

Macrophyte-derived detritus in shallow coastal waters contributes to suspended particulate organic matter and increases growth rates of *Mytilus edulis*

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ABSTRACT: Benthic suspension feeders, such as bivalves, potentially have several different food sources, including plankton and resuspended detritus of benthic origin. We hypothesised that suspension feeders are likely to feed on detritus if it is present. This inference would be further strengthened if there was a correlation between $\delta^{13}\text{C}$ of suspension feeder tissue and $\delta^{13}\text{C}$ of particulate organic matter (POM). Since detritus is characterised by high particulate organic matter (POC):chl *a* ratios, we would also predict a positive correlation between POM $\delta^{13}\text{C}$ and POC:chl *a*. We hypothesised that increasing depth and greater distance from shore would produce a greater nutritional reliance by experimentally transplanted blue mussels *Mytilus edulis* on plankton rather than macrophyte-derived detritus. After deployments of 3 mo duration in 2 different years at depths from 3 to 40 m, *M. edulis* sizes were positively correlated with POM concentrations. POC:chl *a* ratios and $\delta^{13}\text{C}$ of POM and *M. edulis* gill tissue decreased with increasing depth (and greater distance from shore). $\delta^{13}\text{C}$ of POM was correlated with $\delta^{13}\text{C}$ of *M. edulis*. Our results suggest that detritus comprised a large proportion of POM at shallow depths (<15 m), that *M. edulis* ingested and assimilated carbon in proportion to its availability in POM, and that growth of *M. edulis* was higher where detritus was present and POM concentrations were higher.

KEY WORDS: Carbon · Stable isotope analysis · Detritus · Phytoplankton · Seagrass · Kelp · Suspension feeders.

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1. INTRODUCTION

Coastal marine ecosystems are among the most productive in the world (Cebrian 1999). Suspension feeders can be abundant in these ecosystems (Gili & Coma 1998) and can comprise up to 70% of the biomass on some coastal temperate reefs (Newell et al. 1982). Suspension feeders can be important links from primary producers to higher trophic levels—including humans—and perform important regulating services such as filtering water (Gili & Coma 1998).

Phytoplankton are often an important food source for coastal suspension feeders (Doi et al. 2005, Kang et al. 2007). This has been determined through direct methods such as gut content analysis and feeding experiments (Seiderer & Newell 1988, Beninger & Decottignies 2005, Miller & Page 2012). Quantifying the contribution of detritus derived from benthic macrophytes (such as seagrasses and kelps) to suspension feeder diets has been more problematic (Miller et al. 2013), but these sources potentially comprise a substantial proportion of diet in some places (Duggins & Eckman 1997, Schaal et al. 2010). Benthic

macrophytes are highly productive, and much of this production is often not directly consumed by herbivores, so macrophyte-derived detritus might comprise a large proportion of water column particulate organic matter (POM) in the vicinity of large stands of macrophytes and might be an important food source for suspension feeders in those places (Nadon & Himmelman 2006, Miller & Page 2012).

Various lines of evidence support the inference that suspension feeders should be able to consume detritus that originates from benthic macrophytes. Some suspension feeders, such as *Cerastoderma edule*, are able to acquire energy from sediment, suggesting that they can digest detritus (Arambalza et al. 2009, Navarro et al. 2009). In addition, numerous species of suspension feeders display compensatory responses to changes in the quality and/or quantity of suspended particles, for example through selective feeding (Navarro et al. 2009, Hawkins et al. 2013, Arambalza et al. 2018). These responses include varying the rates and efficiencies with which bivalves filter and absorb phytoplankton and detrital food particles according to the quality of that food (Arambalza et al. 2018). The energetic gain and growth experienced by suspension feeders can vary between food sources, with particle digestibility being an important influence (Arambalza et al. 2014).

In fact, many suspension feeders do not eat either only phytoplankton or macrophyte detritus but a mixture of both when it occurs (Langdon & Newell 1990). Langdon & Newell (1990) found that cellulosic detritus and bacteria did not appear to fully meet the requirements of oyster *C. virginica* and the ribbed mussel *Geukensia demissa*. For these bivalve species, other food sources were required, such as phytoplankton, particulate or dissolved organic matter.

Our understanding of how changes in environmental conditions, such as those caused by depth gradients, affect the diet of suspension feeders remains poor. In a low nutrient environment, and in the absence of coastal upwelling, as water becomes deeper, a reasonable prediction is that the contribution of phytoplankton will become greater, because the larger volume of water can support a greater abundance of phytoplankton, and light attenuation will tend to limit the growth of benthic macrophytes.

Unambiguously demonstrating consumption of macrophyte-derived detritus in nature can be elusive, in part because studying gut contents of suspension feeders is difficult or impossible. Stable carbon isotope analysis might help quantify the contribution of macrophyte detritus to suspension feeder diets (Riera & Richard 1996, Fry 1999, Lefebvre & Blin

2009, Nerot et al. 2012, Miller et al. 2013), because marine primary producers typically have distinct $\delta^{13}\text{C}$ (Vander Zanden & Rasmussen 2001, McCutchan et al. 2003). $\delta^{13}\text{C}$ of kelp, seagrass and benthic microalgae are typically higher ($\sim 7\%$) on average than $\delta^{13}\text{C}$ of phytoplankton (Vander Zanden & Rasmussen 2001, McCutchan et al. 2003). Further, $\delta^{13}\text{C}$ of consumers is typically close to that of their diet (Pedersen & Fry 1987, West et al. 2006), so $\delta^{13}\text{C}$ of suspension feeders that consume phytoplankton is likely to be lower than $\delta^{13}\text{C}$ of suspension feeders that consume macrophyte detritus.

Using stable isotopes ($\delta^{13}\text{C}$) alone is unlikely to resolve patterns in the reliance of suspension feeders on macrophyte detritus with depth. For example, phytoplankton composition can vary, and $\delta^{13}\text{C}$ of inshore phytoplankton can be higher than $\delta^{13}\text{C}$ of offshore phytoplankton, making its contribution to POM difficult to distinguish from macrophyte detritus (Nadon & Himmelman 2006, Miller & Page 2012). Inferences are also hampered if samples are taken from within a restricted spatial extent or temporal duration because $\delta^{13}\text{C}$ of most consumer tissues typically reflects integration of diet over months, or sometimes longer (Vanderklift & Ponsard 2003). Measurements conducted over a short duration (e.g. days) might not reflect relevant temporal variability in the $\delta^{13}\text{C}$ of primary producers (Vanderklift & Bearham 2014), potentially producing a biased estimate of source contributions.

