

Impacts of dense crab populations on carbon exchanges across the surface of a salt marsh

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ABSTRACT: Laboratory mesocosm experiments were conducted to quantify the effects of 2 crab species, *Sesarma catenata* and *Cleistostoma edwardsii*, on carbon exchanges across the surface of a south temperate salt marsh. The grapsoid crab *S. catenata* was most abundant in the vegetated marsh flats, and the ocypodoid *C. edwardsii* in the unvegetated tidal creek. Replicate mesocosms of the marsh flats and tidal creek were incubated with and without crabs of the species dominant in that region. Both species enhanced the losses of carbon relative to uptake by the marsh, but they did so via different mechanisms. In the tidal creek, *C. edwardsii* increased the net fluxes of total organic carbon (TOC) by 60 % (or 448 mg C m⁻² d⁻¹), but had no significant impact on community net production (NP). (Bioturbation accounted for 95 % of the enhanced TOC fluxes, and excretion only 5 %). In the marsh flats, *S. catenata* had no measurable impact on the fluxes of TOC, but decreased community NP by 1132 mg C m⁻² d⁻¹ (Ninety-two percent of this reduction was caused through reduction in epibenthic NP through crab grazing of microalgae. Crab respiration accounted for only 8 % of the reduction). The crab effects were sufficient to determine whether, for a tide of a particular tide elevation, the marsh functioned as a carbon source or sink. When crabs were absent, the marsh functioned as a carbon sink at all except the very highest tides that, in turn, accounted for only 3 % of all tides inundating the marsh. When crabs were present, the marsh functioned as a carbon source at 87 %, and all except the very lowest tides.

INTRODUCTION

Crabs are among the most abundant and conspicuous macroinvertebrates on salt marshes. Their population densities can be high, exceeding 500 ind. m⁻² (Krebs & Valiela 1978), with biomasses greater than 30 g dry wt m⁻² (Ringold 1979). Their distributions within salt marshes can vary considerably, with highest densities usually observed on the creek banks and in the tall and medium *Spartina* regions (Wolf et al. 1975, Cammen et al. 1980). When a marsh is inhabited by more than 1 species, the different species may exhibit vertical patterns of zonation (Teal 1958). The distributions of the species depend on their physiological tolerance to environmental gradients (Teal 1958), and their ability to burrow in different sediment types vari-

ously compacted by macrophyte roots (Ringold 1979, Bertness & Miller 1984).

Salt marsh crabs are highly motile, burrow and deposit feed. Their burrows increase the surface area of marshes (Katz 1980), increase soil drainage and oxygen levels (Valiela et al. 1978, Montague 1982), and enhance the production of marsh macrophytes (Bertness 1985). Their burrows can also increase the abundance of meiofauna on marshes through passive deposition (DePatra & Levin 1989) or the creation of suitable microenvironments (Bell et al. 1978). The crabs themselves consume 25 % and assimilate 2.5 % of the macrophyte net production of marshes (Cammen et al. 1980). Their deposit feeding can also significantly affect the taxonomic composition and production of epibenthic microbiota (Foreman 1985) and meiofauna (Hoffman et al. 1984), and increase the level of oxygenation of the surface sediments (Hoffman et al. 1984). Their burrowing and feeding activities increase the rates of sediment (and presumably nutrient) turnover within these systems (Katz 1980).

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One neglected and potentially important impact of the crabs is their influence on material fluxes across the surface of marshes. Concentrations of organic carbon (Agosta 1985) and dissolved nutrients (Yelverton & Hackney 1986) are orders of magnitude higher in the sediments of these systems than in the inundating water. For other macrofauna, bioturbation has been shown to influence nutrient fluxes from submerged freshwater (Graneli 1979, Matishoff et al. 1985) and subtidal marine (Kristensen 1984a, b, Kristensen et al. 1985, Yamada & Kayama 1987) sediments, but the equivalent data are not available for salt marsh crabs.

The purpose of the present study was to quantify the effects of crabs on fluxes of organic carbon across the surface of a salt marsh on the southeast coast of southern Africa. Emphasis was placed on the fluxes of total, dissolved and particulate organic carbon, because these are the fractions (as opposed to the gaseous forms) potentially available for export and biological utilization in the adjoining estuary. The study is part of a larger investigation of the fluxes of organic carbon (Taylor unpubl.) and nutrients (Taylor 1992) between the marsh and estuary.

STUDY SITE

The marsh is located in the middle reaches (33° 40' 37" S, 26° 38' 46" E) of the Kariega estuary, and details of the marsh and estuary are provided in Taylor (1988), and Allanson & Read (1987), respectively. The marsh has an area of 4.2 ha, 80% of which is marsh flats and 20% tidal creek. The marsh flats are covered by dense macrophyte meadows of *Sarcocornia perennis* (Mill.) A. J. Scott, *Chenolea diffusa* Thunb. and *Spartina maritima* (Curtis) Fernald. In terms of area covered, *S. perennis* is the dominant macrophyte, with single-species stands covering 70% of the marsh flats. The tidal creek has no macrophyte vegetation. The estuary is a small marine-dominated, lagoon-like system, and during the present study, salinities were 35‰ along its entire length. In the estuary, adjacent to the marsh, the water column is vertically well mixed. The marsh is submerged twice daily by semidiurnal (ca 12.4 h) tides, and is completely drained of surface water at each low tide.

