

Growth and production of California sea cucumbers (*Parastichopus californicus* Stimpson) co-cultured with suspended Pacific oysters (*Crassostrea gigas* Thunberg)

D.L. Paltzat^{a,c}, C.M. Pearce^{a,*}, P.A. Barnes^b, R.S. McKinley^c

^a Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia, Canada V9T 6N7

^b Centre for Shellfish Research, Malaspina University-College, 900 Fifth Street, Nanaimo, British Columbia, Canada V9R 5S5

^c Centre for Aquaculture and Environmental Research, University of British Columbia/Fisheries and Oceans Canada, 4160 Marine Drive, Vancouver, British Columbia, Canada V7V 1N6

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Abstract

Growth and production of California sea cucumbers (*Parastichopus californicus* Stimpson), co-cultured with suspended Pacific oysters (*Crassostrea gigas* Thunberg), were investigated in a 12-month (January 2004–January 2005) study conducted at two sites of deep-water, suspended oyster culture in British Columbia, Canada. Rates of oyster biodeposition (faeces and pseudofaeces) and the utilization of this particulate material as a food source by *P. californicus* were also examined. Peaks in sedimentation rates through 8.5 m water depth, below the oyster rafts, were observed in April (93.6 g dry wt m⁻² d⁻¹) and July (91.9 g dry wt m⁻² d⁻¹) 2004. At the two study sites, maximum mean total organic carbon deposition rate at 8.5 m depth occurred in July 2004 and amounted to 3123 and 3830 mg dry wt C m⁻² d⁻¹. Maximum mean total nitrogen deposition rate at the two sites was 524 and 568 mg dry wt N m⁻² d⁻¹ which occurred in November and July 2004, respectively. Mean C/N ratios of particulate material in the sediment trap samples collected at the two sites between January and November 2004 ranged between 5.9 and 12.4 and may be considered to be of high nutritional value. Growth and survivorship of sea cucumbers held in experimental trays below the suspended oysters were measured, growth being assessed using split weight as well as muscle and skin wet weights. There were no sea cucumber mortalities in any of the trays deployed at either site during the study. Sea cucumbers grown in trays at both sites successfully utilized biodeposits from the cultured oysters and showed a mean weight increase of 42.9 g in approximately 12 months (average growth rates at both sites ranged from 0.061 to 0.158 g d⁻¹). Overall growth was affected by the absence of visceral organs and the cessation of feeding activity observed in the November 2004 sampling period. Overall mean values (for the two study sites) for organic content were significantly higher in the foregut of the sea cucumbers (24.7% or 224.6 mg g⁻¹ dry sediment) than in the sediment (5.9% or 51.6 mg g⁻¹ dry sediment) or in the hindgut (14.5% or 157.9 mg g⁻¹ dry sediment), showing both active selection of organic material from the sediments and digestion/assimilation of these organics in the gut. Organic material deposited in the trays was assimilated by *P. californicus* at the two study sites with an average efficiency of 40.4%. The successful utilization of the naturally-available biodeposits from the cultured Pacific oysters by California sea cucumbers suggests the feasibility of developing a commercial-scale co-culture system that would both reduce the amount of organic deposition underneath shellfish farms and produce a secondary cash crop.

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1. Introduction

Dense assemblages of filter-feeding bivalves enhance the vertical flow of organic matter towards the benthic environment.

Many studies report that bivalves in suspended raft or long-line culture play a key role in coastal ecosystems due to their high filtration capacity and culture density (e.g. Kautsky and Evans, 1987; Jaramillo et al., 1992; Hatcher et al., 1994). Bivalves, to a large extent, remove small suspended particles and initiate the sedimentation of larger particles of high organic content (i.e. faeces and pseudofaeces) (Kautsky and Evans, 1987). Captured particles

* Corresponding author. Tel.: +1 250 756 3352; fax: +1 250 756 7053.

E-mail address: PearceC@pac.dfo-mpo.gc.ca (C.M. Pearce).

are rejected before ingestion as pseudofaeces or ingested, passed through the digestive tract, and excreted as faeces (collectively termed biodeposits) (Haven and Morales-Alamo, 1966; Navarro and Thompson, 1997; Miller et al., 2002). Although there is no net addition of organic matter, the larger biodeposits become available as an energy source (i.e. carbon and nitrogen) to micro-organisms, and ultimately to higher trophic levels such as benthic macro-invertebrates (Yingst, 1976; Dame and Dankers, 1988).

Soft-sediment communities are often dominated by deposit feeders and the physical and chemical characteristics of the sediments are influenced by the feeding activities of these animals. Like many deposit-feeding organisms, sea cucumbers exploit the sediment layer with the highest and most readily utilizable organic matter (Yingst, 1982). The California sea cucumber (*Parastichopus californicus* Stimpson) occurs in low intertidal and subtidal areas on rock, shell or muddy–sandy sediments or on pilings, and reaches greatest densities in quieter waters from Baja California to the Gulf of Alaska (Cameron and Fankboner, 1989; Kozloff, 1996; Lambert, 1997). This sea cucumber species has become the focus of a limited commercial dive fishery in British Columbia, Washington, and Alaska (Sloan, 1986; Cameron and Fankboner, 1989; Conand and Byrne, 1993) and is highly valued for import into, and re-export from, Hong Kong. Like many other commercially important sea cucumber species, *P. californicus* has previously been fished extensively in British Columbia and Washington to meet the increased demand for its longitudinal muscles and *bêche-de-mer*, the market name for the dried product from the body wall of holothurians, in southeast Asia (Conand and Byrne, 1993). An early period of growth in capacity and landings in the 1980s led to over-exploitation of the fishery in British Columbia.

Oyster growers in British Columbia have found that juveniles and sub-adults of *P. californicus* can form a significant population within the community of organisms that settle and grow on the oyster culture gear (B. Stevenson, Viking Bay Ventures, pers. comm.). The sea cucumbers have been observed to clean the detritus from the oysters and ingest the organic material (D. Paltzat, pers. obs.). The organic matter deposited by the shellfish as faeces and pseudofaeces may represent a significant proportion of the energy (Stuart et al., 1982) potentially available to *P. californicus* in the vicinity of oyster farms. Ahlgren (1998) showed that muscle development of California sea cucumbers reared inside floating net pens at a salmon (*Oncorhynchus* sp.) rearing facility in southeast Alaska was significantly greater than that of sea cucumbers feeding in their natural environment. That work suggests that this species of sea cucumber is capable of consuming fouling debris (e.g. fish faeces, excess fish food, algae, etc.) and could turn harmful fouling into a marketable product (sea cucumber biomass). Integrated multi-trophic aquaculture (IMTA) has the potential to increase the efficiency and productivity of intensive monoculture systems while reducing waste loadings and environmental impacts (Chopin et al., 2001; Neori et al., 2004). IMTA technology has been applied to sea cucumber production in China where *Stichopus* (= *Apostichopus*) *japonicus*, the temperate species in the western Pacific, has been successfully grown, without supplemental feeding, on artificial reefs placed in shrimp ponds (Chen, 2003). However, in other parts of the world, suitable culture methods for commercially exploited

sea cucumber species have not yet been developed or are in experimental stages (Hagen, 1996; Ramofafia et al., 1997; Kang et al., 2003).

In the present study, field investigations were undertaken to examine the feasibility of growing California sea cucumbers, *P. californicus*, in co-culture with Pacific oysters, *Crassostrea gigas* (Thunberg), the oyster species farmed in British Columbia. Sedimentation rates of biodeposits from the cultured oysters were determined and samples of the particulate material were analyzed for organic carbon and nitrogen content. Utilization of this material as a food source by *P. californicus* was measured quarterly over a 12-month period by monitoring growth (i.e. changes in overall weight and muscle and skin wet weights) and survivorship of the sea cucumbers *in situ* under oyster culture rafts.

2. Materials and methods

2.1. Study sites

Field studies were conducted at two established *C. gigas* culture sites in Village Bay (VB), Quadra Island (49°59'N, 124°11'W) and Gorge Harbour (GH), Cortes Island (50°05'N, 125°01'W), British Columbia (Fig. 1). At the farms, oysters are cultured on strings suspended from rafts in the upper 6 m (approximately) of the water column at an average density of 1077 individuals m⁻². Approximately 15 dozen oysters are cultured on each string and the rafts contain 250 strings (ca. 45,000 individuals per raft) (J. Rendall, Bee Islets Co-op, pers. comm.). The two study sites were approximately 17 km apart. Village Bay is relatively exposed and has direct tidal flushing from the Strait of Georgia. The oyster farm in VB is located in the northwest section of the bay which reaches a maximum depth of 19 m. The farm produces both raft and long-line cultured oysters. The site contains 36 rafts which cover a surface area of approximately 1500 m² as well as long-lines, near the back of the bay. Gorge Harbour is a semi-restricted water body, with tidal exchange from the Strait of Georgia occurring through a single narrow opening along the southwest shore of the embayment. The basin in GH is depositional and has a maximum depth of 30 m around the oyster farm. Tidal ranges of 1–2 m and tidal current velocities of 16.0–37.5 cm s⁻¹ and 7.5–10.0 cm s⁻¹ in surface and deeper (13–15 m) waters, respectively, have been documented for GH (Hay and Company Consultants, Inc., 2001; Richardson and Newell, 2002). The oyster rafts used at this study site were located in the Bee Islets lease, which contains approximately 150 rafts covering a surface area of ca. 44,800 m² (J. Rendall, Bee Islets Co-op, pers. comm.).