The knowledge acquired to date allows several testable predictions about consumption of detritus by suspension feeders. If rates of growth of suspension feeders are proportional to POM concentrations (if, for example, suspension feeders engaged in non-selective feeding), then a logical prediction is that suspension feeders are likely to feed on detritus if it is present. This inference would be further strengthened if there was a correlation between $\delta^{13}\text{C}$ of suspension feeder tissue and $\delta^{13}\text{C}$ of POM. Detritus is characterised by high particulate organic matter (POC):chl *a* ratios (Cloern et al. 1995), so we can also predict a positive correlation between POM $\delta^{13}\text{C}$ and POC:chl *a* if macrophyte detritus comprised a significant proportion of POM in shallow waters. Alone, each of these predictions would provide weak support for the inference that suspension feeders consumer macrophyte-derived detritus, but together they provide stronger support.

The purpose of our investigation was to test these predictions: to evaluate the presence of macrophyte detritus in POM and the relative importance of this detritus to the diet and growth of suspension feeders

across a range of depths and distances from shore. We hypothesized that shallower depth and shorter distance from shore would result in a greater proportion of macrophyte detritus in POM and greater use of this resource by suspension feeders.

2. MATERIALS AND METHODS

2.1. Study area

Our study focused on a transect extending offshore along the 31.850°S latitudinal parallel, approximately 18 km north-west of Perth, south-western Australia. The area is oligotrophic and upwelling is absent: nitrate concentrations are typically $<0.5 \mu\text{mol l}^{-1}$, phosphate concentrations $<0.2 \mu\text{mol l}^{-1}$, and pelagic primary productivity is low (Lourey et al. 2006). The region is characterised by low rainfall in summer (mean = 35.6 mm during the period from December to February; Australian Bureau of Meteorology, www.bom.gov.au/climate/averages/tables/cw_009225.shtml).

The biomass of benthic macrophytes is high, and seagrass and macroalgae are abundant. The small kelp *Ecklonia radiata* (C.Ag.) is the dominant species of macroalgae on hard surfaces (Kirkman 1984, 1989, Wernberg et al. 2006, Bearham et al. 2013) and occurs from shallow water (2 m) to depths exceeding 50 m (Staehr & Wernberg 2009).

We chose 9 sites situated at depths of 3 m (500 m from shore), 5 m (2.0 km from shore), 10 m (3.1 km from shore), 15 m (4.5 km from shore), 20 m (5.6 km from shore), 25 m (7.4 km from shore), 30 m (10.3 km from shore), 35 m (13.9 km from shore) and 40 m (20.4 km from shore). More detailed information on the environmental conditions present at the sites can be found in Bearham et al. (2013) and Vanderklift & Bearham (2014).

2.2. Survey design and data collection

We deployed *Mytilus edulis* (obtained from Blue Lagoon Mussels, Cockburn Sound, latitude $-32^{\circ}10.012$, longitude $115^{\circ}43.588$) at each site from December to March in the austral summers of 2008/2009 and in 2009/2010. Approximately 300–400 *M. edulis* spat (2008/2009: mean spat height = 24.82 mm, mean dry mass = 0.54 g; 2009/2010: mean spat height = 20.31 mm, mean dry mass = 0.29 g) were enclosed around 2.5 m lengths of 20 mm diameter hemp rope with cotton mussel stocking. The

stockings disintegrated after approximately 20 d; by then *M. edulis* were attached to the rope. At each site, 4 ropes were secured to a mooring at one end and suspended vertically in the water column by attaching a float to the opposite end. Consequently, the mussels were suspended in the water column approximately 2–4 m above the substrate. Moorings were attached to a surface line for controlled deployment and retrieval.

After 88 d (2008/2009) or 105 d (2009/2010) all mussels were collected. For ropes from which sufficient *M. edulis* were retrieved, shell length and total mass measurements were taken for 25 individual mussels; otherwise all individuals were used. Tissue was removed from the shell and placed into a numbered aluminium dish, which was dried at 60°C for 12 h and then weighed (μg). Shell length was also measured (mm); in 2008/2009 100 mussels were retrieved from each of 5 sites (5, 10, 15, 20 and 35 m). Mortality of mussels limited the number of individuals retrieved in 2009/2010 to a total of 92, with 11 individuals retrieved from the 5 m site, 0 from the 10 m site, 0 from the 15 m site, 59 from the 20 m site, 3 from the 25 m site, 10 from the 30 m site and 9 from the 40 m site.

Gill tissues were dissected and then dried by sublimation in a freeze drier (Labconco FreeZone 2.5) before being crushed into a fine powder using a mixer mill (Retsch MM400). Sixteen individuals from each site (5, 10, 15, 20 and 35 m) were analysed from 2008/2009, while in 2009/2010 almost all individuals that were retrieved were analysed; the only exception was the 20 m site, where 26 mussels were analysed (rather than the 59 obtained).

Gill tissue was used in the study because it has a higher metabolic turnover than other mussel tissue. Previous studies have found little difference between $\delta^{13}\text{C}$ in gill, adductor muscle and digestive tissue (Cabanellas-Reboredo et al. 2009). Nonetheless, a comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of gill tissue and adductor muscle was made to ensure that differences in the uptake of these elements by different tissues did not bias the results. To that end, 18 mussels were dissected and both muscle and gill tissue samples obtained. These samples were processed using identical methods to the samples above. No significant difference was observed between the tissue types in this study (means: $\delta^{13}\text{C}$ gill = 20.87, SE ± 0.35 ; muscle 20.57, SE 0.19; $\delta^{15}\text{N}$ gill = 6.03, SE 0.07; vs. muscle 6.02, SE 0.35).

Water samples were collected once per month (with an initial and final sampling) at each site during each of the deployments from less than 2 m above the sea floor by Niskin bottles to give a total of 5 sam-

pling points. Two litres of seawater were filtered through a pre-ashed and weighed glass microfibre filter (Whatman GF/F; diameter 47 mm; pore size 0.7 μm) for measurement of POM, POC and $\delta^{13}\text{C}$. An additional 4 l of seawater were filtered through a pre-ashed and weighed glass microfibre filter (Whatman GF/F; diameter 25 mm; pore size 0.7 μm) for the analysis of pigment composition and concentration by high performance liquid chromatography (HPLC). One litre of seawater was filtered for measurement of chlorophyll *a* (chl *a*) (Whatman GF/F; diameter 25 mm; pore size 0.7 μm). Filters for analysis of POM were frozen on site and stored at -20°C in the laboratory; filters for analyses of pigments and chl *a* were stored in liquid nitrogen on site and stored at -80°C . In 2008/2009 a total of 70 water samples were filtered for measurement of POM, 50 for chl *a*, 47 for $\delta^{13}\text{C}$ and 48 for pigment analyses. In 2009/2010 126 water samples were filtered for measurement of POM, 101 for chl *a*, 133 for $\delta^{13}\text{C}$ and 87 for pigment analyses.