MATERIALS AND METHODS

Crab distribution. Crab densities and biomasses on the marsh were determined by using (0.5 × 0.5 × 0.5 m) quadrats randomly placed (using a compass and a table of random numbers) on the marsh. Crabs were removed from burrows within quadrats by rapidly forc-

ing a knife at an angle, alongside and then into each burrow. To check the efficiency of this method, 8 quadrats were sampled as above, and then immediately excavated to 0.5 m. The contents were then sieved (1.25 mm mesh size) to remove unsampled crabs. The mean percentage recovery (\pm S.D.) using the abbreviated method was $78 \pm 9\%$ for *Sesarma catenata* and $95 \pm 4\%$ for *Cleistostoma edwardsii*, which was considered adequate for the present purpose. Crab ash-free dry weight (AFDW) was determined as loss of dry weight on ignition at 495°C for 5 h. Loss of inorganic crab weight due to carbonate combustion, and loss as CO₂, was checked by parallel ignition of 'Analar' CaCO₃ samples: on no occasion was correction for this potential source of error necessary.

Organic carbon fluxes. Two experiments were conducted, each employing 6 replicate mesocosms. Details of the mesocosms and tidal-simulation system are provided in Taylor (1992). The first experiment involved mesocosms of the marsh flats, and the second, mesocosms of the tidal creek. Separate experiments were conducted for the 2 regions, because for this marsh they are well differentiated with unique sediment characteristics, and plant and crab communities (Taylor 1988). In each experiment, 3 mesocosms were incubated with crabs of the species dominant in that region, and 3 without. The field surveys were used to determine the number and size of crabs to be added to each mesocosm.

The mesocosms were intact 0.3 × 0.3 × 0.1 m blocks of marsh surface collected with associated plants and macrofauna. The blocks were collected prior to each experiment from regions of the marsh known to support mean densities of the respective crab species. The blocks and the crabs added to the mesocosms, were collected during spring lunar-tidal phases, to match flooding in the laboratory with that in the field; the marsh is flooded most frequently and extensively during spring lunar-tidal phases, and frequently remains completely exposed during neap tides (Taylor 1988). The matching of the laboratory and field tides also served to minimize possible variability arising from endogenous, tidally linked, crab activity rhythms (Williams et al. 1985).

Crabs collected with the marsh blocks were carefully removed (using forceps) from all the mesocosms immediately the blocks were returned to the laboratory. Removal was carried out under infrared lights not visible to crabs to minimize disturbance of the marsh surface. After all the crabs had been removed, 5 *Sesarma catenata* crabs, weighing 0.20 g AFDW each, were added to each of the 3 marsh flats mesocosms designated to receive crabs. The equivalent tidal creek mesocosms each received 35 *Cleistostoma edwardsii* crabs, with an average individual weight of 0.01 g AFDW.

The stocking values were the mean numbers and mean individual biomasses determined for the 2 regions from the field surveys. The crabs were allocated to alternate rather than random mesocosms, to ensure the with- and without-crab mesocosms were equally subjected to possible microgradients within the constant environment room.

For 2 d immediately following the crab additions, all mesocosms were subjected to 4 semidiurnal (12.4 h) tides, during which fluxes were not measured. The purpose of these tides were to flush the mesocosms of materials mobilized during block collection, and allow the added crabs to settle. The marsh flats mesocosms were then subjected to 9 semidiurnal (12.5 h) tides, and the tidal creek mesocosms to 15, these being the average numbers of field tides inundating the respective regions during 14 d semilunar (neap-spring-neap) tidal cycles (Taylor 1988).

The water used to inundate the mesocosms was collected from mid-channel in the estuary adjacent to the marsh. The water was collected at high tide, to ensure that it would be typical of that normally inundating the marsh. The water was stored in the dark, at 5°C until use, a period always less than 72 h. During each tide, the marsh flats and tidal creek mesocosms were inundated for 125 and 200 min, respectively, to match the mean duration of inundation of the 2 regions in the field (Taylor 1988). These characteristics were determined from topographic surveys of the marsh, surveys of the areal inundation of the marsh at different elevation tides, and 12 mo water level records at the junction of the marsh and estuary (Taylor 1988). The horizontal water flow over the marsh that occurs during tides in the field was not simulated in the mesocosms.

The mesocosms were arranged below sodium and halogen light banks. Incident photosynthetically active radiation at the sediment surface was 92 ± 4.3 (SD) $\mu\text{E m}^{-2} \text{s}^{-1}$ ($n = 15$), slightly lower than that known to cause light saturation of benthic microalgal photosynthesis (Rasmussen 1983). Temperatures at the marsh surface in the mesocosms were maintained at $23 \pm 0.9^\circ\text{C}$, which corresponds with the summer mean weekly temperature 5 cm above the marsh surface in the field (Taylor 1988). The mesocosms were exposed to 10 h dark : 14 h light photoperiod, determined from published tables of sunrise and sunset (South African Tide Tables 1987).

The mesocosms were inundated with water collected at high tide at the junction of the marsh and estuary. The water was collected within 36 h of use, and stored in the dark at 5°C. Flow into the mesocosms was regulated at 0.30 l min^{-1} using Gampmeter Type GT flow meters. The inundating water was filtered through $100 \mu\text{m}$ filters prior to flooding. After each tide, water from each mesocosm was drained into an acid-

cleaned, darkened, ice-enclosed glass bottle. Duplicate water samples for analysis were collected from the inflowing water during inundation, and from the outflowing water in each glass bottle after complete drainage of the mesocosms. One of the duplicate influent and effluent samples were filtered through ashed, pre-rinsed Whatman GF/F filter paper, and the filtrate used for determining concentrations of dissolved organic carbon. The unfiltered samples were used to estimate total organic carbon (TOC). Concentrations of particulate organic carbon (POC) were determined by difference. After filtration, the water samples were stored at -15°C , in the dark until analysis. Concentrations were determined using a Beckman 915B Total Organic Carbon Analyzer, after removal of inorganic carbon by acid sparging. Precision of the analytical technique, as applied, and expressed as percentage coefficient of variation, was between 3 and 6% at DOC concentrations of 3 to 10 mg C l^{-1} ($n = 9$).