2.2. Water column characteristics

As part of a concurrent ecological study conducted by the Centre for Shellfish Research (CSR), Malaspina University-College, submersible temperature data loggers (Onset Computer Corporation, Pocasset, MA, USA) were suspended for 14 months below a central experimental oyster raft at both study sites. The temperature data loggers were positioned at four depths: 3.0, 5.0, 8.5, and 10.0 m at VB and 3.0, 8.5, 18.5, and 23.5 m at GH. Water temperature measurements were recorded every 15 min by the moored instruments except for breaks when the data were downloaded during each of the quarterly sampling periods. Also in conjunction with the CSR's concurrent ecological interactions study, water column profiles were run at both sites on sampling dates in January, April, and July 2004 to determine salinity and chlorophyll (*a*, *b*, and *c1+c2*) using a YSI 6600 multi-parameter water-quality monitoring sonde (YSI Inc., Yellow Springs, OH, USA). Values for salinity and chlorophyll are reported at depths of approximately 8.5 m in January, 8.0 m in April, and 10.1 m in July 2004. These correspond to depths at which sediment traps were placed and the depth at which sea cucumbers were held.

2.3. Sea cucumber growth and production

Sub-adult sea cucumbers (contracted length: 8–13 cm) for the field studies were collected from the oyster farms at VB and GH. Animals were taken directly off the

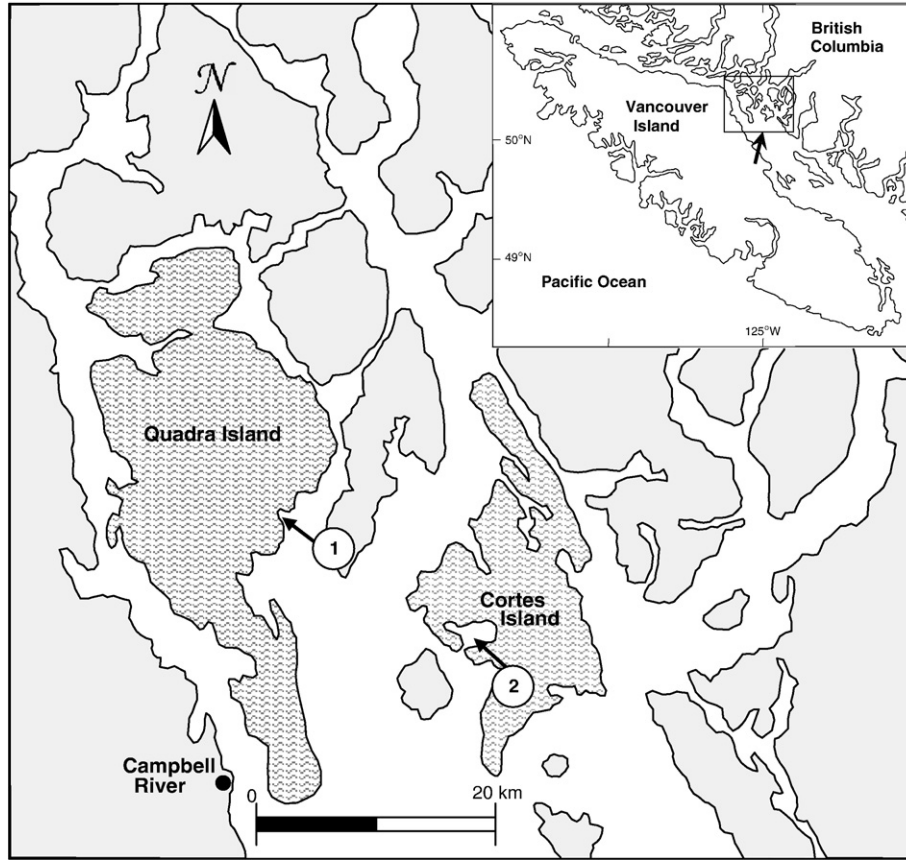


Fig. 1. Location of the oyster culture sites. 1 Village Bay; 2 Gorge Harbour.

oyster strings on the culture rafts in January 2004. Prior to placement in the experimental trays, body length and width were measured for all individuals. Length and width measurements were taken at the points of greatest dimensions on

contracted individuals. Full contraction was assumed to be the point at which no further shortening occurred during handling. These linear measurements were used in the formulation of a size index (SI) = length × width × 0.01 (Yingst, 1982). Body

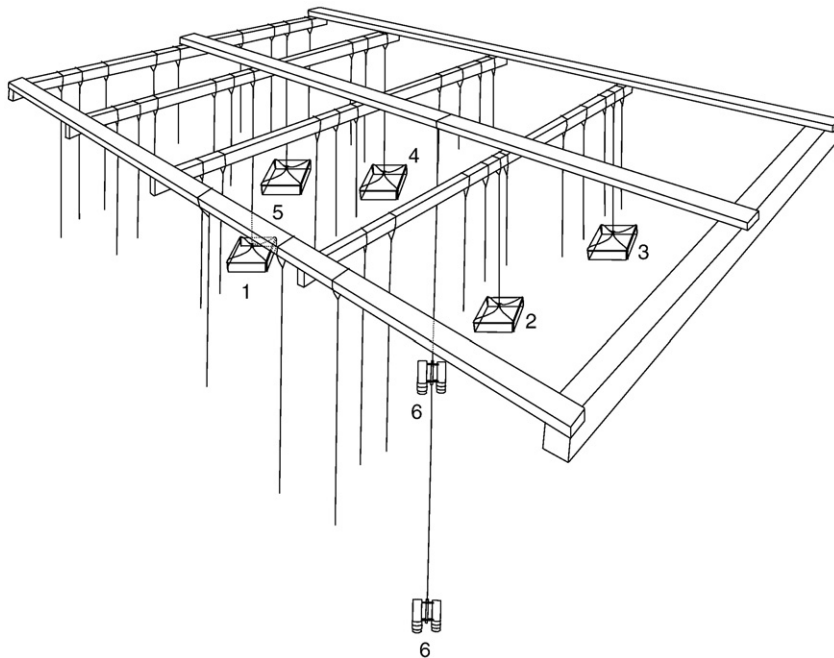


Fig. 2. Diagrammatic representation of experimental tray, control tray, and sediment trap arrangement below the culture rafts. 1–4 Experimental trays; 5 Control tray; 6 Sediment traps.

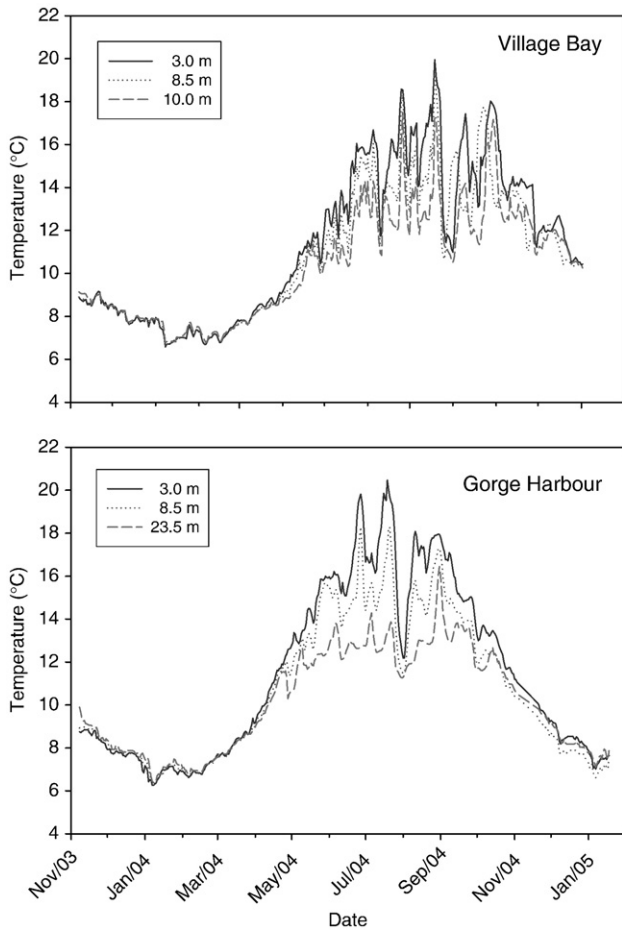


Fig. 3. Water temperature in Village Bay and Gorge Harbour from November 2003 to January 2005. Data are average daily temperatures at each depth.

wet weight measurements were taken, using a digital balance, after external water was removed from specimens by blotting them on a paper towel. Six sea cucumbers were placed in each of four experimental trays which were deployed below each of three culture rafts at both study sites. An additional 18 sea cucumbers were randomly collected from the oyster strings at both sites to get a baseline measurement of split weight (excluding cloacal and coelom water) and muscle and skin wet weights.