Each filter for POM analysis was thawed and then dried at 70°C for 12 h and weighed. The original weight of the filter was subtracted to obtain the total weight of suspended solids present. The filter was then placed in a muffle furnace at 450°C for 4 h and then re-weighed in order to obtain a measurement of the weight of the particulate inorganic matter present in the sample by subtraction of the initial filter weight. The weight of the POM was calculated as the difference between the weights of the total weight of suspended solids and the weight of the particulate inorganic matter. All measurements were then divided by the volume of water filtered to give a concentration of each parameter in mg l^{-1} .

Concentrations of chl *a* were obtained from extraction of the filters in the laboratory using a Turner 10-AU fluorometer. The fluorometer was calibrated using primary standards of ultrafiltered seawater samples at 35 ppt and 2 chl *a* samples within the expected range ($0\text{--}0.1 \text{ mg m}^{-3}$). An ultrafiltered seawater sample at 35 ppt was used to ensure calibration accuracy throughout.

Stable isotope analyses of POM and mussel gill tissue were performed by Natural Isotopes Pty Ltd using an elemental analyser (ANCA-GSL, Europa) coupled with a continuous flow isotope ratio mass spectrometer (20-20 IRMS, Europa). Filters were acidified to remove inorganic carbon prior to analysis of $\delta^{13}\text{C}$. The analytical precision derived from repeated measurements of an internal standard of *Fucus vesiculosus* (which had been previously calibrated against International Atomic Energy Agency or National Institute of Standards and Technology standards) was ± 0.17 for $\delta^{13}\text{C}$.

Filters for pigment analyses were extracted over 15–18 h in an acetone solution before analysis by HPLC using a C_8 column and binary gradient system with an elevated column temperature following the method of Clementson (2013). Pigments were identified by retention time and absorption spectrum from a photo-diode array (PDA) detector and concentrations of pigments were determined from commercial and international standards (Sigma; DHI).

2.3. Data analysis

POM and POC measurements were averaged for each station across each deployment. We used linear regression analysis to test for relationships between mean *M. edulis* mass and shell length, mean concentrations of POM, mean $\delta^{13}\text{C}$ and depth.

We tested 2 predictions about the nature of the regression between $\delta^{13}\text{C}$ POM and $\delta^{13}\text{C}$ of *M. edulis*. First, if *M. edulis* feed non-selectively on POM, then the slope of the regression should be 1. Second, the intercept of the regression should be similar to the difference expected between a consumer and its diet, because the stable isotope ratios of a consumer's tissues should differ from those of its diet in a predictable way (Vanderklift & Wernberg 2010).

Since chl *a* of detritus degrades rapidly in the euphotic zone (Nelson 1993), the relative contribution of detritus and phytoplankton (using chl *a* concentrations as a measure of phytoplankton abundance) to POM was characterised by POC:chl *a* ratios. A high POC:chl *a* ratio (>200 , Table 1, Parsons et al. 1977). indicates that detritus probably comprises a high proportion of POM while a low POC:chl *a* ratio indicates that phytoplankton probably comprise most of the POM (Cifuentes et al. 1988). We used linear regression analysis to test for relationships between (untransformed) POC or POC:chl *a* ratios and POM $\delta^{13}\text{C}$.

The study area is characterised by low rainfall in summer (and therefore has minimal terrestrial input), so we hypothesise that a positive correlation should exist between POM $\delta^{13}\text{C}$ and POC:chl *a* ratios if macrophyte detritus comprised a large proportion of POM inshore, and a lower proportion offshore. We would expect no correlation if phytoplankton were dominant everywhere (Miller et al. 2013). All analyses were performed and assessed for statistical significance using SPSS 17.0 (IBM) or R version 3.5.1 (R Development Core Team 2010).

To further investigate the potential contribution of phytoplankton and detritus, canonical analysis of

Table 1. Particulate organic matter (POC):chl *a* ratios for different regions. Blanks indicate no $\delta^{13}\text{C}$ values reported

Reference	Region	Source	POC:chl <i>a</i> ratio	$\delta^{13}\text{C}$
Present study	Western Australia Indian Ocean	Present study	100–250 (Fig. 5)	
Cifuentes et al. (1988)	Delaware River estuary	Detritus	>200	
Francois et al. (1993)	Open Indian Ocean	Phytoplankton?	100–1000 mostly 200–800	–22.6 from samples >500 (reflecting terrestrial sources)
Jakobsen & Markager (2016)	Danish/Baltic Sea	Phytoplankton	7.5–86	
Caperon et al. (1976)	Coastal Pacific Ocean – Hawaiian Islands, Kaneohe Bay	Possible detritus– waste discharge	127–146	Surface samples

principal coordinates (Anderson & Willis 2003) was used to test whether pigment composition varied among depths, and axis scores were correlated with concentrations of pigments to determine which pigments contributed most to patterns observed. Analyses were conducted on Hellinger distances calculated from untransformed data, using the Primer 6 software package (Clarke & Gorley 2006).

3. RESULTS

POM concentrations explained much of the variance in, and were positively correlated with, *Mytilus edulis* dry mass (2008/2009: $R^2 = 0.78$, $p < 0.001$; 2009/10: $R^2 = 0.91$, $p < 0.001$; Fig. 1) and shell length (2008/2009: $R^2 = 0.90$, $p < 0.001$; 2009/2010: $R^2 = 0.96$, $p = 0.003$; Fig. 1) in both deployments. POM concentrations were not well correlated with depth (2008/2009: $R^2 = 0.00$, $p = 0.89$; 2009/2010: $R^2 = 0.05$, $p = 0.72$; see dot size in Fig. 1). $\delta^{13}\text{C}$ of POM and mussel gill tissue were positively correlated with each other and increased with depth. This relationship was significant for both deployments (see Fig. 4).

Chl *a* concentrations were a weaker predictor of *M. edulis* dry mass, and this was not statistically significant in either deployment (2008/2009: $R^2 = 0.28$; 2009/2010: $R^2 = 0.41$; Fig. 1). POC:chl *a* ratios decreased with depth—a pattern which is consistent with an increase in phytoplankton biomass with increasing depth (Fig. 2).

