospio jubata	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Spionidae	558839	Prionospio lighti	10	3	6	1	0	6	0	37	19	27	10	24	2	1	0	17	4	16	87	16	68
Polychaeta	Spionidae	131164	Prionospio steenstrupi	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	2	0	0
Polychaeta	Spionidae	334829	Spiophanes berkeleyorum	5	10	11	1	2	6	1	2	1	1	0	4	4	5	1	0	0	0	0	0	0
Polychaeta	Spionidae	334830	Spiophanes duplex	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Polychaeta	Spionidae	131121	Dipolydora quadrilobata	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Polychaeta	Spionidae	131124	Dipolydora socialis	0	0	0	0	0	0	0	5	2	6	0	0	0	0	0	1	0	0	0	0	0
Polychaeta	Spionidae	129619	Polydora sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Polychaeta	Sternaspidae	338196	Sternaspis affinis	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	1	0	0	0	0	0
Polychaeta	Syllidae	333450	Exogone (Parexogone) molesta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Polychaeta	Terebellidae	322588	Terebellinae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Terebellidae	330867	Polycirrus californicus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Polychaeta	Terebellomorpha	152292	Terebellomorpha	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Polychaeta	Trichobranchidae	983	Trichobranchidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Trichobranchidae	129717	Terebellides sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Trochochaetidae	131576	Trochochaeta multisetosa (Juv.)	0	0	0	0	0	0	0	3	0	1	0	0	0	0	1	0	0	0	0	0	0
Sagittoidea	Sagittoidea	5949	Sagittoidea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scaphopoda	Gadilidae	138027	Siphonodentalium	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	0	0

Supplementary Table 3.3 Redundancy analysis of benthic fluxes against environmental drivers measured in the Salish Sea in May/July 2011, and September 2013.

Sequential tests for stepwise model (R^2 = 0.583. Adj. R^2 = 0.444)					
Variable	**AICc**	***F***	***P***	**Prop.**	**Cumul.**
Chla:Phaeo (ln)	36.47	7.19	0.005	0.188	0.188
Prokabun (ln)	34.69	5.38	0.005	0.145	0.333
Porosity	32.32	3.21	0.015	0.074	0.407
Depth	33.21	4.00	0.005	0.088	0.495
Temp	32.27	3.17	0.015	0.088	0.583

Supplementary Table 3.4 Percent variation explained by individual axes and relationships between RDA coordinate axes and orthonormal variables from redundancy analysis of benthic fluxes against environmental drivers measured in the Salish Sea in May/July 2011, and September 2013.

Variation explained by individual axes (%)					Relationships between RDA coordinate axes and orthonormal X variables (multiple partial correlations)				
	Explained variation out of fitted model (%)		Explained variation out of total variation (%)		Chla: Phaeo (ln)	Prokabun (ln)	Porosity	Depth	Temp
Axis	Ind.	Cumul.	Ind.	Cumul.					
1	46.91	46.91	27.33	27.33	-0.771	-0.496	-0.024	0.405	-0.001
2	25.04	71.95	14.59	41.92	-0.381	0.752	0.130	0.057	-0.336
3	21.16	93.11	12.33	54.25	-0.027	-0.137	0.250	0.628	0.332
4	4.24	97.36	2.47	56.73	-0.230	-0.028	-0.258	-0.562	0.874
5	2.64	100.00	1.54	58.27	-0.455	-0.411	0.924	0.351	0.114

Supplementary Table 3.5 Redundancy analysis of benthic fluxes against functional diversity indices measured in the Salish Sea in May/July 2011, and September 2013. N = abundance, Simp = Simpson's diversity index, FRic = functional richness, FEve = functional evenness, CWM = community-level weighted means of trait values, Feed = feeding types, SSD = sub-surface deposit feeders, Fn = funnel feeders, Ri = reworking types, S.mod = surface modifiers, Mi = mobility, Lmt = limited movement, Slow = slow movement through the sediment matrix.

Sequential tests for stepwise model (R^2 = 0.678. Adj. R^2 = 0.414)					
Variable	**AICc**	***F***	***P***	**Prop.**	**Cumul.**
FRic	40.30	6.29	0.005	0.197	0.197
CWM.Mi.Lmt	35.92	3.03	0.025	0.083	0.279
CWM.Feed.SSD	35.66	2.86	0.045	0.060	0.340
FEve	36.66	3.53	0.025	0.057	0.396
CWM.Ri.S.mod	36.23	3.24	0.030	0.045	0.442
CWM.Mi.Slow	34.63	2.20	0.075	0.060	0.502
N	37.54	4.16	0.015	0.045	0.547
Simp	36.37	3.34	0.010	0.050	0.597
CWM.Feed.Fn	35.53	2.77	0.015	0.081	0.678

Supplementary Table 3.6 A) Percent variation explained by individual axes and B) relationships between RDA coordinate axes and orthonormal variables from redundancy analysis of benthic fluxes against functional diversity indices measured in the Salish Sea in May/July 2011, and September 2013.