For each chemical component, areal net fluxes per tide, F_m ($\text{mg m}^{-2} \text{ tide}^{-1}$), were computed for each mesocosm as follows:

$$F_m = (O - I) V/A$$

where I = concentration in influent water (mg l^{-1}); O = concentration in effluent water (mg l^{-1}); V = volume of water drained from mesocosm (l); and A = area of top of sediment block (m^2). This computation assumes the volume of water leaving each mesocosm is the same as that entering. This was checked, and retention by the marsh blocks found to be between 2 and 8% of influent volume.

Crab respiration. Weight-specific respiration rates of *Sesarma catenata* and *Cleistorstoma edwardsii*, as oxygen uptake per unit AFDW, were determined using a Gilson Single Valve Differential Respirometer. The crabs used for the respiration measurements were those used earlier in the mesocosm experiments, to allow direct comparison of the carbon losses via respiration and bioturbation. Prior to the respiration measurements, the crabs were equilibrated in prefiltered (Whatman GF/F), autoclaved estuarine water at room temperature for 2 h, to ensure gut clearance. Crabs were then placed in 50 ml experimental flasks, which each contained 10 ml prefiltered autoclaved estuarine water. The central well in each flask contained 500 mm^2 fluted Whatman GF/C filter paper soaked in 1.5 ml 10% KOH, which served as a CO_2 trap. Control treatments were as for experimental treatments, except the flasks were incubated without crabs. Experimental and control flasks were allowed to equilibrate for 15 min before valve closure, and changes in gas volume then monitored for 3 h. Flasks were incubated at 23°C , the same temperature at which the mesocosms were incubated.

Respiratory oxygen consumption rates were converted to carbon equivalents assuming respiratory quotients (RQ) of 0.71 and 1.0. Since RQ values vary depending on substrate respired (0.71 for lipid, 0.80 for protein, and 1.0 for carbohydrate; Lampert 1984), and the metabolic substrates of *Sesarma catenata* and *Cleistostoma edwardsii* on the marsh were not known, respiratory rates were calculated using both the minimum and maximum RQ values.

Crab excretion. Weight-specific rates of excretion of DOC were measured using crabs removed from the mesocosms. Crabs were rinsed and gently scrubbed with a soft brush to remove dissolved and attached particulate material, and then equilibrated for 2 h in pre-filtered (Whatman GF/F), autoclaved estuarine water, at room temperature. The crabs were then incubated in 50 ml prefiltered, autoclaved estuarine water for 4 h, at 23 °C. Water samples for analysis were collected before and after incubation, filtered and analyzed as above. Replicates in which crabs had produced fecal pellets were discarded. Control measurements were conducted in duplicate, using containers incubated with estuarine water, without crabs.

Epibenthic respiration and photosynthesis. Epibenthic respiration and photosynthetic rates were determined using 2.0 ml surface sediment samples incubated in a Gilson Respirometer (Umbreit et al. 1972). At the start and end of each mesocosm experiment, six 3 mm deep sediment samples were collected from the marsh surface using a 100 mm diameter core. At the end of the mesocosm experiments, sediment samples were collected from random positions within each mesocosm, and pooled. Sediment samples could not be collected from the mesocosms prior to the experiments without causing significant disturbance of the systems. Therefore, before each experiment, the sediments were collected in the field immediately adjacent to the sites of collection of the mesocosm blocks. During incubation in the Gilson Respirometer, the sediment samples in the flasks were shaken horizontally at 65 traverses min^{-1} (amplitude of each traverse = 275 mm). The measured rates therefore represent potential values.

To measure the potential rates of sediment (or epibenthic) respiration, the flasks were incubated in the dark at 22.0 ± 1.0 °C, equivalent to the summer temperature employed for the mesocosms. Incubation lasted 11 h. Measurements were not made for the first 3 h, during which oxygen uptake rates were high, and largely non-biological. For the next 4 h, readings representing total oxygen uptake were recorded hourly. Mercuric chloride (0.1 ml 1%) was then added to each flask as a metabolic inhibitor, and after 15 min equilibration, volume changes equivalent to nonbiological

uptake were recorded for a further 4 h. Rates of biological oxygen uptake were determined by difference, and assumed to measure community respiration of the surface sediments. This assumption was considered valid, because at the E_h values ($> +350$ mV) exhibited by the marsh surface sediments (Taylor 1988), aerobic respiration with oxygen as the major terminal electron acceptor, is the dominant respiratory pathway (Sorenson et al. 1979).

Rates of epibenthic net photosynthesis (NP) were determined as for community respiration, except the flasks were incubated in the light ($90 \mu\text{E m}^{-2} \text{s}^{-1}$) for 8 h, and the oxygen changes were not partitioned into biological and nonbiological components using mercuric chloride. Rates of gross photosynthesis (GP) were determined by adding estimates of dark oxygen uptake to light oxygen production measured in parallel treatments. The oxygen exchange rates were converted to carbon equivalents using a factor of 0.32. Chlorophyll *a*, corrected for phaeophytin degradation products, was determined according to Sartory (1985).