$\delta^{13}\text{C}$ of POM and depth were positively correlated (2008/2009: $R^2 = 0.77$, $p = 0.03$; 2009/2010: $R^2 = 0.73$, $p < 0.01$; Fig. 3), with $\delta^{13}\text{C}$ of POM lower at deeper offshore sites (–18.8‰ at 3 m to –23.2‰ at 35 m in 2009; –18.6‰ at 3 m to –23.1‰ at 35 m in 2010). Similarly, *M. edulis* gill $\delta^{13}\text{C}$ was positively correlated with depth in both deployments (2008/2009: $R^2 =$

0.68, $p < 0.001$. 2009/2010; $R^2 = 0.91$, $p < 0.001$; Fig. 3), and tended to be lower at deeper offshore sites (–19.8‰ at 10 m to –21.6‰ at 35 m in 2009, and –20.7‰ at 5 m to –23.4‰ at 40 m in 2010). $\delta^{13}\text{C}$ of *M. edulis* gill was positively correlated with $\delta^{13}\text{C}$ of POM in both 2008/2009 ($R^2 = 0.65$, $p < 0.0001$; Fig. 4) and 2009/2010 ($R^2 = 0.72$, $p < 0.0001$; Fig. 4).

The correlation between POM $\delta^{13}\text{C}$ and POC:chl *a* was positive and statistically significant in 2009/2010 ($R^2 = 0.47$, $p = 0.04$, Fig. 5), but not in 2008/2009 ($R^2 = 0.06$, $p = 0.22$, Fig. 5). During 2009/2010, POM $\delta^{13}\text{C}$ was positively correlated with POC concentrations, although the amount of variance accounted for was relatively modest ($R^2 = 0.35$, $p = 0.09$, Fig. 5); this pattern was also present in 2008/2009 ($R^2 = 0.12$, $p = 0.55$, Fig. 5). In 2008/2009 POC was positively correlated with chl *a* and accounted for a proportion of the variance ($R^2 = 0.84$, $p < 0.01$, Fig. 5).

Constrained ordination revealed differences in pigment composition among sites in both deployments, with a tendency for shallow sites (3–15 m) to be visually distinct from deeper (20–40 m) sites (Fig. 6). In each case there was a high correlation of axis scores with concentrations of lutein, which tended to be present in higher concentrations at shallow sites (Fig. 6).

4. DISCUSSION

Our results suggest that macrophyte detritus is an important component of POM in shallow water and that the proportion of macrophyte detritus in POM decreases with depth: we infer this because sites in shallow water had higher POC:chl *a* ratios and higher concentrations of lutein (which is found in seagrass). Correspondingly, our results suggest that the food sources used by the suspension-feeding *Mytilus*

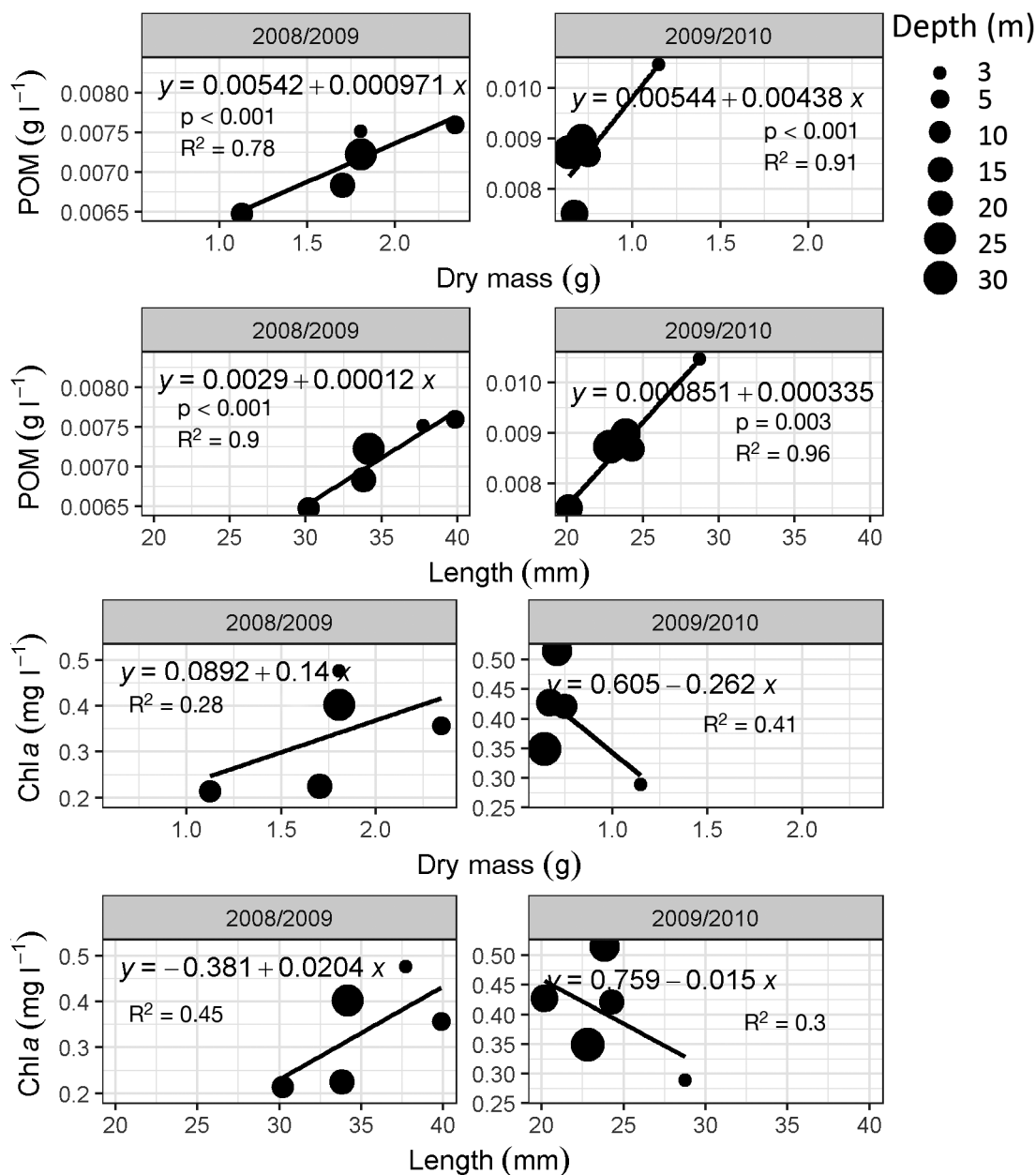


Fig. 1. Comparison of average dry mass (g), shell length (mm), chlorophyll a (mg l⁻¹) and particulate organic matter concentration (POM; g l⁻¹) at each of the sites in 2008/2009 (left) and 2009/2010 (right) using linear regression. Results from linear regression indicated in corner of scatter plot. Depth of the site is indicated by the size of the point on the figure from 3 m smallest to 40 m largest

edulis changed from predominantly benthic detritus to predominantly pelagic phytoplankton with increasing depth (and distance from shore): the main evidence for this inference is that $\delta^{13}\text{C}$ of *M. edulis* tissue was correlated with $\delta^{13}\text{C}$ of POM. *M. edulis* grew to larger sizes at sites with higher mean concentrations of POM during both deployments.