A)

Variation explained by individual axes (%)				
	Explained variation out of fitted model (%)		Explained variation out of total variation (%)	
Axis	Ind.	Cumul.	Ind.	Cumul.
1	44.58	44.58	30.23	30.23
2	28.93	73.51	19.61	49.84
3	18.21	91.72	12.34	62.18
4	4.50	96.22	3.05	65.24
5	3.04	99.26	2.06	67.29
6	0.74	100.00	0.50	67.80

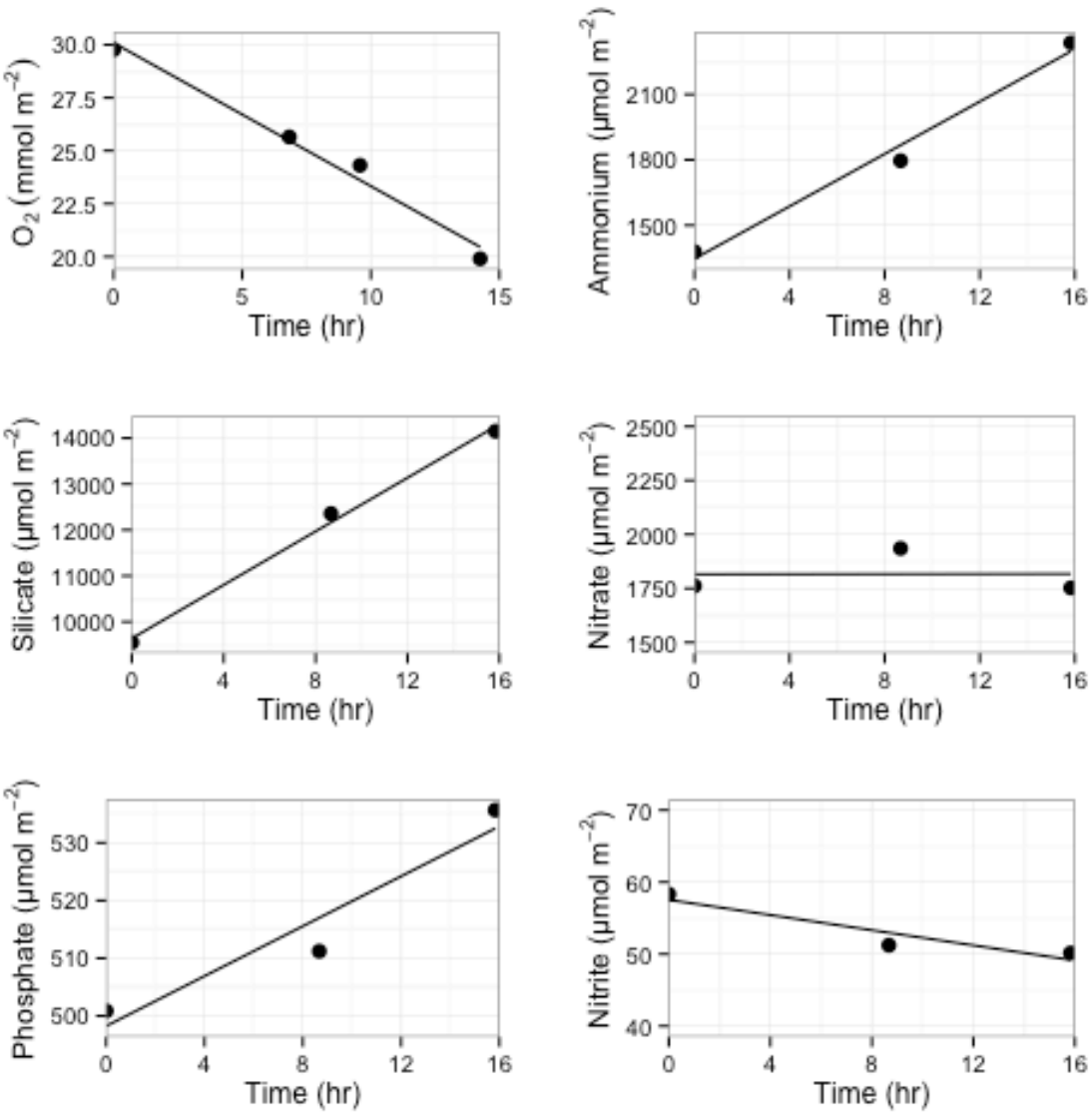
B)