RESULTS

Seven species of crabs were observed on the marsh, but in terms of numbers and biomass 2 species dominated, the grapsoid *Sesarma catenata* Ortm. and the ocypodoid *Cleistostoma edwardsii* McLeay. The vertical distributions of the 2 species differed, with *C. edwardsii* having maximum densities in the tidal creek, between 0.9 and 1.1 m above mean sea level (MSL), and *S. catenata* in the marsh flats, between 1.2 and 1.3 m above MSL (Table 1). For all quadrats in which the species were observed, *C. edwardsii* showed mean densities ($386 \pm 127 \text{ ind. m}^{-2}$, $\pm 95\%$ CL) an order of magnitude higher than *S. catenata* ($47 \pm 8 \text{ ind. m}^{-2}$, $\pm 95\%$ CL), but *C. edwardsii* individuals were an order of magnitude smaller; 0.01 vs 0.19 g AFDW ind.^{-1} . The mean areal biomass of *S. catenata* ($8.7 \pm 1.0 \text{ g AFDW m}^{-2}$) exceeded *C. edwardsii* ($3.8 \pm 0.6 \text{ g AFDW m}^{-2}$) by a factor of 2.3.

In both regions, whether crabs were present or not, the mean net fluxes of TOC (calculated for the 3 replicates and all tides combined) were directed from the marsh surface to the water column, mainly as DOC (Fig. 1, Table 2). (Positive flux values indicate net loss from the marsh surface to the water column, and negative values, net uptake). The mean fluxes of all three organic carbon fractions were greater from the tidal creek than from the marsh flats. In the tidal creek, *Cleistostoma edwardsii* significantly enhanced the mean net fluxes of all 3 organic carbon fractions. The fluxes of TOC were enhanced by $224 \text{ mg C m}^{-2} \text{ tide}^{-1}$ (or $60.5 \text{ mg C m}^{-2} \text{ h}^{-1}$), and most (66%) of this was in

Table 1 *Sesarma catenata* and *Cleistostoma edwardsii*. Densities and ash-free dry weights (AFDW) of crabs at different elevations on the marsh. MSL: mean sea level

Elevation (m above MSL)	<i>S. catenata</i>		<i>C. edwardsii</i>	
	Density (ind. m ⁻²)	Biomass (g AFDW m ⁻²)	Density (ind. m ⁻²)	Biomass (g AFDW m ⁻²)
0.81–0.90	0	0	9 ± 22	1.06 ± 3.73
0.91–1.00	3 ± 6	0.1 ± 0.2	535 ± 43	5.16 ± 3.80
1.01–1.10	32 ± 12	7.8 ± 8.5	560 ± 22	5.41 ± 1.91
1.11–1.20	46 ± 29	8.5 ± 10.1	193 ± 33	1.67 ± 2.8
1.21–1.30	92 ± 27	14.1 ± 13	0	0
1.31–1.40	23 ± 14	6.3 ± 7.3	0	0
Mean + 95 % CL (n)	47 ± 8 (38)	8.7 ± 1.0 (38)	386 ± 127 (72)	3.8 ± 0.6 (72)

the particulate form. In the marsh flats, the mean fluxes were higher from the mesocosms with crabs than from those without, but the differences between the with- and without-crab mesocosms were not statistically significant.

The weight-specific rates of DOC excretion were 146 ± 76 and $328 \pm 178 \times 10^{-3}$ mg C g⁻¹ AFDW h⁻¹ for *Sesarma catenata* and *Cleistostoma edwardsii*, respectively. With biomasses of *S. catenata* and *C. edwardsii* being 11.1 and 3.9 g AFDW m⁻², the areal rates of crab excretion of DOC were 1.6 mg C m⁻² h⁻¹ in the marsh flats and 1.3 mg C m⁻² h⁻¹ in the tidal creek. For both species, the carbon losses via respiration were greater than the excretory losses. Assuming a RQ of 0.71, the areal rates of respiration by *S. catenata* and *C. edwardsii* were 2.5 and 2.0 mg C m⁻² h⁻¹, respectively (Table 3). Assuming a RQ of 1.0, the equivalent values were 3.6 and 2.8 mg C m⁻² h⁻¹.

In the marsh flats, *Sesarma catenata* decreased the potential rates of epibenthic NP and GP, but not respiration (Table 4). *Cleistostoma edwardsii* in the tidal creek had no significant impact on epibenthic NP, GP or R. Both species decreased the chlorophyll *a* contents of the surface sediments (presumably through grazing), and increased rates of specific GP (or GP per unit chlorophyll). *S. catenata* lowered the rates of gross photosynthesis relative to respiration (GP:R), but *C. edwardsii* increased this ratio, suggesting differential consumption of autotrophic microalgae by *S. catenata*, and heterotrophic bacteria or meiofauna by *C. edwardsii*.

The relative impacts of the 2 species on the different processes regulating carbon fluxes at the marsh sur-