High Flow™ (Fukui North America, Eganville, ON, Canada) oyster grow-out trays (L×W×H: 56.25×56.25×21.25 cm) were used as the experimental units. Tray bottoms were lined with a solid PVC insert (thickness: 0.156 cm) to prevent

loss of biodeposits, tray sides were reinforced with a wire panel (mesh size: 0.625 cm), and tray tops were covered with wire panels of the same mesh size to prevent the sea cucumbers from escaping.

In January 2004 the trays were deployed 2.5 m below the oyster strings (8.5 m water depth) and were positioned towards the centre of each of the rafts to capture maximal deposition (Fig. 2). One tray without sea cucumbers (control) was placed below each of the three culture rafts, at the same depth as the experimental trays, at both study sites. The culture rafts were non-randomly selected due to constraints of the farm operation. Rafts with oysters that were approximately one-year old were used in the study. Field observations and sampling were carried out three times over the course of 10 months in VB. The VB experiment had to be terminated in November 2004, after 10 months, when the oysters reached commercial size and were harvested. Field observations and sampling in GH were carried out every 3 months for 12 months to obtain data throughout an annual growth cycle. Control trays and one randomly selected experimental tray were sampled at each of the three study rafts at both sites for every sampling period. Trays were carefully hauled to the surface and a sample (1 l) of particulate material in the trays was collected and frozen at -4 °C prior to freezing at -18 °C at the laboratory. After removing the sea cucumbers, the experimental trays became control trays and were placed back in their respective places under the rafts until the next sampling period.

Sea cucumber survivorship was documented when animals were removed from the trays. The sampled sea cucumbers from each experimental tray were held separately in Ziploc® bags filled with seawater and dissected within 1 h of sampling. Prior to dissection, contracted body length, width, and wet weight were measured for all individuals. After dissection, a split weight was measured for each. Particulate material in the first 50 mm and the last 50 mm of the gut tract was removed and frozen (-18 °C). Faecal material was collected from the Ziploc® bags. Each sample was kept individually for comparison with the particulate material from the trays. The difference between the fore- and hindguts was assumed to be equal to the amount of that material that was removed during passage through the digestive tract. The muscle bands were separated from the skin and both parts of the body wall were blotted on paper towel for 5 s and weighed.

At both study sites, sediment traps [each trap consisting of a double array of PVC canisters, (10 cm i.d., 50 cm high) following the design of Barnes and Edmonson (unpub. data)] were deployed under the culture rafts for 3 d during each sampling period, one trap at the same water depth as the experimental trays (“shallow” traps) and one trap below the experimental trays at ~2 m above sediment surface (“deep” traps) (Fig. 2). A total of six sediment traps were deployed (two at each of the three experimental rafts) at both sites. Particulate organic matter (POM) in the sediment traps from both sites was collected and kept on ice until frozen (-18 °C) at the laboratory prior to processing. Two deep sediment trap samples were lost in GH in January 2004 and one shallow sediment trap sample was lost in VB in November 2004.

2.4. Determination of organic matter, total organic carbon, total nitrogen, and C/N ratio

Samples of tray sediments and gut contents were thawed, weighed, and dried to a constant weight at 60 °C. For tray sediments, three replicate samples were taken from the dried material from each sample date. All samples were ground to

Table 1

ANOVA results for the fixed effects model for depth, site, and time on sedimentation rate, total organic carbon (TOC) deposition rate, total nitrogen (TN) deposition rate, and C/N ratio in shallow and deep sediment traps deployed under oyster culture rafts in Village Bay and Gorge Harbour from January to November 2004

Source of variation	Sedimentation rate				TOC deposition rate				TN deposition rate				C/N			
	df	MS	F	P	df	MS	F	P	df	MS	F	P	df	MS	F	P
Depth (De)	1	0.09	10.39	0.005	1	0.14	7.55	0.010	1	0.15	8.01	0.008	1	0.001	0.46	0.503
Site (Si)	1	0.02	1.89	0.517	1	0.08	4.10	0.052	1	0.07	3.54	0.070	1	0.13	90.92	<0.001
Time (Ti)	3	0.23	27.70	<0.001	3	0.51	27.90	<0.001	3	0.69	37.79	<0.001	3	0.03	20.40	<0.001
De×Si	1	0.00	0.41	0.568	1	0.05	0.92	0.346	1	0.02	0.88	0.356	1	0.001	0.91	0.347
De×Ti	3	0.01	1.32	0.409	3	0.04	0.84	0.482	3	0.03	1.47	0.244	3	0.001	0.86	0.472
Si×Ti	3	0.08	9.55	<0.001	3	0.13	3.04	0.045	3	0.08	4.18	0.014	3	0.02	13.78	<0.001
De×Si×Ti	3	0.02	2.30	0.286	3	0.06	1.65	0.200	3	0.04	1.93	0.147	3	0.002	1.07	0.379
Residual	29	0.01			29	0.01			29	0.02			29	0.001		
Total	45				45				45				45			

2.5. Statistical analysis of data

2.5.1. Sedimented material in traps

A mean value was calculated for each pair of sediment canisters and this trap mean became the replicate used in statistical analyses. Separate three-way ANOVAs were conducted to assess the effect of depth, site, and time on sedimentation rate, TOC deposition rate, TN deposition rate, and C/N ratio. TOC and TN deposition rates and C/N ratio data were \log_e transformed to obtain normality and homogeneity of variances prior to statistical analyses.

2.5.2. Sedimented material in trays and sea cucumbers

Separate three-way ANOVAs were conducted to assess the effect of tray (i.e. experimental or control), site, and time on TOC and TN concentration and C/N ratio in sedimented tray material. C/N ratio data required \log_e transformation to obtain homogeneity of variances.

A mean value was calculated for the six sea cucumbers in each tray and this tray mean became the replicate used in statistical analyses. Separate three-way ANOVAs were conducted to assess the effect of sediment position (tray sediment, foregut, or hindgut), site, and time on organic content (TOC+TN) in tray sediments on which sea cucumbers fed and on TN and C/N ratio (only foregut and hindgut for TN and C/N ratio). A *t*-test was used to compare the calculated assimilation efficiencies between VB and GH experimental sea cucumbers.

2.5.3. Sea cucumber growth

Growth of animals was analyzed for all sample periods using split weight and muscle and skin wet weights. Growth rates were calculated for increases and decreases in wet weights for sea cucumbers from both sites and are reported as an average (of the six sea cucumbers per tray) for the experimental trays sampled at each time period for both sites (i.e. “tray” is the replicate unit used in statistical analyses). Growth rates were calculated as:

$$(w_t - w_i) / t$$

where w_t is the mean weight (g) at the time of analysis, w_i is the initial weight (g), and t is the length of the growth period in days. The January 2005 data from GH are presented in the tables and figures, but were not included in data comparisons or statistical analyses since data for this sample period in VB were not taken.

Separate two-way ANOVAs were conducted to assess the effect of site and time on split weight, size index, and muscle and skin wet weights of sea cucumbers grown in trays. Growth data were transformed to \log_e to improve normality and homogeneity of variances.

For all data sets, normality was evaluated using the Shapiro–Wilk test and homogeneity of variances was evaluated using Levene’s test. Where there were significant interactions in the ANOVAs, treatment differences were assessed with a one-way ANOVA or *t*-tests (depending on number of treatments). Tukey tests were used to identify means that differed significantly, where appropriate. Data analyses were carried out using SPSS 12.0® (SPSS Inc., Chicago, IL, USA) for Windows.

3. Results

3.1. Water column characteristics

Water temperature in VB and GH followed a seasonal pattern, the lowest values being recorded from winter (January) to early spring (April) (Fig. 3). Water temperatures in VB and GH at a depth of 8.5 m ranged from a seasonal daily mean low of 6.6 °C and 6.3 °C in winter to a summer mean high of 18.4 °C and 18.3 °C, respectively. Salinities at the oyster rafts in VB and GH were 28.60‰ (8.6 m) and 28.75‰ (8.3 m) in January, 26.00‰ (8.5 m) and 26.80‰ (8.7 m) in April, and 29.00‰ (9.9 m) and 29.16‰ (10.1 m) in July 2004, respectively (P. Barnes, unpub. data). Mean chlorophyll concentrations around the oyster rafts, measured during the same environmental study and at the same depths given for salinities above, were 2.6 and 2.4 $\mu\text{g l}^{-1}$ in January, 4.3 and 4.7 $\mu\text{g l}^{-1}$ in April, and 3.4 and 3.5 $\mu\text{g l}^{-1}$ in July 2004 at VB and GH, respectively (P. Barnes, unpub. data).

3.2. Organic matter, total organic carbon, total nitrogen, and C/N ratio

3.2.1. Sedimented material in traps

Sedimentation rates were significantly affected by the factors depth and time and the interaction between site and time (Table 1). Sedimentation rates were significantly higher in shallow traps than in deep traps (Fig. 4). Sedimentation rates differed significantly across sample dates, but these differences were dependent on the interaction with site. For VB, rates were highest in April and were significantly higher in this month than in January or July. For GH, rates were highest in July and were significantly higher in this month than in January or November (Fig. 4).