Relationships between RDA coordinate axes and orthonormal X variables (multiple partial correlations)									
Axis	N	Simp	FRic	FEve	CWM. Feed. SSD	CWM. Feed. Fn	CWM. Ri. S.mod	CWM. Mi. Lmt	CWM. Mi. Slow
1	0.474	0.384	0.727	-0.009	0.512	0.288	0.207	-0.035	-0.001
2	0.173	0.420	0.404	-0.048	-0.183	-0.133	0.558	0.204	0.026
3	-0.042	-0.280	-0.108	0.034	-0.179	0.393	0.205	-0.700	-0.162
4	-0.317	0.016	0.044	-0.348	0.497	-0.018	-0.284	-0.176	-0.256
5	-0.576	-0.502	-0.377	0.448	-0.504	-0.298	-0.353	0.400	-0.516
6	0.161	0.494	-0.246	0.435	0.303	-0.134	0.191	-0.044	-0.097

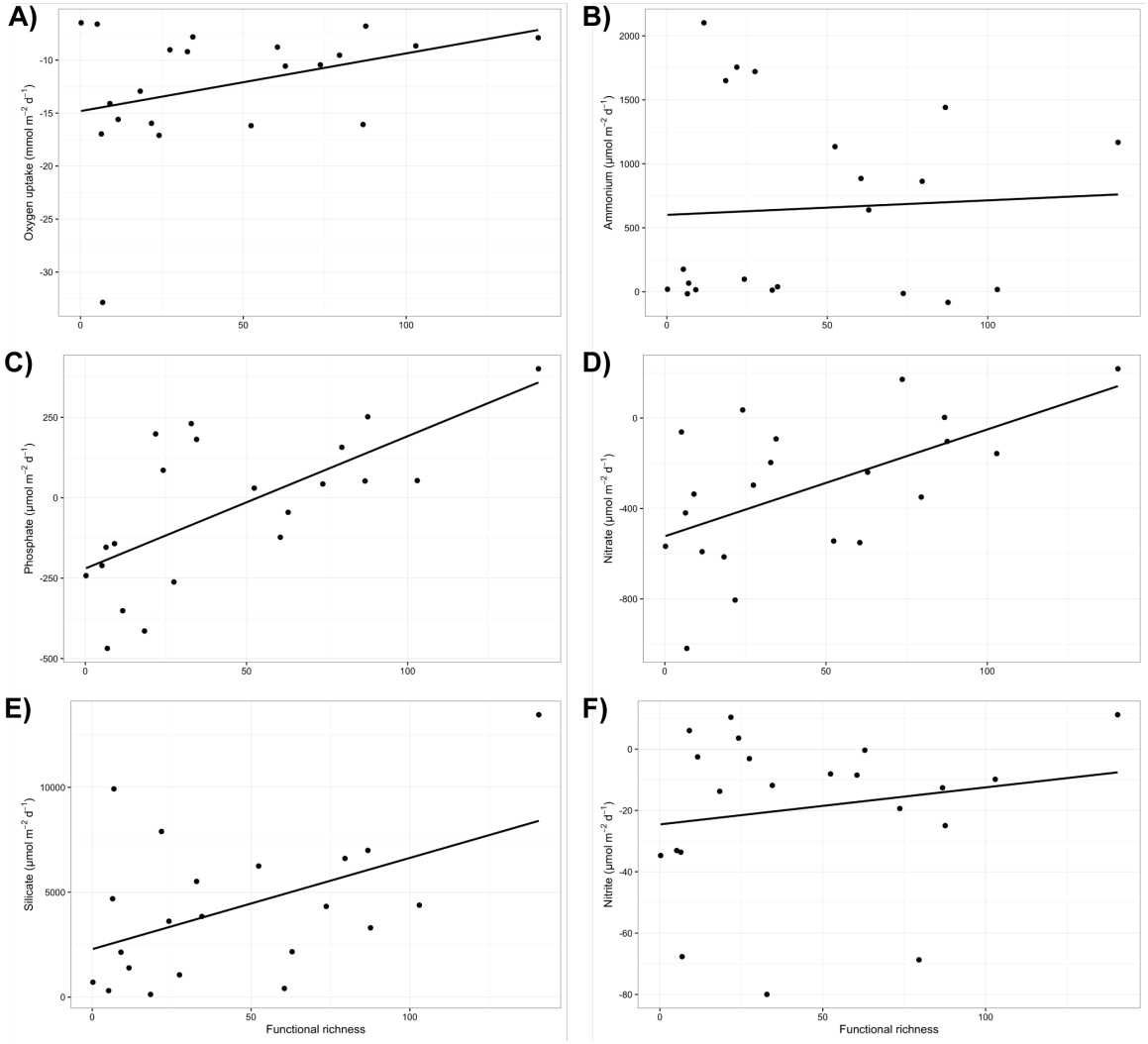
Supplementary Table 3.7 Results of the variation partitioning of the benthic fluxes between environmental variables and functional diversity indices. X1 = variation explained by the redundancy analysis (RDA) model of environmental variables, X2 = variation explained by the RDA model of functional diversity (FD) indices, a = variation explained by environmental variables only, b = intersection of the variation explained by redundancy analysis (RDA) models of environmental variables and functional diversity indices, c = variation explained by FD indices only, and d = residual variation (unexplained variation).