$\delta^{13}\text{C}$ of *Ecklonia radiata* in this region varies from -17.6 to -22.5‰ (mean = 19.8‰) in summer (Van-

derkluft & Bearham 2014). Seagrasses are also common in shallow (<15 m) sheltered areas, predominantly the taxa *Amphibolis griffithii* and *Posidonia* spp. (Kirkman & Kuo 1990). The seagrass *P. sinuosa* has $\delta^{13}\text{C}$ of -11.2 to -14.2‰ while $\delta^{13}\text{C}$ of *A. griffithii* averages -15.2‰ in Marmion Lagoon (authors' unpubl. data). Suspension feeders such as ascidians, sponges and bivalves are also abundant (Keesing et al. 2013).

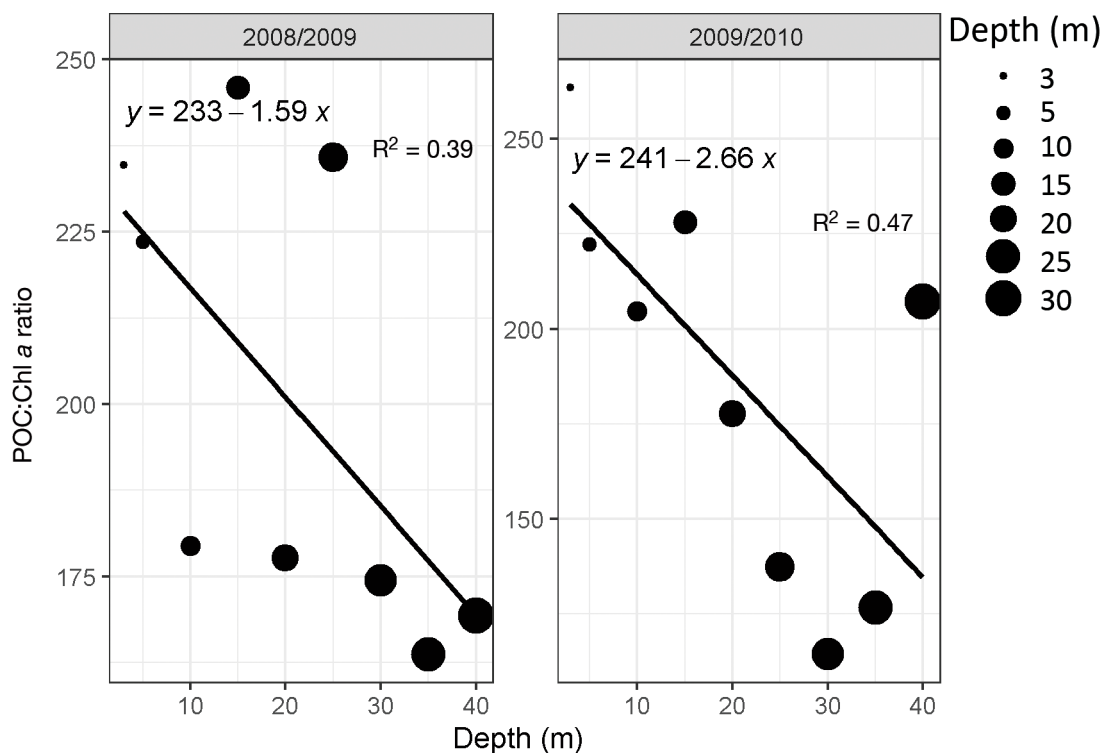


Fig. 2. Relationship between the POC:chl *a* ratio and depth from monthly sampling during 2008/2009 and 2009/2010. POC: particulate organic carbon. Linear regression results are indicated on the plot as well as a *p*-value where analysis is statistically significant. Depth of the site is indicated by the size of the point on the figure from 3 m smallest to 40 m largest

In 2009/2010, when chl *a* concentrations were relatively low throughout the deployment, $\delta^{13}\text{C}$ of POM was correlated with POC concentrations but not with chl *a* concentrations. In addition, POC concentrations were not correlated with chl *a* concentrations, suggesting that POC were not dominated by phytoplankton biomass. In the same deployment, POM $\delta^{13}\text{C}$ was positively correlated with POC:chl *a* ($R^2 = 0.47$, $p = 0.04$), which is also consistent with the hypothesis that macrophyte detritus comprised a larger proportion of POM at shallow sites, because $\delta^{13}\text{C}$ of benthic macrophytes tends to be higher than that of phytoplankton (Vander Zanden & Rasmussen 2001, McCutchan et al. 2003). The dominant macroalgae *E. radiata* has a $\delta^{13}\text{C}$ in this region of between -17.6 and -22.5 ‰ (mean = -19.8 ‰) in summer (Vanderklift & Bearham 2014), while the seagrass *Posidonia sinuosa* ranges from -11.22 to -14.21 ‰ (M. A. Vanderklift unpubl. data). During this deployment, POM $\delta^{13}\text{C}$ was weakly correlated with POC concentrations ($R^2 = 0.35$, $p = 0.09$) but not chl *a* concentrations ($R^2 = 0.06$, $p = 0.22$), providing further support that detritus contributed to POM $\delta^{13}\text{C}$.

In contrast, in 2008/2009 there was no correlation between POM $\delta^{13}\text{C}$ and POC:chl *a* ($R^2 = 0.06$, $p = 0.22$;

Fig. 5), but POC concentrations were positively correlated with chl *a* concentrations ($R^2 = 0.84$, $p < 0.01$), suggesting that POC was influenced to some extent by phytoplankton concentrations during this deployment. This relationship may have been influenced by higher chl *a* concentrations observed late (February/March) during the deployment at shallower sites (3 to 10 m). When the March data for these sites was excluded from the analyses, then POM $\delta^{13}\text{C}$ did correlate with POC:chl *a* ($R^2 = 0.21$; positive relationship).