Deposition rates of TOC were significantly affected by the factors depth and time and the interaction between site and time (Table 1). TOC deposition rate was significantly higher in shallow traps than in deep traps (Fig. 5A). TOC deposition rate varied seasonally [VB ($F_{3,23}=22.52$, $P<0.001$); GH ($F_{3,22}=11.02$, $P<0.001$)] with mean concentrations significantly lower in winter than in summer at both sites. Tukey tests showed that TOC deposition rate was significantly lower in January than in all other sampling periods at both study sites (Fig. 5A).

Deposition rates of TN were also significantly affected by the factors depth and time and the interaction between site and time (Table 1). TN deposition rate was significantly higher in shallow traps than in deep traps (Fig. 5B). The rate of TN deposition varied seasonally [VB ($F_{3,23}=30.33$, $P<0.001$); GH ($F_{3,22}=13.31$, $P<0.001$)] with mean concentrations significantly lower in winter than in summer at both sites. As with TOC deposition rates, Tukey tests revealed that TN

Table 2

ANOVA results for the fixed effects model for tray (experimental versus control), site, and time on sediment total organic carbon (TOC), total nitrogen (TN), and C/N ratio in trays deployed under oyster culture rafts in Village Bay and Gorge Harbour from January to November 2004

Source of variation	TOC				TN				C/N			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Tray (Tr)	1	1814.64	8.21	0.007	1	41.33	8.49	0.006	1	0.23	0.89	0.351
Site (Si)	1	124.69	0.56	0.457	1	1.59	0.33	0.571	1	0.06	0.23	0.632
Time (Ti)	2	1051.97	4.76	0.014	2	31.32	6.44	0.004	2	0.30	1.16	0.324
Tr × Si	1	2.36	0.01	0.918	1	0.08	0.02	0.900	1	0.34	1.32	0.258
Tr × Ti	2	523.93	2.37	0.106	2	14.97	3.08	0.057	2	0.17	0.67	0.520
Si × Ti	2	183.77	0.83	0.443	2	4.47	0.92	0.407	2	0.11	0.43	0.656
Tr × Si × Ti	2	35.92	0.16	0.851	2	0.06	0.01	0.987	2	0.24	0.95	0.397
Residual	40	221.99			40	4.87			40	0.26		
Total	52				52				52			

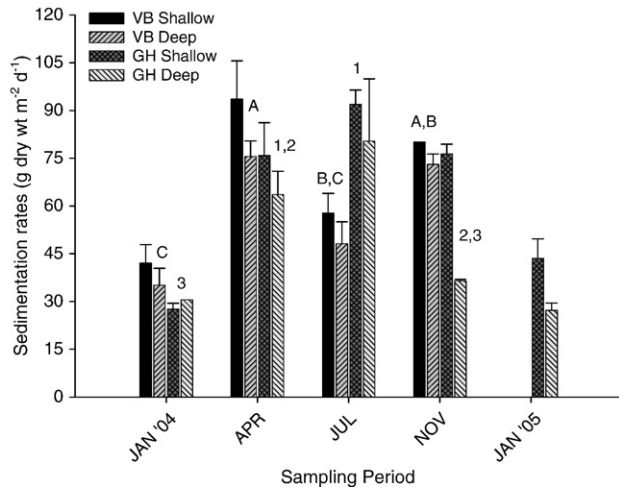


Fig. 4. Total particulate material sedimentation rate in shallow and deep sediment traps deployed under oyster culture rafts in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005. Data are means ($n=3$) for both shallow and deep traps in each sampling period and error bars indicate SE. Different letters and numbers above bars indicate significant ($P<0.05$) differences among times at VB and GH, respectively.

a uniform consistency with a mortar and pestle, which was acid-washed and dried in a drying oven at 109 °C for 10 min between samples. The ground samples were stored frozen (−18 °C) in muffled scintillation vials until determination of organic matter and total organic carbon (TOC) and total nitrogen (TN) content. The frozen samples were subdivided for determination of organic matter content (50 mg) and TOC and TN (30 mg). The organic matter content was measured as weight loss on ignition at 475 °C for 6 h in a muffle furnace. The differences between the organic content of the hindgut and foregut samples (mg) were assumed to be equal to the quantity of organic matter removed per gram of dry material during passage through the digestive tract (Yingst, 1976). TOC and TN were determined by high-temperature combustion using a Carlo Erba NA-1500 Elemental Analyzer (CE Elantech, Inc., Lakewood, NJ, USA), with acetanilide as a standard (Verardo et al., 1990). TOC was calculated as the difference between the total carbon content and inorganic carbon content obtained from the analysis of calcium carbonate using a Model 5011 (or Model CM5014) CO₂ Coulometer (UIC, Inc., Instruction Manual for CO₂ Coulometer 1985 (1999)). All TOC and TN data were converted to percentages of total dry weight of sample. The TOC and TN weight data were used to calculate a TOC/TN ratio, referred to throughout the text as C/N ratio.

The efficiency with which the organic carbon present in the oyster biodeposits was utilized by the experimental animals was determined by comparing the fraction of organic matter in the foregut with that in the hindgut (Conover, 1966). It is assumed that the organic component of the food in the foregut is the only fraction significantly affected by the digestive process and that the inorganic component is insoluble and passes through the gut unaltered. The assimilation efficiency was calculated as follows:

$$U' = [(F' - E') / (1 - E') F'] \times 100$$

where F' is the ash-free dry weight (AFDW)/dry weight (DW) ratio of the ingested food in the foregut, and E' is the AFDW/DW ratio of the egested material in the hindgut (Conover, 1966).

To compare TOC and TN in the sediment trap samples, the contents from the bottom of each trap were thawed, poured into acid-washed 50-ml polycarbonate centrifuge tubes, and centrifuged at 4000 rpm for 30 min at room temperature (M. Soon, University of British Columbia, pers. comm.). Seawater overlying the sediment pellet was removed by vacuum filtration and the remaining sediment pellet was scraped into acid-washed crucibles and 2 ml of 0.2- μ m filtered seawater was added to remove any remaining particles on the tube walls. The additional seawater in the crucibles was removed by vacuum filtration. The sediment samples were dried to a constant weight at 60 °C and ground to a uniform consistency and stored frozen (−18 °C) in muffled scintillation vials

until analysis of TOC and TN using the methods described above for the gut contents. The filtrate from the sediment trap samples was not analyzed for dissolved components due to the small contribution from the dissolved fraction, which adds little to the overall total organic content (M. Soon, University of British Columbia, pers. comm.). Sediment trap deposition rates of TOC and TN were estimated as the product of sedimentation rates and their chemical elements (i.e. carbon or nitrogen). The TOC and TN data were used to calculate a TOC/TN ratio, referred to herein as a C/N ratio.

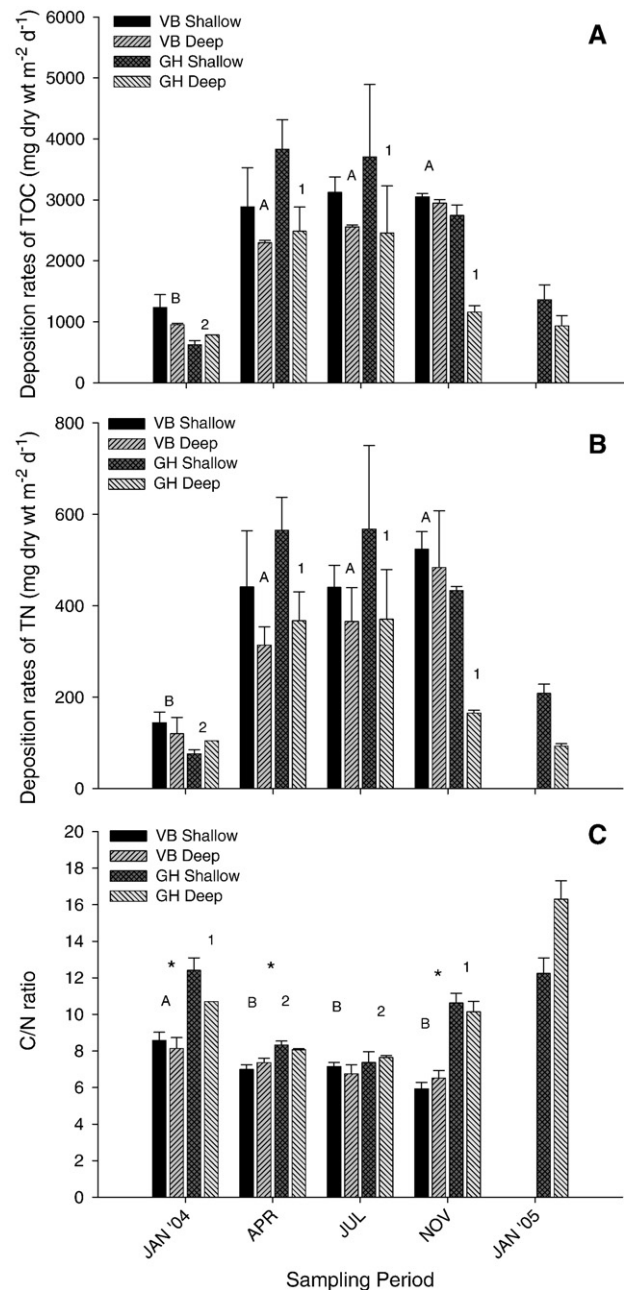


Fig. 5. (A) Total organic carbon (TOC) deposition rate, (B) total nitrogen (TN) deposition rate, and (C) C/N ratio in shallow and deep sediment traps deployed under oyster culture rafts in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005. Data are means ($n=3$) for both shallow and deep traps in each sampling period and error bars indicate SE. * indicates a significant ($P<0.05$) site effect within sampling period. Different letters and numbers above bars indicate significant ($P<0.05$) differences among times at VB and GH, respectively.

deposition rate was significantly lower in January than in all other sampling periods at both study sites (Fig. 5B).