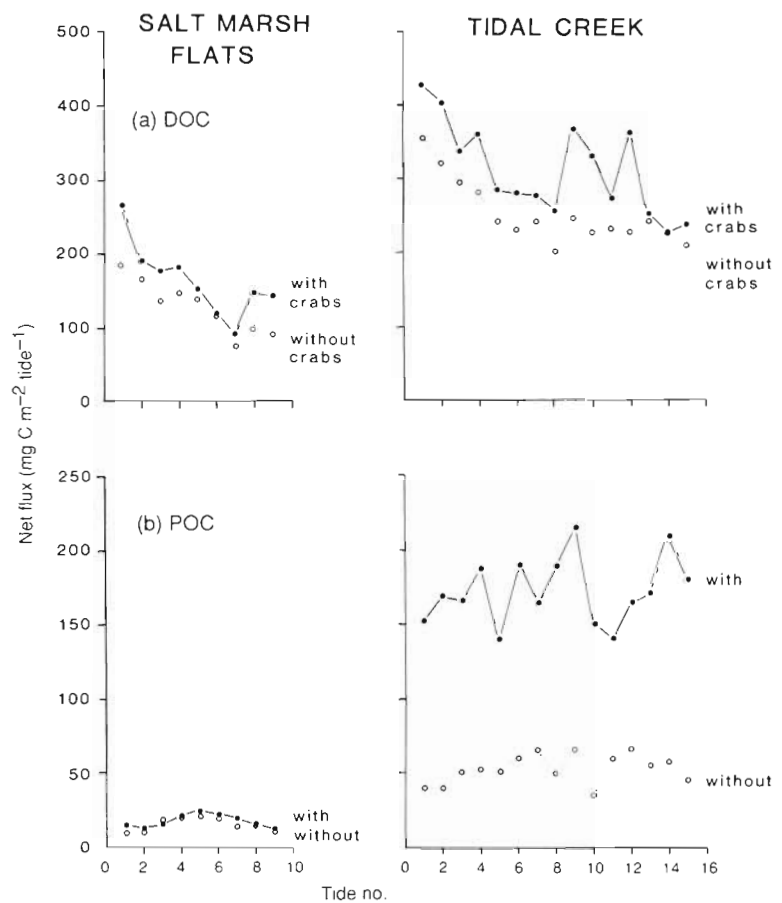


Fig. 1 *Sesarma catenata* and *Cleistostoma edwardsii*. Tidal net fluxes of DOC and POC from mesocosms of the marsh flats (with and without *S. catenata*) and tidal creek regions (with and without *C. edwardsii*), over a simulated, average semilunar tidal cycle (equivalent to 9 and 15 semidiurnal tides in the respective regions). Each point represents the mean ($n = 3$) net flux per semidiurnal tide, for either the with- or without-crab treatments

face are summarized in Table 5. In both regions (and especially in the tidal creek), the crab-enhanced fluxes of TOC were large compared to the carbon losses via crab excretion. The remainder of the TOC fluxes were a result of crab bioturbation. In the tidal

Table 2. *Sesarma catenata* and *Cleistostoma edwardsii*. Comparison of mean net fluxes of organic carbon ($\text{mg C m}^{-2} \text{ tide}^{-1}$, $\pm 95\% \text{CL}$) in the presence and absence of crabs in mesocosms of the marsh flats (with and without *S. catenata*) and tidal creek (with and without *C. edwardsii*). Each flux value represents the mean fluxes from 3 replicate mesocosms, for all tides combined. No. of tides in parentheses

Component	Mean net flux			
	Marsh flats		Tidal creek	
	With crabs	Without crabs	With crabs	Without crabs
TOC	+188 \pm 50.7 (26)	+152 \pm 33.4 (26)	+590 \pm 136 (44)	+366 \pm 69.5 (44)
DOC	+169 \pm 25.0 (26)	+135 \pm 16.6 (26)	+381 \pm 29.3 (44)	+304 \pm 24.0 (44)
POC	+19 \pm 5.0 (26)	+17 \pm 4.6 (26)	+209 \pm 33.4 (44)	+62 \pm 13.0 (44)

Table 3. *Sesarma catenata* and *Cleistostoma edwardsii*. Mean ($\pm 95\% \text{CL}$) mass-specific respiration rates expressed in oxygen and carbon terms. $n = 15$ and 19 for *S. catenata* and *C. edwardsii*, respectively

Species	Mean AFDW per individual (g)	O_2 consumption ($\mu\text{g O}_2 \text{ g}^{-1} \text{ h}^{-1}$)	CO_2 equivalence ($\mu\text{g C g}^{-1} \text{ h}^{-1}$) assuming:	
			RQ = 0.71	RQ = 1.0
<i>S. catenata</i>	0.09 \pm 0.04	611 \pm 27	229 \pm 10	325 \pm 14
<i>C. edwardsii</i>	0.016 \pm 0.004	1370 \pm 38	514 \pm 14	731 \pm 20

creek, bioturbation by *Cleistostoma edwardsii* accounted for 99 % of the hourly and 94 % of the daily TOC fluxes attributable to the crabs. In the marsh flats, where *Sesarma catenata* had less impact on the fluxes of TOC, the equivalent values were 88 and 47 %. (Bioturbation is used here to describe sediment disturbance, breakup and resuspension of feces,

and damage to macrophytes and microbiota during crab feeding, burrowing, and locomotion.) In both regions, the carbon losses via crab respiration were small compared to the effects of the crabs on rates of epibenthic NP. In the marsh flats, where epibenthic NP was decreased most by the crabs, respiratory losses were equivalent to 16 % (hourly) and 14 % (daily) of the

Table 4. *Sesarma catenata* and *Cleistostoma edwardsii*. Effects of crabs on mean ($\pm 95\% \text{CL}$) rates of respiration (R), net (NP) and gross (GP) photosynthesis, specific rates of GP, GP:R ratios, and chlorophyll *a* contents of surface sediments of the marsh flats (with and without *S. catenata*) and tidal creek (with and without *C. edwardsii*) mesocosms. No. of sediment sample measurements in parentheses