We also found higher concentrations of lutein at shallower sites. Lutein is a xanthophyll commonly found in green plants, including seagrasses (Casazza & Mazzella 2002) and is also found in some red macroalgae and unicellular green algae such as the Chlorophyceae. It tends to degrade slowly relative to other plant pigments (Bianchi & Findlay 1991). The higher concentrations of lutein in shallow water are consistent with the inference that detritus from benthic macrophytes (such as seagrasses and red macroalgae) comprises a substantial proportion of POM in shallow water, where those macrophytes are most abundant.

Phytoplankton biomass is typically low (0 to 1 mg m^{-3}) in the region during summer (Lourey et al. 2006),

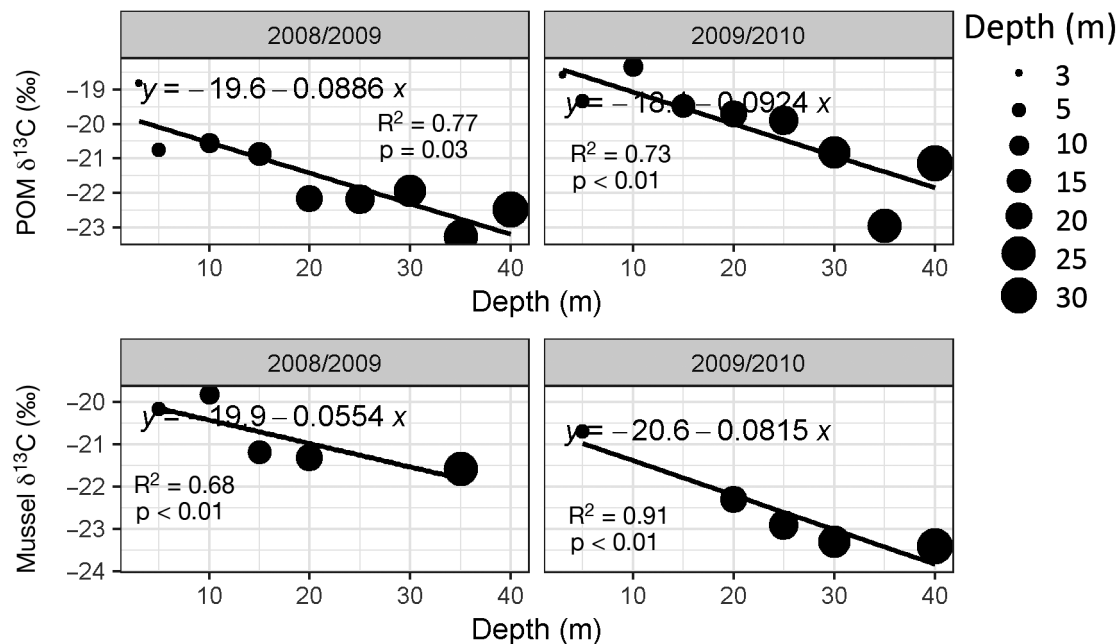


Fig. 3. Scatter plots comparing depth to average $\delta^{13}\text{C}$ values for particulate organic matter (POM; top) and *Mytilus edulis* tissue (bottom) for 2008/2009 (bottom) and 2009/2010 (bottom). *M. edulis* were not obtained from some sites due to mortality. Depth of the site is indicated by the size of the point on the figure from 3 m smallest to 40 m largest

but *E. radiata* has been shown to provide, on average, 254 g fresh weight $\text{m}^{-2} \text{d}^{-1}$ of detritus (254–538 g C $\text{m}^{-2} \text{yr}^{-1}$) through erosion (de Bettignies et al. 2013). Seagrasses such as *P. sinuosa* and *A. griffithii* are also abundant in the area, and although comparable estimates of detritus production do not exist, they are not heavily grazed and production of detritus is likely to be substantial. The magnitude of this contribution and the widespread distribution of kelps and seagrasses in the study area make it likely detritus derived from these macrophytes will contribute substantially to the diet of suspension feeders that feed non-selectively. Our studies support this, and other studies have confirmed that some suspension feeders can consume particles of detritus. Levinton et al. (2002) found that kelp detritus was potentially a source of nutrition for suspension feeders (*Crassostrea gigas*, *Mytilus trossulus*) during laboratory feeding experiments. They found that these bivalves can distinguish among particles with varying chemical composition and respond by changing clearance rates and selectivity. Clearance rates of mussels and oysters were significantly higher for aged (4 d) kelp detritus than for fresh kelp particles.

It is possible that resuspended benthic microalgae can also contribute to diet of suspension feeders, especially in shallow water. Kendrick et al. (1997) found that winter storm swells resuspended nutrients increasing microalgal growth rates in Marmion

Lagoon. However, patterns in $\delta^{13}\text{C}$ and POC:chl a ratios suggest that they are less likely than detritus to be a major food source for the mussels in this study.

We found strong positive correlations ($R^2 = 0.90$ – 0.96) between POM concentrations and *M. edulis* size, which supports the inference that they fed non-selectively. We also found strong positive correlations between $\delta^{13}\text{C}$ of POM and *M. edulis* gill tissue ($R^2 = 0.86$ – 0.93), which is consistent with the inference that *M. edulis* assimilated carbon in proportion to its availability. Combined with the evidence that macrophyte detritus comprised a large proportion of the POM at shallow (<15 m) sites, these patterns are consistent with ingestion and assimilation of macrophyte detritus by *M. edulis* in our study, especially at shallow inshore sites.

Explaining patterns in $\delta^{13}\text{C}$ of suspension feeders is not always simple. Nadon & Himmelman (2006) urged caution when interpreting decreasing $\delta^{13}\text{C}$ with increasing distance from shore. Inferences that are derived from indirect estimates of $\delta^{13}\text{C}$ of inshore or offshore phytoplankton can generate overestimates of the importance of macrophytes to benthic consumers. POM comprises a variety of different particles and mussels might select specific particle types (Ward & Shumway 2004, Nerot et al. 2012).