Mean C/N values were significantly affected by the factors site and time and the interaction between site and time (Table 1). In comparing sites at each sampling period, C/N ratios in VB were significantly lower than those in GH in all sampling periods but July [January ($t_{0.05,3} = -4.90$, $P < 0.05$); April ($t_{0.05,5} = -3.78$, $P < 0.05$); November ($t_{0.05,4} = 17.86$, $P < 0.001$)] (Fig. 5C). C/N ratios varied seasonally [VB ($F_{3,23} = 9.20$, $P < 0.001$); GH ($F_{3,22} = 35.82$, $P < 0.001$)] with mean

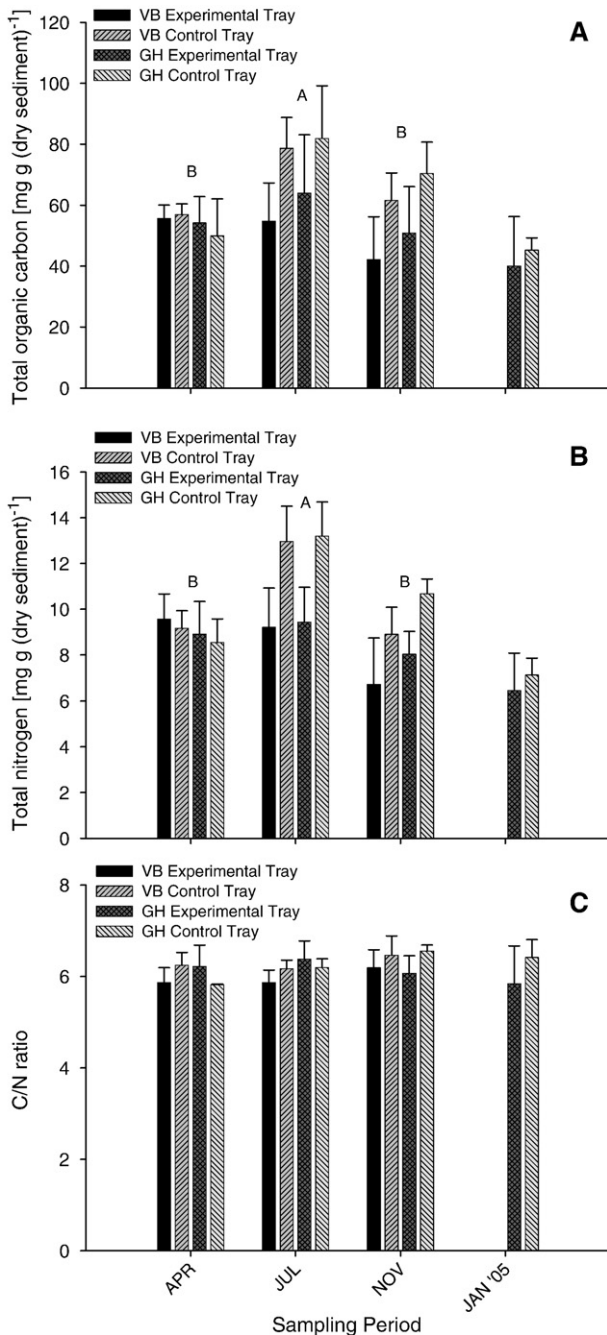


Fig. 6. (A) Total organic carbon (TOC), (B) total nitrogen (TN), and (C) C/N ratio of sediments collected in experimental and control trays deployed under oyster culture rafts in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005. Data are means from the three rafts ($n=3$) in each sampling period and error bars indicate SE. Different letters above bars indicate significant ($P < 0.05$) differences among times at both sites.

concentrations significantly higher in winter than in summer at both sites. Tukey tests showed that C/N ratios in VB were significantly higher in January than in any other month. For GH, C/N ratios were significantly higher in January and November than in April and July (Fig. 5C).

3.2.2. Sedimented material in trays and sea cucumbers

TOC of sediment deposited in the trays was significantly affected by the factors tray (experimental versus control) and time (Table 2). Sediment TOC was significantly lower in trays with sea cucumbers (experimental) than those without (control) (Fig. 6A). For VB and GH, sediment TOC was highest in July and this was significantly higher than in April and November (Fig. 6A).

TN of sediment deposited in the trays was also significantly affected by the factors tray (experimental versus control) and time (Table 2). Sediment TN was significantly lower in trays with sea cucumbers (experimental) than those without (control) (Fig. 6B). For VB and GH, sediment TN was highest in July and this was significantly higher than in April and November (Fig. 6B). C/N ratios in the tray sediments were not significantly affected by any experimental factors (Table 2, Fig. 6C).

The organic content (TOC + TN) of sediment from the trays and fore- and hindguts of sea cucumbers was only significantly affected by the factor position (tray, foregut, or hindgut) (Table 3). The organic content of foregut sediment from sea cucumbers feeding in the trays at both VB and GH was significantly higher than that of the hindgut, whereas the organic content of the tray sediment was significantly lower than that of both the fore- and hindguts at both sites (Table 4). The efficiency with which sediments in the trays from VB and GH (containing an average of 5.93% and 5.92% organic matter, respectively) were utilized (39.10% and 41.70%, respectively) did not differ significantly from each other ($t_{0.05,16} = 0.56$, $P = 0.580$) (Table 4).

TN content of sediment from the fore- and hindguts of sea cucumbers was significantly affected by the factor position (foregut or hindgut) and the interaction between position and time (Table 3). TN content was significantly higher in the foregut than in the hindgut in all sampling periods (Table 5).

C/N ratios of sediment were significantly affected by the factors position and site and the interaction between site and time (Table 3). C/N ratios were significantly lower in the foregut than in the hindgut (Table 5). In November, C/N ratios in the foreguts and hindguts of sea cucumbers in GH were significantly lower than those of sea cucumbers in VB ($t_{0.05,2} = 4.83$, $P < 0.05$) (Table 5). There were no other significant differences between sites in any other sampling periods.

There was an obvious reduction in feeding activity of the holothurians in November. Among the animals from the trays, only 25% of the sea cucumbers from either site were seen to produce faecal pellets. At both sites, sediment was absent in the digestive tract of 66.7% of holothurians from the trays. Most of these animals lacked internal organs (e.g. gonad, circulatory system, and respiratory trees), the intestines had not completely degenerated but were reduced in length and diameter, and the colour was a dull yellow-brown. In January 2005, the majority (76.5%) of holothurians harvested from the trays in GH had regenerated their digestive tract and internal organs and had resumed feeding, as evidenced by sediment in the gut.

3.3. Sea cucumber growth and survivorship

Split weight (g) of experimental sea cucumbers was significantly affected by the factors site and time and the interaction between site and time (Table 6). Individual comparisons (t -tests) between sites at each sampling period, however, failed to reveal any significant site differences (Fig. 7). Split weight in both VB and GH peaked in July. In VB, split weight in July was significantly higher than in any other

Table 3

ANOVA results for the fixed effects model for sediment position (tray, foregut, or hindgut), site, and time on organic content (total organic content (TOC)+total nitrogen (TN)), TN, and C/N ratio of sediment from the experimental trays or from the foregut and hindgut of *Parastichopus californicus* cultured under oyster culture rafts in Village Bay and Gorge Harbour from January to November 2004

Source of variation	Organic content (TOC+TN) (tray, foregut, and hindgut)				TN (foregut and hindgut)				C/N (foregut and hindgut)			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Position (P)	2	1.20	101.42	<0.001	1	34.10	107.37	<0.001	1	1.66	17.31	<0.001
Site (Si)	1	0.02	1.97	0.170	1	1.14	3.59	0.071	1	0.47	4.90	0.037
Time (Ti)	2	0.01	0.94	0.400	2	0.39	1.22	0.314	2	0.09	0.88	0.427
P×Si	2	0.001	0.08	0.922	1	0.01	0.03	0.864	1	0.03	0.35	0.562
P×Ti	4	0.02	1.67	0.179	2	1.96	6.18	0.007	2	0.26	2.72	0.087
Si×Ti	2	0.01	0.74	0.486	2	0.44	1.38	0.271	2	0.75	7.82	0.003
P×Si×Ti	4	0.001	0.10	0.983	2	0.05	0.17	0.843	2	0.05	0.53	0.597
Residual	35	0.01			23	0.32			23	0.10		
Total	53				35				35			