Variable	Marsh flats		Tidal creek	
	With crabs	Without crabs	With crabs	Without crabs
NP ($\text{mg C m}^{-2} \text{ h}^{-1}$)	-9 + 6 (7)	16 + 7 (7)	31 + 10 (7)	35 + 14 (6)
GP ($\text{mg C m}^{-2} \text{ h}^{-1}$)	36 + 11 (7)	65 + 18 (7)	45 + 12 (7)	56 + 14 (6)
R ($\text{mg C m}^{-2} \text{ h}^{-1}$)	45 + 14 (7)	49 + 17 (7)	14 + 4 (7)	21 + 9 (6)
Chlorophyll <i>a</i> (mg m^{-2})	31 + 4 (5)	82 + 12 (5)	54 + 8 (5)	82 + 25 (6)
Specific GP ($\text{mg C mg chl a}^{-1} \text{ h}^{-1}$)	1.2	0.8	0.8	0.7
GP:R	0.8	1.3	3.2	2.7

reduction in epibenthic NP (Table 5). In the tidal creek, the relative contribution of respiratory losses was greater than in the marsh flats, and equivalent to 75 % (hourly) and 70 % (daily) of the reduced epibenthic NP.

Table 6 summarizes the effects of the crabs on the daily carbon budgets of the 2 regions. Both species enhanced the carbon losses relative to uptake by the marsh (by $1204 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the marsh flats and $505 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the tidal creek), but they did so via different mechanisms. In the marsh flats, *Sesarma catenata* decreased community NP by $1132 \text{ mg C m}^{-2} \text{ d}^{-1}$, but their effects on TOC fluxes were small and not statistically significant. In the tidal creek, *Cleistostoma edwardsii* enhanced the fluxes of TOC, but had no significant impact on community NP.

DISCUSSION

On the Kariega marsh, *Cleistostoma edwardsii* and *Sesarma catenata* occupy similar vertical positions to the sand and mud fiddler crabs, *Uca pugnator* and *U. pugnax* respectively, on the marshes of the southeast USA (Teal 1958, Colby & Fonseca 1984). *C. edwardsii*, like *U. pugnator*, occupies the coarser-grained substrata of the creek banks and the regions of the marsh flats closest to the tidal creek. *S. catenata* and *U. pugnax* occur higher up the marsh in the vegetated regions with finer, more consolidated sediments. The mean densities of *S. catenata* (47 ind. m⁻²; on the marsh, and used in the mesocosm experiments, lie in the mid- to lower range reported for *U. pugnax* (0 to >500 ind. m⁻²; Table 7).

For *C. edwardsii*, the mean densities (390 m⁻²) were generally higher than those reported for *U. pugnator*, in part because most previous studies employed 5 mm mesh compared to the 1.25 mm mesh used in the present study. Krebs & Valiela (1978) compared the densities of *U. pugnax* on Great Sippewissett Marsh using 2 and 5 mm mesh, and noted the 5 mm mesh underestimated densities by almost 80 %.

Comparison of the flux estimates from the mesocosms with those measured between the marsh and estuary in the field (Taylor unpubl.) and between other marsh-estuarine systems, indicates the patterns ob-

Table 5. *Sesarma catenata* and *Cleistostoma edwardsii*. Impact of crabs on the hourly (mg C m⁻² h⁻¹) and daily (mg C m⁻² d⁻¹) carbon exchanges at the marsh surface. Symbol denotes the impact of crabs on the process rates, and not the direction of flux. (+) value indicates crabs increased rate, (-) crabs decreased rate

Type of carbon exchange	<i>S. catenata</i>		<i>C. edwardsii</i>	
	Hourly	Daily	Hourly	Daily
Non-gaseous C exchanges				
TOC flux	(+)17	(+)72	(+)72	(+)488
DOC flux	(+)16	(+)68	(+)23	(+)154
POC flux	(+) 1	(+) 4	(+)49	(+)334
Crab DOC excretion	(+) 2	(+)38	(+) 1	(+) 31
TOC bioturbation ^a	(+)15	(+)34	(+)71	(+)457
Gaseous C exchanges				
Crab C respiration ^b	(+) 4	(+) 86	(+) 3	(+) 67
Epibenthic GP	(-)29	(-)696	(-)11	(-)264
Epibenthic NP	(-)25	(-)600	(-) 4	(-) 96
Epibenthic respiration	(-) 4	(-) 96	(-) 7	(-)170

^a Effect of crabs on TOC flux minus crab DOC excretion
^b RQ = 1.0

served in the mesocosms are realistic. On annual time scales, most marshes export DOC and POC (Nixon 1980, Dame et al. 1986), and this applied to the mesocosms of both regions over the 9 to 14 simulated tides. For the marsh flats, the mean TOC fluxes (137 g C m⁻² yr⁻¹) were similar to the fluxes of 100 to 200 g C m⁻² yr⁻¹ predicted for salt marshes by Nixon (1980). For the tidal creek, the fluxes of 430 g C m⁻² yr⁻¹ were higher. Based on previous field measurements of fluxes between the marsh and estuary over 42 tides, the mean annual net flux of TOC from the marsh to the estuary has been estimated to be 5 g C m⁻² yr⁻¹ (Taylor un-

Table 6. *Sesarma catenata* and *Cleistostoma edwardsii*. Impacts of crabs on the daily carbon budget (mg C m⁻² d⁻¹) at the marsh surface. Symbols not in parentheses represent direction of net flux: + values denote net loss to water column; - values net uptake by marsh surface. Effects of crabs are denoted using parenthesized symbols: (+) indicates crabs enhanced the process; (-) indicates crabs reduced the rate. nd: not determined