Bivalves may increase clearance rates with increasing food quality and preferentially reject poor qual-

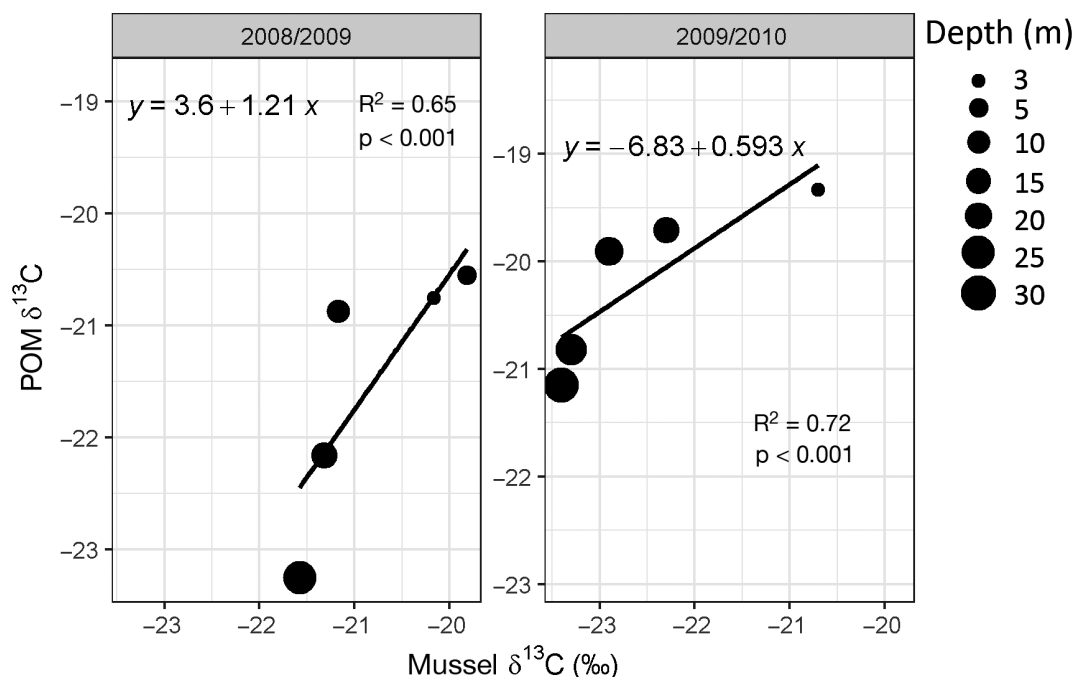


Fig. 4. Plots comparing $\delta^{13}\text{C}$ ratios for POM and *Mytilus edulis* tissues from the same station. Left regression represents 2008/2009; right regression represents 2009/2010 data. Station depths indicated on the plot. Depth of the site is indicated by the size of the point on the figure from 3 m smallest to 40 m largest

ity material in pseudofeces (Newell & Jordan 1983, Iglesias et al. 1992). They may also reduce clearance rates when food is of poor quality (Bayne et al. 1989) and select certain species of phytoplankton, avoiding those that have high concentrations of cellulose (Levinton et al. 2002). This selectivity is mostly accomplished on the gills of oysters (*Crassostrea* spp.) and on the palps of *Mytilus* spp. (Ward et al. 1997, 1998).

The feeding characteristics of suspension-feeding bivalves such as *M. edulis*, may vary with size and with variables such as temperature, as well as the quality and quantity of seston available (Bayne et al. 1989). There are 3 behavioural responses that have been observed in *M. edulis* that might act together to increase the ingestion rate of filtered organics (Bayne et al. 1989): firstly, a change in the rate at which material is filtered from suspension; secondly, a change in the proportion of this material being rejected as pseudofaeces; and lastly, an increase in the efficiency with which organic material is selected from particles filtered for ingestion (Bayne et al. 1989). By altering one or more of these 3 factors, bivalves are able to increase or decrease adsorption rates for organics as required. In this study we found low planktonic biomass may have resulted in *M. edulis* feeding indiscriminately rather than choosing to feed selectively, unlike bivalves that occur in other locations such as Georges Bank.

Previous studies (Fry 1988, Hobson et al. 1995) have also suggested that some inshore to offshore gradients observed in $\delta^{13}\text{C}$ of suspension feeders may be at least partially due to high phytoplankton productivity at shallow sites where increased rates of photosynthesis use a greater proportion of dissolved carbon, which would tend to decrease fractionation so that $\delta^{13}\text{C}$ of phytoplankton becomes more similar to that of dissolved carbon sources (i.e. become higher). Fry (1988) observed a depth-related decrease in $\delta^{13}\text{C}$ of 1.2‰ in scallop *Placopecten magellanicus* (−16.8 to −18‰) on Georges Bank (0–160 m) and suggested that this pattern might reflect a gradient in phytoplankton productivity because Georges Bank is located far from sources of kelp or benthic microalgae. The differences in $\delta^{13}\text{C}$ of POM between shallow and deep sites in our study were much larger (2008/2009: 4.4‰; 2009/2010: 4.5‰), during a period that encompassed relatively low phytoplankton biomass (average chl *a* 0.35 mg m^{−3}). In addition, no relationship (2008/2009) or a positive relationship (2009/2010; $R^2 = 0.47$ $p = 0.04$) was observed between POC:chl *a* and $\delta^{13}\text{C}$. Since macrophyte detritus is characterised by high POC:chl *a* ratios, it is more likely that patterns in detritus concentration resulted in a lower $\delta^{13}\text{C}$ of POM (and in turn of $\delta^{13}\text{C}$ of *M. edulis* tissue) at shallow sites in our study.