Table 4

Percent organic content (total organic carbon+total nitrogen) of tray sediment and material in foregut and hindgut, and assimilation efficiency of organic matter ingested by *Parastichopus californicus* cultured under oyster culture rafts in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005

Sampling period	Site	% Organic content			% Assimilation efficiency
		Tray sediment (mean±SE)	Foregut (mean±SE)	Hindgut (mean±SE)	(mean±SE)
April 2004	VB	6.52±0.54	29.93±1.95	13.79±2.07	57.87±4.06
	GH	6.31±0.63	27.96±1.43	14.83±1.80	30.27±11.30
July 2004	VB	6.40±1.43	25.69±1.44	14.56±1.75	45.77±22.53
	GH	6.99±1.26	26.54±1.10	15.98±0.90	50.70±12.55
November 2004	VB	4.89±1.60	21.09±2.66	15.72±1.47	14.17±6.53
	GH	2.94±0.99	25.70±1.59	16.17±2.78	57.86±25.80
January 2005	GH	4.65±1.78	14.83±2.26	9.85±2.53	27.97±6.41
Overall mean	VB	5.93±0.53	25.57±2.55	14.69±0.56	39.10±12.91
	GH	5.92±0.57	23.76±3.48	14.21±1.71	41.70±8.57

Data are means of tray means ($n=3$, ±SE) for both sites at each sampling period.

Table 5

Percent total organic carbon (TOC %), percent total nitrogen (TN %), and C/N ratio of foregut and hindgut contents of *Parastichopus californicus* feeding on organic matter deposited in trays in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005

Sampling period	Site	Foregut			Hindgut		
		TOC (%) (mean±SE)	TN (%) (mean±SE)	C/N (mean±SE)	TOC (%) (mean±SE)	TN (%) (mean±SE)	C/N (mean±SE)
April 2004	VB	24.73±1.63	5.20±0.35	4.76±0.14	11.41±1.50	2.17±0.36	5.50±0.28
	GH	22.94±0.85	5.02±0.58	4.96±0.17	12.45±1.50	2.32±0.25	5.79±0.21
July 2004	VB	21.47±1.21	4.22±0.24	5.10±0.02	12.27±1.48	2.29±0.27	5.37±0.09
	GH	22.05±0.86	4.49±0.24	5.01±0.11	13.46±0.78	2.66±0.01	5.21±0.18
November 2004	VB	11.65±1.97	3.49±0.49	5.46±0.22	13.33±1.31	2.39±0.17	5.95±0.24
	GH	21.32±1.26	4.38±0.37	4.89±0.22	13.48±2.29	3.05±0.08	4.79±0.07
January 2005	GH	12.10±1.99	2.57±0.25	4.28±0.39	8.16±2.09	1.58±0.31	4.86±0.13
Overall mean	VB	21.27±2.06	4.30±0.49	5.10±0.20	12.34±0.56	2.28±0.06	5.61±0.18
	GH	19.26±2.48	4.12±0.02	4.78±0.20	11.87±1.74	2.40±0.36	5.21±0.24

Data are means of tray means ($n=3$, ±SE) for both sites at each sampling period.

Table 6

ANOVA results for the fixed effects model for site and time on split weight, size index, and muscle and skin wet weight data from *Parastichopus californicus* grown under oyster culture rafts in Village Bay and Gorge Harbour from January to November 2004

Source of variation	Split weight				Size index				Muscle wet weight				Skin wet weight			
	df	MS	F	P	df	MS	F	P	df	MS	F	P	df	MS	F	P
Site (Si)	1	0.01	7.07	0.017	1	0.04	5.01	0.040	1	0.05	18.70	0.001	1	0.02	13.1	0.002
Time (Ti)	3	0.44	253.10	<0.001	3	0.44	60.9	<0.001	3	0.41	165.27	<0.001	3	0.25	178.5	<0.001
Si×Ti	3	0.01	7.17	0.003	3	0.08	10.7	<0.001	3	0.01	3.73	0.045	3	0.01	9.52	0.001
Residual	16	0.002			16	0.007			16	0.003			16	0.001		
Total	24				24				24				24			

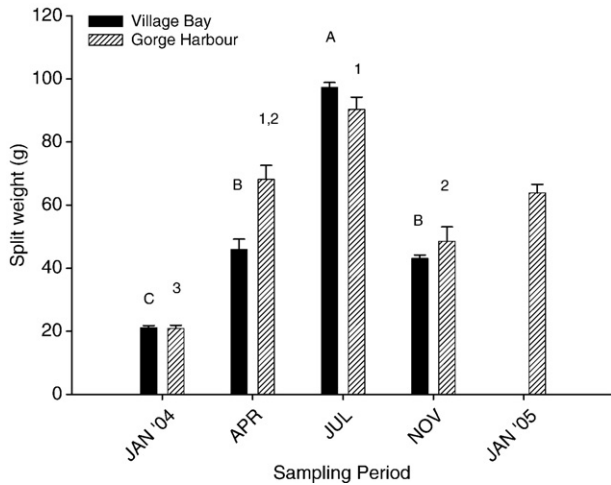


Fig. 7. Mean split weights of *Parastichopus californicus* grown in trays under oyster culture rafts in Village Bay and Gorge Harbour from January 2004 to January 2005. Data are means from the three rafts ($n=3$) for each site at each sampling period and error bars indicate SE. Different letters and numbers above bars indicate significant ($P<0.05$) differences among times at VB and GH, respectively.

sampling period while in GH split weight in July was significantly higher than in January and November but not significantly different from April (Fig. 7). After a full 12 months of growth, split weight at GH differed significantly among the sampling periods ($F_{4,15}=83.67$, $P<0.001$). A Tukey test revealed that split weight was significantly higher in January 2005 than in January 2004. For the period January–July 2004, the average increase in split weight in VB was 0.42 g d^{-1} (± 0.10) while the average increase in GH was 0.38 g d^{-1} (± 0.05). A seasonal effect was observed with the growth rate becoming negative in the fall and winter. The overall mean growth rate of sea cucumbers during the 10 and 12 month growth periods in VB and GH, including the period with negative growth, was 0.08 g d^{-1} (± 0.01) and 0.12 g d^{-1} (± 0.02), respectively. There were no sea cucumber mortalities in any of the trays deployed at either site during the study.

Sea cucumber size index (SI) was significantly affected by the factors site and time and the interaction between site and time (Table 6). In comparing sites at each sampling period, sea cucumbers in VB were significantly larger than those in GH in July ($t_{0.05,2}=4.77$, $P<0.05$), but there were no other significant site comparisons within sample periods (Table 7). One-way ANOVAs on sample date within both sites revealed significant effects of sample date on SI [VB ($F_{3,12}=47.37$, $P<0.001$); GH ($F_{3,12}=15.32$, $P<0.001$)]. Animals from VB were significantly larger in July than in January, April, or November (Table 7). There were no significant differences in SI for animals from GH collected in April,

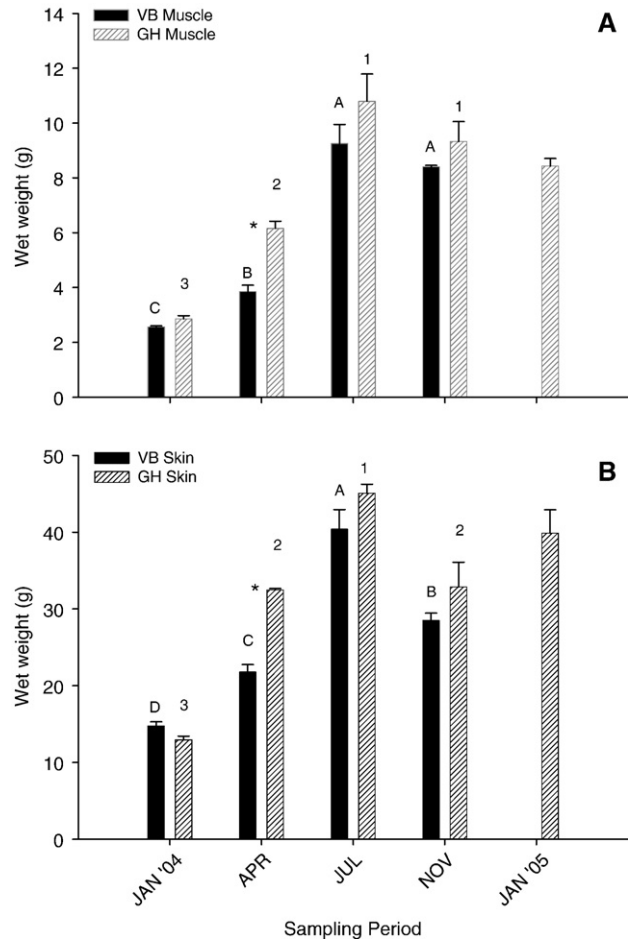


Fig. 8. Mean (A) muscle wet weights and (B) skin wet weights of *Parastichopus californicus* grown in trays under oyster culture rafts in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005. Data are means from the three rafts ($n=3$) for each site at each sampling period and error bars indicate SE. * indicates a significant ($P<0.05$) site effect within sampling period. Different letters and numbers above bars indicate significant ($P<0.05$) differences among times at VB and GH, respectively.