	Marsh flats (<i>S. catenata</i>)			Tidal creek (<i>C. edwardsii</i>)		
	With crabs	Without crabs	Effect of crabs ^a	With crabs	Without crabs	Effect of crabs ^a
TOC net flux ^b	+376	+304	(+)72	+1180	+723	(+)448
Epibenthic NP ^c	+660	-396	(-)264	-192	-168	(-)24
<i>Sarcocornia</i> NP ^d	-1068	-1068	0	nd	nd	nd
Community NP ^e	-332	-1464	(-)1132	-120	-168	(-)48
Balance d ^{-1f}	+44	-1160	1204	+1060	+555	505

^a Mean rates with crabs minus mean rates without
^b Calculated from hourly rates, assuming 2.1 and 3.7 h inundation in the marsh flats and tidal creek regions, and both regions inundated twice daily. Includes excretory losses
^c Calculated from data in Table 4 assuming a 12 h light:12 h dark regime, and subtracting dark respiration from net production
^d From Christie (1981), and assumed to be the same in the presence and absence of crabs
^e Epibenthic NP plus *Sarcocornia* NP minus crab respiration
^f Community NP minus TOC net flux

Table 7. Comparison of the densities of the crab populations on the Kariega Marsh with crab populations on other marshes and mud and sandflat regions in the U.S. nd: not determined

Marsh	Species	Crab size (>mm)	Density (ind. m ⁻²)	Source
Kariega Marsh, South Africa	<i>Sesarma catenata</i>	1.25	47 ^a	Present study
	<i>Cleistostoma edwardsii</i>	1.25	390 ^a	
Great Sippewissett, MA	<i>Uca pugnax</i>	5	113 ^a	Krebs & Valiela (1978)
		2	401 ^a	
Little Sippewissett, MA	<i>Uca pugnax</i>	nd	34–42 ^b	Katz (1980)
Smith Cove, RI	<i>Uca pugnax</i>	5	42–109 ^a	Bertness & Miller (1984)
Dutchman Creek, NC	<i>Uca pugnax</i>	2	18–42 ^a	Cammen et al. (1984)
	<i>U. minax</i>	2	0–2 ^a	
Oak Island, NC	<i>Uca pugnax</i>	2	10–40 ^a	
	<i>U. minax</i>	2	0–3 ^a	
Snow's Marsh, NC	<i>Uca pugnax</i>	2	6–29 ^a	Cammen et al. (1984)
	<i>U. minax</i>	2	0–5 ^a	
Walden Creek, NC	<i>Uca pugnax</i>	2	14–45 ^a	Cammen et al. (1984)
	<i>U. minax</i>	2	0–10 ^a	
Shackleford Banks, NC	<i>Uca pugilator</i>	5	34–65 ^a	Colby & Fonseca (1984)
Bell Creek, NC	<i>Uca pugnax</i>	1	12–42 ^a	Ringold (1979)
	<i>U. minax</i>	1	0–6 ^a	
Sapelo Island, GA	<i>Uca pugnax</i>	nd	0–61 ^c	Teal (1958)
	<i>U. pugilator</i>	nd	0–52 ^c	
	<i>Sesarma reticulatum</i>	nd	0–30 ^c	
	<i>S. cinereum</i>	nd	0–2 ^c	
Reynold's Marsh, GA	<i>Uca pugnax</i>	0.5	27–196 ^a	Wolf et al. (1975)
Matanzas Inlet, FL	<i>Uca pugnax</i>	nd	156–205 ^c	Genoni (1991)
Oak Creek, CA	<i>Pachygrapsus crassipes</i>	nd	40 ^c	Willason (1981)
	<i>Hemigrapsus oregonensis</i>	nd	90 ^c	
Pirhana Creek, CA	<i>Pachygrapsus crassipes</i>	nd	4 ^c	Willason (1981)
	<i>Hemigrapsus oregonensis</i>	nd	60 ^c	

^a Determined by sediment sieving
^b Determined from burrow densities
^c Crabs removed by visual selection rather than sieving

publ.). This is small compared to the fluxes observed from the mesocosms of both regions, and several factors probably account for this.

In the present experiments, the mesocosms of the 2 regions were incubated separately, whereas in the field water flows between the 2 regions resulting in the recycling and retention of material within the marsh (Welsh 1980). Therefore on a flood tide, some fraction of the POC resuspended in the tidal creek (by bioturbation and other processes) would be deposited on the higher, densely vegetated marsh flats (Gleason et al. 1979), decreasing the POC loss from the marsh. Also, in the field the creek sediments at the mouth of the marsh are inhabited by dense populations of filter-feeding bivalves (*Solen cylindraceus*) and anomuran crustaceans (*Upogebia africana*) (Hodgson 1987), which retain particulate material leaving the marsh (Dame et al. 1984, Chrzanowski et al. 1986). Because

the marsh blocks were only 0.3 m deep, and were collected in the middle of the marsh (where these filter feeders were absent), the mesocosm flux values are probably overestimates. Some proportion of the organic carbon lost from the mesocosms was probably also caused by marsh disturbance during block collection and crab removal. Considerable care was taken to minimize this disturbance, but some disruption (and presumably release of organic carbon) was unavoidable.

The mesocosm experiments demonstrated that both species enhanced the losses of carbon relative to uptake by the marsh, one by increasing the fluxes of organic carbon, and the other by reducing epibenthic NP (Table 6). The reasons for the different effects of the 2 species are not known for certain. Data are not available on the sediment organic carbon pools in the 2 regions, or on the feeding and burrowing behavior of the

2 species. The sediments are, however, coarser grained, and presumably less consolidated in the tidal creek than the marsh flats, and this may account for the greater bioturbation effects of *Cleistostoma edwardsii* in the tidal creek. The mud (subsieve < 63 μm) contents of the tidal creek sediments were < 300 mg g^{-1} dry wt, compared to > 900 mg g^{-1} dry wt in the marsh flats (Taylor 1988). Cross-incubation of the 2 species in mesocosms of the 2 regions would have allowed the contributions of crab behavior and the properties of the marsh regions to be differentiated, but these experiments still need to be conducted.