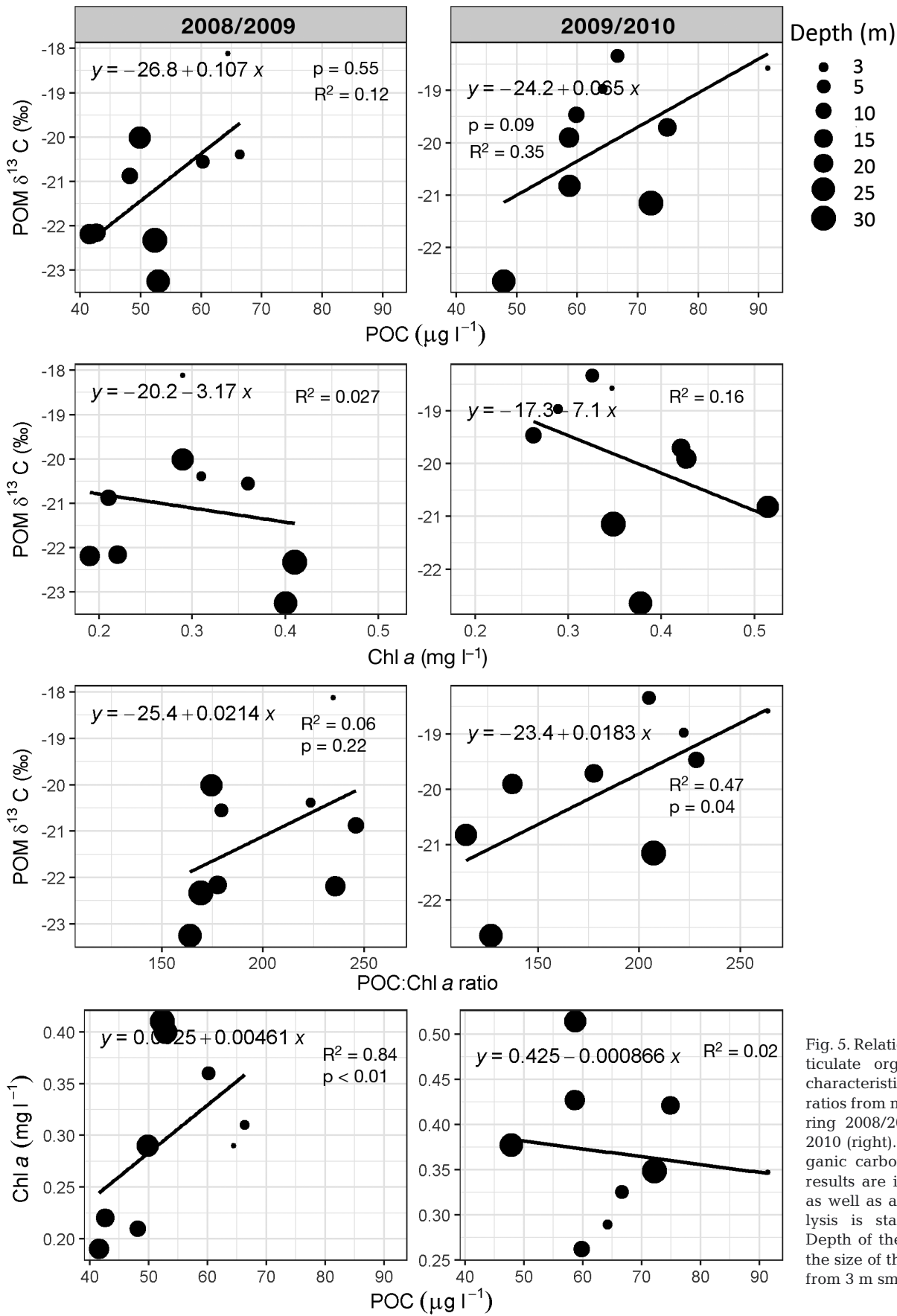


Fig. 5. Relationships between particulate organic matter (POM) characteristics and POM $\delta^{13}\text{C}$ ratios from monthly sampling during 2008/2009 (left) and 2009/2010 (right). POC: particulate organic carbon. Linear regression results are indicated on the plot as well as a p-value where analysis is statistically significant. Depth of the site is indicated by the size of the point on the figure from 3 m smallest to 40 m largest

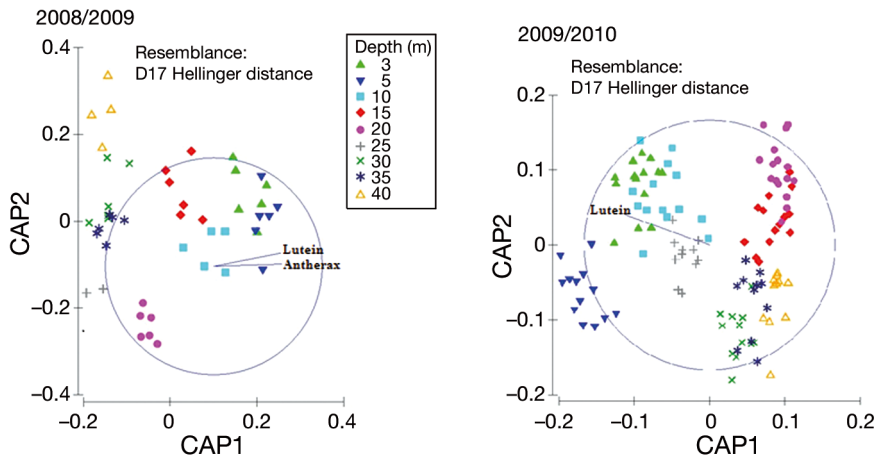


Fig. 6. Distribution of sites compared to pigment concentrations obtained through pigment analysis. Plots were visualized using CAP (canonical analysis of principal coordinates) analyses with a Hellinger distance algorithm with no transformation. Depth of the site (in m) is indicated by the shape of the point from 3 to 40 m

This study was conducted in an area with low phytoplankton concentrations (by international standards). This may have resulted in the mussels feeding more on detritus than they otherwise would have. In our study [chl *a*] ranged from 0.1 to 0.7 mg m⁻³, with an average chl *a* concentration of 0.35 mg m⁻³. Widdows et al. (1979) found no pseudofaeces were produced at 4.5 mg l⁻¹ total seston by *M. edulis* kept in laboratory conditions. At no point during this study did chl *a* concentrations exceed 0.7 mg l⁻¹.

Our results support the inference that macrophyte-derived detritus comprises a substantial proportion of POM in shallow water, and likely contributes to the diet of suspension feeders. Any decrease in the biomass of benthic macrophytes will therefore potentially have broader consequences for the ecosystem. Such changes might occur due to increasing water temperature (Pearce & Feng 2007, Wernberg et al. 2010, Bearham et al. 2013), changes to bottom water velocities as storm patterns change (Frederiksen & Frederiksen 2007), increases in nutrient concentrations (Thompson et al. 2009) and reduced light due to declining water quality (Connell et al. 2008).

5. CONCLUSIONS

We found rates of growth of suspension feeders were proportional to POM concentrations, indicating suspension feeders are likely to feed on detritus if it is present. This inference was further strengthened since there was a correlation between $\delta^{13}\text{C}$ of suspension feeder tissue and $\delta^{13}\text{C}$ of POM. We also found a positive correlation between POM $\delta^{13}\text{C}$ and POC:chl *a*. These results support the inference that experimentally transplanted blue mussels *Mytilus edulis* consumed a large proportion of macrophyte detritus at shallow inshore sites and that increasing

depth and greater distance from shore produced a greater reliance on plankton. Growth of *M. edulis* was higher where detritus was present and POM concentrations were higher.

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