July, or November, but animals were significantly bigger in these 3 months than in January (Table 7).

Muscle wet weight (g) of sea cucumbers was significantly affected by site and time and the interaction between these two factors (Table 6). In comparing sites at each sampling period, muscle wet weights were significantly higher in GH than in VB in April ($t_{0.05,2}=-4.95$, $P<0.05$), but there were no other significant site comparisons at any other date

Table 7

Mean size of *Parastichopus californicus* grown in trays in Village Bay (VB) and Gorge Harbour (GH) from January 2004 to January 2005

Sampling period	Site	Contracted length (cm) (mean \pm SE)	Contracted width (cm) (mean \pm SE)	Animal size index (mean \pm SE)
January 2004	VB	9.56 \pm 0.62	2.62 \pm 0.06	0.11 \pm 0.02 ^C
	GH	10.39 \pm 0.26	2.70 \pm 0.14	0.25 \pm 0.01 ²
April 2004	VB	15.66 \pm 0.29	3.14 \pm 0.17	0.41 \pm 0.07 ^B
	GH	17.76 \pm 0.49	3.32 \pm 0.16	0.50 \pm 0.07 ¹
July 2004	VB	19.40 \pm 0.57	4.97 \pm 0.18	0.86 \pm 0.02 ^A
	GH	15.45 \pm 1.09	5.13 \pm 0.20	0.65 \pm 0.02 ^{1*}
November 2004	VB	12.27 \pm 0.58	4.10 \pm 0.19	0.48 \pm 0.02 ^B
	GH	11.09 \pm 0.49	3.96 \pm 0.14	0.43 \pm 0.02 ¹
January 2005	GH	11.85 \pm 0.28	4.82 \pm 0.15	0.56 \pm 0.05

Data are means of tray means ($n=3$, \pm SE) for each sampling period. Superscripted letters and numbers next to animal size index indicate significant differences among times within VB and GH, respectively. * indicates a significant site effect within sampling period.

(Fig. 8A). One-way ANOVAs of sample date within both sites revealed significant effects of sample date on muscle wet weight [VB ($F_{3,12}=93.97$, $P<0.001$); GH ($F_{3,12}=75.73$, $P<0.001$)]. Muscle wet weights of sea cucumbers grown in trays peaked in July at both sites and were significantly higher in July and November than in January and April 2004 (Fig. 8A). **The average muscle growth rate between January and July 2004 was the same for both sites, averaging 0.04 g d^{-1} (± 0.01).**

Body wall (skin) wet weight (g) of these same holothurians was also significantly affected by the factors site and time and the interaction between site and time (Table 6). In comparing sites at each sampling period, sea cucumbers in VB had significantly lower skin wet weight than those in GH in April ($t_{0.05,2}=-8.52$, $P<0.05$), but there were no other significant site comparisons at any other date (Fig. 8B). One-way ANOVAs of sample date within both sites revealed significant effects of sample date on body wall wet weight [VB ($F_{3,12}=101.89$, $P<0.001$); GH ($F_{3,12}=83.63$, $P<0.001$)]. All pair-wise comparisons among sample dates in VB and GH were significant except for April and November in GH (Fig. 8B). **For the period January–July 2004, the average growth rate in skin wet weight in VB was 0.14 g d^{-1} (± 0.04) whereas the average increment in GH was 0.18 g d^{-1} (± 0.03).**

4. Discussion

4.1. Total particulate deposition in Village Bay and Gorge Harbour

Seasonal changes in sedimentation rates and TOC and TN deposition are related to biodeposits produced by the cultured oysters, which have been found to correspond to water temperature and Chl *a* concentrations (Kautsky and Evans, 1987; Hatcher et al., 1994; Hayakawa et al., 2001). High rates of biodeposition from oysters have been shown to coincide with periods of higher water temperatures (Loosanoff, 1958; Haven and Morales-Alamo, 1966). Increased feeding activity of oysters in British Columbia occurs between the end of May and mid-September (Quayle, 1969). Mean sedimentation rates in GH peaked ($91.9 \text{ g dry wt m}^{-2} \text{ d}^{-1}$) in July when water temperature was $15.1 \text{ }^\circ\text{C}$ (8.5 m) and chlorophyll concentration was $3.5 \mu\text{g l}^{-1}$ (10.1 m). Sedimentation rates in VB were also high in July ($57.8 \text{ g dry wt m}^{-2} \text{ d}^{-1}$). High rates of sedimentation ($23 \text{ g dry wt m}^{-2} \text{ d}^{-1}$) from oyster rafts were observed by Hayakawa et al. (2001) when chlorophyll concentrations were elevated in the 0–5 m layer between May and mid-September. They reported that total means ranged from 2.9 to $11 \text{ g dry wt m}^{-2} \text{ d}^{-1}$ among stations in the Ofunato estuary, Japan.

During the present study, a general pattern of decreasing sedimentation with increasing water depth was found at both study sites. Sedimentation rates in GH were significantly lower at 24 m than at 8.5 m. Patterns of TOC and TN deposition have been reported to decrease with depth (Lampitt et al., 1990; González et al., 2000; Garcia-Ruiz et al., 2001). **The difference between sedimentation rates at the different depths observed in the present study suggests that dispersion by water currents is an important factor (Hayakawa et al., 2001).**

In this study, the TOC content represents only a small fraction of the particulate material in the sediment traps. Depending on season, the TOC content of the shallow sediment trap samples ranged from a low of 22.5 mg g^{-1} in winter to a high of 54.6 mg g^{-1} in summer. These values are slightly lower but comparable

with the TOC content ($65\text{--}76 \text{ mg g}^{-1}$) of sediment trap samples from oyster rafts in Japan (Hayakawa et al., 2001). Kusuki (1977) reported TOC values of $30\text{--}120 \text{ mg g}^{-1}$ and TN values of $4\text{--}15 \text{ mg g}^{-1}$ for biodeposits of *C. gigas* (cf. Hayakawa et al., 2001). Mean TN values for sediment in the shallow traps in the present study ($6.14\text{--}9.97 \text{ mg g}^{-1}$) are comparable with other TN values reported for biodeposits of *C. gigas* ($4\text{--}15 \text{ mg g}^{-1}$) (Kusuki, 1977).

Mean C/N ratios of particulate material in the sediment trap samples from VB and GH throughout this study ranged between 5.9 and 12.4 and may be considered to be of high nutritional value. C/N ratios between 4 and 8 indicate phytoplankton, faecal material, and other easily degraded material of high nutritional value (Kautsky and Evans, 1987), whereas C/N ratios of 10 or greater characterize detritus, sediment, and other mineralized material of low nutritional value (Strickland, 1960; Parsons et al., 1977). The C/N ratios reported here fall into the range of previously measured C/N ratios of biodeposits from other suspension-feeding bivalves (e.g. mussels) (Miller et al., 2002; Giles and Pilditch, 2004).

Nutritional enrichment of faeces and pseudofaeces is provided by the attachment of micro-organisms (Newell, 1965). Bacteria colonizing faecal material will increase the nitrogen content and lower the C/N ratio of this potential food resource (Kautsky and Evans, 1987). The nitrogen content of food is an important indicator of its nutritional value (Russel-Hunter, 1970; Boyd and Goodyear, 1971; Kautsky and Evans, 1987). Consumption and assimilation of faecal material by *P. californicus* is likely related to the bacteria associated with this material, which makes it a desirable food source for the sea cucumbers (Newell, 1965; Hauksson, 1979; Stuart et al., 1982). Relatively low C/N ratios (~ 6) in the experimental tray sediments may be explained by a high bacterial content as shown by the TN content of the sediment. Sea cucumbers in the trays selected and digested organic matter with a high nitrogen content as shown by the significantly higher TN values and lower C/N ratios in the foregut than the hindgut.

Deposit-feeding holothurians feed mainly on bacteria associated with organic material as well as diatoms, cyanophytes, and foraminifera (Bakus, 1968; Moriarty, 1982; Yingst, 1982). It appears that holothurians assimilate micro-organisms with higher efficiency than organic detritus in the sediments (Fenchel, 1972; Yingst, 1976). Bacteria and nitrogenous components of organic matter have been shown to be an important food source for *Holothuria atra* and *Stichopus tremulus* (Moriarty, 1982). Moriarty (1982) showed that values for organic carbon and nitrogen and muramic acid (bacteria) were generally lower in the hindgut than in the foregut due to digestion and assimilation. Sediment enriched by bacteria has also been suggested to be an important source of food for *Actinopyga mauritiana* (Ramofafia et al., 1997) and for *S. tremulus* (Hauksson, 1979). It appears, therefore, that particulate organic matter settling from the oyster rafts, containing oyster biodeposits rich in organic carbon and nitrogen, constitutes a major potential food source for *P. californicus*.