	Df	R^2	**Adj.** R^2
[a+b] = X1	5	0.583	0.444
[b+c] = X2	9	0.678	0.414
[a+b+c] = X1+X2	14	0.889	0.629
Individual fractions			
[a] = X1|X2	5		0.214
[b]	0		0.229
[c] = X2|X1	9		0.185
[d] = Residuals			0.371

Supplementary Figure 3.1 Typical changes in concentration of oxygen (O_2), ammonium, silicate, nitrate, phosphate and nitrite. Data are from incubation #16 collected in the Strait of Georgia East (SoGE-16) in September 2013.



Supplementary Figure 3.2 Relationships between functional richness (FRic) and A) oxygen uptake, B) ammonium, C) phosphate, D) nitrate, E) silicate, and F) nitrite. All units are in μmol m^{-2} d^{-1}, except for oxygen which is in mmol m^{-2} d^{-1}.

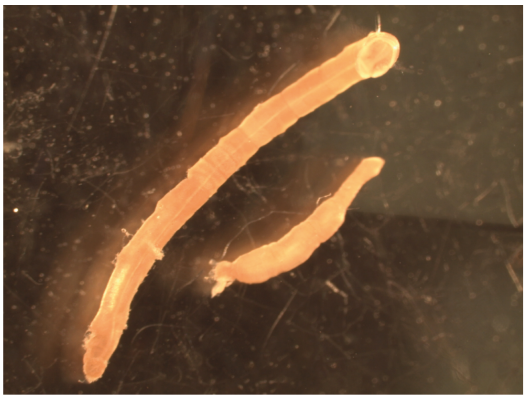


Supplementary Figure 3.3 Representative images of macrofauna identified and discussed in this thesis.

A

Paraprionospio pinnata

B



Maldane sarsi

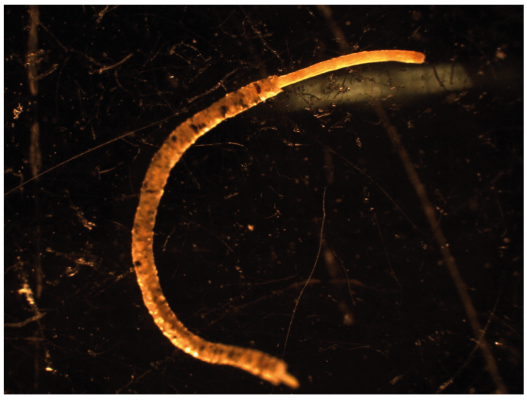
C

Prionospio lighti

D

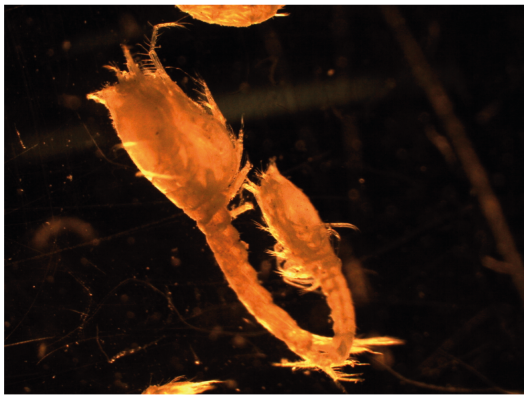
Bipalponephtys cf. cornuta

E



Galathowenia oculata

F



Cumella sp.