Potentially, the crab effects on the carbon budgets of salt marshes can be partitioned into the effects of the crabs themselves (e.g. Cammen et al. 1980, Hoffman et al. 1984, Foreman 1985) and the effects of their burrows (e.g. Katz 1980, Montague 1982). Because both the with- and without-crab mesocosms contained pre-existing burrows, the present experiments quantified the impacts of the crabs. The experiments were conducted on a time scale of days to minimize laboratory enclosure effects, and therefore did not address the longer-term effects of the crabs such as their seasonal carbon accumulation in biomass, or their carbon loss through gamete release or detachment of exuviae. The crab surveys and mesocosm experiments were also conducted in summer or under simulated summer conditions, and the effects of the crabs at other times of the year may have been different. A laboratory mesocosm approach was adopted in preference to field enclosure experiments for several reasons. The mesocosms al-

lowed total exclusion of the crabs, whereas in the field deep burrows might have provided crabs with access to without-crab controls. Unless the field enclosures had been far apart, which would have increased substrate variability and made detection of the crab effects more difficult, materials released or mobilized by the crabs (from both the with-crab enclosures and the general marsh surface) might also have been transferred (through tidal flow) to the controls. The laboratory approach also allowed partial control of the ambient environment.

Using the flux and epibenthic production data from the mesocosms, and the data from a survey of the marsh area inundated by different elevation tides (Taylor 1988), it has been possible to quantify the effects of the crabs on the exchanges of carbon m^{-2} , averaged for the entire marsh (Table 8). The marsh is inundated by tides ranging in maximum elevation from 0.7 to > 1.8 m above MSL, with the mean maximum tide elevation being 1.1 m above MSL (Taylor 1988). When tides are too low to inundate the marsh (< 0.7 m above MSL), the marsh apparently functions as a carbon sink, whether crabs are present or not. However, for higher tides the direction of the net exchanges of carbon vary depending interactively on tide elevation and the presence or absence of crabs. If crabs are absent, the marsh functions as a carbon sink at all except the highest (> 1.6 m above MSL) tides, which are in turn relatively rare. Water levels reach or exceed this elevation at only 3 % of tides (Taylor 1988). When crabs are present, the marsh serves as a carbon source

Table 8. Effects of crabs on carbon fluxes (m^{-2}) averaged over the entire marsh for tides of different elevations. MSL: mean sea level; NP: net community production. Symbols as in Table 2

Max. tide elevation (m above MSL)	Frequency ^d (%)	Area flooded ^b ($\times 10^3 \text{ m}^2$)		Net fluxes ^c for total marsh ^d (g C h^{-1})						
		Tidal creek	Marsh flats	TOC flux	With crabs		Without crabs			Crab effects ^e Net
					NP ^f	Net	TOC flux	NP ^f	Net	
0.7	96	0	0	0	-623	-623	0	-2154	-2154	1531
0.8	87	0.03	2.48	+397	-623	-226	+247	-2154	-1907	1681
1.0	62	1.40	5.07	+937	-623	+314	+605	-2154	-1549	1863
1.2	33	9.77	5.74	+1789	-623	+1166	+1274	-2154	-880	2046
1.4	12	17.28	6.72	+2618	-623	+1995	+1916	-2154	-238	2233
1.6	3	27.2	6.80	+3519	-623	+2896	+2642	-2154	+488	2408
1.8	1	34.44	7.56	+4288	-623	+3665	+3241	-2154	+1087	2578

^a Frequency with which tides inundating the marsh reach elevation; based on 12 mo continuous water level records measured at the junction of the marsh and estuary in the field (Taylor 1988)

^b Based on surveys of areal extent of marsh inundation by 14 tides (Taylor 1988)

^c Calculated by multiplying hourly TOC flux and community NP values from Table 6 with area of each region inundated at high tide

^d Includes exposed plus inundated regions

^e Values in presence of crabs minus values in absence of crabs

^f Rates assumed to be the same whether marsh inundated or not

for all except the lowest (0.8 m above MSL) tides, and this accounts for 87 % of the tides inundating the marsh (Taylor 1988).

In conclusion, the crab community appears to have considerable impact on the carbon fluxes across the surface of this marsh. For the marsh as a whole, the 2 species enhanced the net loss of carbon, *Cleistostoma edwardsii* by increasing TOC fluxes, and *Sesarma catenata* by reducing epibenthic NP. The quantity of organic carbon mobilized from the tidal creek by *C. edwardsii* ($163 \text{ g C m}^{-2} \text{ yr}^{-1}$) was approximately 30 times the annual TOC flux from the entire marsh to the estuary ($5 \text{ g C m}^{-2} \text{ yr}^{-1}$, Taylor 1988). Similarly, the reduction in epibenthic carbon fixation ($96 \text{ g C m}^{-2} \text{ yr}^{-1}$) caused by *S. catenata* was equivalent to almost 25 % of the annual net production of *S. perennis* ($390 \text{ g C m}^{-2} \text{ yr}^{-1}$; Christie 1981). The overall impacts of the crabs were sufficient to determine the direction of net flux of carbon, and depending on tide elevation, whether the marsh functioned as a carbon source or sink.

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