4.2. Organic content and holothuroid assimilation efficiency

Assimilation efficiencies of sea cucumbers in the field cannot be measured precisely because it is difficult to provide the animals

with diets of known organic composition (Yingst, 1976; Moriarty, 1982). The assimilation efficiencies of *P. californicus* in the present study were calculated using the composition of the foregut and hindgut on the assumption that most of the ash content of the diet is insoluble and therefore passes through the digestive tract unaltered so that it can be compared with the organic materials being digested (Conover, 1966). Data in the literature indicate that, for several species of holothurians, very little change in the inorganic material occurs during digestion (Hammond, 1981; Moriarty, 1982). Hammond (1981) used alkalinity measurements to show that less than 0.25% of ingested inorganic material was dissolved in the gut of holothurians. Moriarty (1982) reported that no statistically significant differences in carbonate content could be determined between foregut and hindgut. This is consistent with the carbonate data determined between the fore- and hindguts of sea cucumbers in the present study.

The organic content (TOC and TN) of sediment found in the foregut of animals in the present study was significantly higher than that in the trays and reflects the capacity of *P. californicus* to selectively ingest organic matter from the sediments. Ahlgren (1998) showed that *P. californicus*, feeding in its natural habitat, selectively ingests organic material. While *P. californicus* appears to selectively ingest organics, the closely-related species *P. parvimensis* does not seem to selectively ingest organic matter from shallow subtidal sediment (Yingst, 1974, 1982).

The overall efficiency with which organic material deposited in the trays was assimilated by *P. californicus* in the present study was higher than the 24.3% ($\pm 2.3\%$ SE) assimilation efficiency reported by Ahlgren (1998) for the utilization by *P. californicus* of organic material in salmon net-pen fouling. Assimilation efficiencies of holothurian deposit feeders are reported as generally being close to 30% (Hauksson, 1979). The ranges of assimilation efficiencies in the present study overlap somewhat with those in the literature but the overall efficiencies are higher than the 21.2% ($\pm 11.3\%$ SD) and 26.8% ($\pm 11.1\%$ SD) efficiencies with which *P. parvimensis* (Yingst, 1976) and *S. tremulus* (Hauksson, 1979), respectively, utilize organic matter in bottom sediments. The efficiency with which deposit feeders assimilate organic matter in the sediments is related to its quality or composition of the sediment (Yingst, 1976, 1982; Hauksson, 1979) and may also be influenced by seasonal differences in the quantity of organic matter in the sediments (Hauksson, 1979). Seasonal variations in the quantity and quality of organic matter may affect assimilation efficiencies, but this has not been examined for any deposit-feeding holothurian.

4.3. Sea cucumber growth

Despite the economic importance of sea cucumbers in many coastal areas, very few papers report on growth rates of sea cucumbers. The few such that are available are mainly on tropical species either in the field (Ebert, 1978; Shelley, 1981, 1985; Conand, 1988) or reared in land-based tanks (Ramofafia et al., 1997; Battaglione et al., 1999).

Growth of *P. californicus* is thought to be slow, taking from 4 to 5 years for an adult weight of 500 g to be reached (Department of Fisheries and Oceans Canada, 1999). Market size of commer-

cially-harvested sea cucumbers ranges from 218 to 489 g (split weight — viscera and internal fluids removed) (Department of Fisheries and Oceans Canada, 1999). Sea cucumbers grown in trays did not reach market size by the end of this field study. Average final split weights for sea cucumbers were 43.6 g (after 10 months) and 63.8 g (after 12 months) for VB and GH, respectively. Since age of recruitment to the fishery is thought to be at least 4 years (Department of Fisheries and Oceans Canada, 1999), it is estimated that sea cucumbers grown below the oyster farms would require 3 to 4 years to reach market size. A previous study that evaluated parameters for sea cucumber (*P. californicus*) aquaculture and enhancement in British Columbia showed that growth was positive during 2 years in suspended and on-bottom cages and indicated that the low end of market size (368 g round weight or 211 g split weight) could be reached after the third year (Sutherland, 1999). However, evaluation by commercial sea cucumber processors indicated that these animals, as well as the ones from our study, were not of acceptable quality due to their small size. The small size makes the muscle meat more time consuming and costly to remove (Paddy Wong, Paladin International Seafood Sales Ltd., pers. comm.).

P. californicus showed a seasonal change in its feeding behaviour. Seasonal feeding activity in the field has been previously reported for several species of holothurians (Tanaka, 1958; Swan, 1961; Mosher, 1965; Jespersen and Lützen, 1971; Dimock, 1977; Yingst, 1982; Fankboner and Cameron, 1985; Singh et al., 1999). The annual reduction in feeding activity by *P. californicus* is associated with annual resorption of the gut in the fall or winter, animals becoming dormant until regeneration of the gut (Yingst, 1982; Fankboner and Cameron, 1985). These holothurians do not completely regenerate their digestive tract for approximately 2 months, although feeding commences after 3 to 4 weeks once minimal gut connection is formed (Yingst, 1982).

Little is known about the factors that induce seasonal feeding activity (i.e. visceral atrophy) in holothurians (Singh et al., 1999). Occurrence of seasonal visceral atrophy and the resulting seasonal feeding behaviour might be influenced by changes in temperature, day length, and/or food availability/quality; however, there are no clear data on the potential factors that may induce such behaviour (Byrne, 1985; Fankboner and Cameron, 1985). The observed seasonal change in feeding behaviour of *P. californicus* in the trays in November 2004 coincided with significantly higher amounts of sediment in the experimental trays (674.5 g dry wt), but with significantly lower organic content (50.9 mg g⁻¹ dry sediment), suggesting that *P. californicus* may have been responding to the quality (i.e. organic content) rather than the quantity of sediment in the trays.

Food quality can influence the composition of the body wall (Ahlgren, 1998). Sea cucumbers from VB and GH lost 29% and 27% of their body wall (i.e. skin) wet weight between July and November, respectively. Autumnal visceral loss and shrinkage of the body wall have been reported in the commercially-harvested western Pacific sea cucumber *S. japonicus* (Tanaka, 1958; Suguri, 1965). Body wall wet weight is known to fluctuate seasonally (Ahlgren, 1998) and has been reported to reach its lowest values immediately prior to visceral regeneration (Fankboner and Cameron, 1985). The body wall of these thick-skinned holothurians

functions as a nutrient reserve, mainly for proteins (Prim et al., 1976). Although data were unavailable for VB, skin wet weight of sea cucumbers from GH showed an increase in January 2005, supporting the view that sea cucumbers recover weight in their body wall when feeding activity resumes (Fankboner and Cameron, 1985). Shrinkage of the body wall, which exceeded 25%, also suggests a nutrient factor regulating visceral atrophy in *P. californicus* (Fankboner and Cameron, 1985).

4.4. Feasibility of a commercial-scale Pacific oyster and California sea cucumber co-culture system

Limited knowledge of holothurian growth rates and the various methods used to measure weight and length make it difficult to interpret the growth of *P. californicus* in this study. However, 100% survival and positive growth rates at VB and GH do support a case for the feasibility of successful culture of this commercially important species in IMTA systems. Growth rates obtained for *P. californicus* in the trays indicated that the biodeposits and other sedimented material (and the associated micro-organisms) were a good food source (i.e. rich in carbon and nitrogen) for the sea cucumbers.

Biodeposition from suspended bivalve culture has been demonstrated to increase local deposition of organic matter to the benthos (Kautsky and Evans, 1987; Jaramillo et al., 1992; Hatcher et al., 1994; Chamberlain et al., 2001). Increased organic sedimentation may lead to carbon and nitrogen accumulation in the sediments, followed by increased oxygen consumption, anoxia, and denitrification (Kaspar et al., 1985). The resulting changes in the characteristics of the sediments under the farms may select for species that are more tolerant of finer textured sediments of high organic content (Tenore et al., 1982). The ability of *P. californicus* to utilize oyster biodeposits suggests that sea cucumbers can thrive in these areas with higher nutrient input. Ahlgren (1998) demonstrated that *P. californicus* is capable of using salmon net-pen fouling composed of fish faeces, excess fish food, algae, and other particulate organic material. This provides evidence that sea cucumbers would be a good candidate for culture in IMTA systems with either cultured finfish or filter-feeding shellfish. The natural occurrence of sea cucumbers on oyster culture strings and below the farms also makes them appealing for IMTA systems with oysters.

Most simply put, IMTA attempts to rear two or more compatible aquatic species together and has the objective of maximizing production using organisms that make use of various feeding levels and niches (Bardach, 1986; Folke and Kautsky, 1992). Integrated coastal aquaculture includes elements that reduce the dependency on external environments for food and energy, reduce waste nutrients among the culture components, assist in utilizing nutrients efficiently, and increase stability of the systems by reducing potential environmental impacts and producing multiple market products (Folke and Kautsky, 1992). Placement of sea cucumbers in productive habitats with higher nutrient loads to utilize the waste particulate material from organisms of different trophic levels may reduce the potential environmental impacts of aquaculture operations. Culturing sea cucumbers with oysters has the potential to increase efficiency in the utilization of the energy initially

introduced into the aquaculture system and could result in increased productivity and diversification in the rearing of commercially important species (Tenore et al., 1974).

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