

Role of microbial mats in Sulaibikhat Bay (Kuwait) mudflat food webs: evidence from $\delta^{13}\text{C}$ analysis

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ABSTRACT: Although microbial mats are known worldwide to contribute to trophic bases in shallow marine embayments, their role has yet to be ascertained for similar habitats in the Arabian Gulf region. In this study, stable carbon isotope analysis in conjunction with faecal and gut analyses were employed to evaluate the relative importance of microbial mats in the nutrition of macrofaunal consumers and their contribution to the exceptional biodiversity, abundance and biomass of species inhabiting Sulaibikhat Bay mudflats (2000–2001) in the absence of extensive macro-vegetation. Microbial mats were mainly composed of diatoms and cyanobacteria (approx. 70 and 30% respectively), with a reduction in the latter with decreasing intertidal gradient. Faeces of 5 out of the 6 species analysed contained both mat components at varying degrees. Diatoms occurred rarely in faeces of the high intertidal consumers, while cyanobacteria dominated the faeces of those occurring at lower levels. Gut analysis revealed that 6 out of the 9 species analysed contained mat residues. Primary producers had distinct $\delta^{13}\text{C}$ values with microbial mats showing a heavy signature (-15.3‰) in comparison to the halophyte *Salicornia herbacea* (-24.7‰), phytoplankton (-21.6‰) and the mangrove *Avicennia marina* (-28.1‰). The $\delta^{13}\text{C}$ values for herbivorous, omnivorous and carnivorous macrofauna ranged between -9.4 and -15.3‰ . It appears from this investigation that microbial mats form the primary source of nutrition for both benthic and pelagic macrofaunal species within the bay including commercially important species, and that selective assimilation/digestion of cyanophytes from the mats is the likely explanation for the relatively high enrichment in the $\delta^{13}\text{C}$ signatures of species located along the higher intertidal zone.

KEY WORDS: Arabian Gulf · Microbial mats · Grazers · Gut/faecal analysis · Stable isotope · Food webs · Reclamation

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INTRODUCTION

The Arabian Gulf is part of the Indo-Pacific Ocean, one of the most productive bodies of water in the world, and is characterised by high pelagic and benthic productivity. Although marine autotrophs have been identified for the Gulf region (IUCN 1987) and some estimates of their production have been made (Sheppard et al. 1992, Jones et al. 2002; GPP in $\text{g cm}^{-2} \text{yr}^{-1}$: phytoplankton 26–200, algae 500–1900, mangrove 500), their relative importance in contributions to coastal food webs is unknown. Due to the sedimentary characteristics of the Arabian Gulf, sand and mudflat habitats dominate intertidally especially along the

north-western coast. These habitats support a high benthic macrofaunal production (Clayton 1986, Jones 1986, Bishop & Khan 1999) despite the absence of conspicuous macro-vegetation due to the harsh climate with extreme temperatures (atmospheric: 0 to 50°C; surface water: 10 to 39°C winter and summer respectively) and salinities (40 to 50‰). Mudflats are covered with a dense microalgal community (Clayton 1986, Jones 1986) referred to as diatom/cyanobacteria-dominated microbial mats (Hoffman 1996). Microstratification is a major characteristic of mats and is associated with the distinctive metabolic groups of micro-organisms each occupying the strata of its optimal growth in relation to the vertical gradient within

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the mat of light, oxygen, redox potential and concentration of sulphide. The top layer is usually supersaturated with oxygen and therefore is occupied by the primary producers, which gives this layer its green coloration. Beneath this layer ambient oxygen decreases as organic matter is intensely decomposed by sulphur bacteria resulting in an anaerobic zone (anoxic 'black' layer). The top layer of these laminated mats and its associated microphytobenthos has been suggested as an important source of primary productivity supplying dense populations of gastropods and other faunal communities (Sheppard et al. 1992). It may contribute more to primary production in the Gulf than mangroves and salt marsh halophytes due to their high productivity, rapid turnover and direct utilisation by grazers (Price et al. 1993). Due to high salinity and low winter temperatures, natural mangroves are absent from Kuwait and reduced in size and extent along the Western Gulf coast as far south as Oman.

Jones et al. (1996) described a cycle on oil-impacted mudflats on the Gulf coast of Saudi Arabia, where after widespread destruction of intertidal macrofauna, microbial mats flourished across the entire intertidal area. The visible mats contracted back to their original zone, around high water, as the grazing macrofauna re-established on the shore, demonstrating a correlation between recovery of macrofaunal diversity and mat regression. These authors proposed that a dynamic relationship may exist on the mid- and lower shore where the mat is grazed as fast as it is produced. They also suggested that visible layers of mat only exist on the top of the shore where grazers are excluded due to high temperature and desiccation.

Soft mud intertidal flats form the most common shoreline type in the north of Kuwait, extending several kilometres seawards and representing approximately 50% of the Kuwaiti coast. Despite the lack of mangroves, high benthic species diversity and abundance is associated with these habitats (Jones & Clayton 1983, Clayton 1986, Wright et al. 1990, Al-Zaidan 1999), suggesting that these mudflats are highly productive. From estimates of distribution and calculations of microbial mat production within the coastal waters of Kuwait, mudflats and their associated microphytobenthos may be more productive in terms of gross primary production than rock, corals and seagrass habitats (Jones et al. 2002).

However, as evidence of the importance of microbial mats in the Gulf is circumstantial, the present investigation seeks to provide experimental evidence for the role of these mats in intertidal food webs. Two approaches were attempted: a conventional analysis of gut and faeces of mudflat benthic macrofauna, coupled with the technique of stable isotope analysis. The application of stable carbon isotope analysis to food web studies in the marine environment has been con-

ducted on a range of coastal environments (Smith & Epstein 1970, Haines 1976a,b, Fry et al. 1984, Rodelli et al. 1984, Bouillon et al. 2000, Dittel et al. 2000, Moncreiff & Sullivan 2001). The present work describes the first systematic application of the technique to food web studies in the Arabian Gulf.

MATERIALS AND METHODS

Study area. Kuwait Bay is a semi-estuarine bay located along the northern province of the Kuwaiti coast (Fig. 1a). It extends 48 km inland from the Arabian Gulf, and is 40 km long and 25 km wide at the mouth. The Bay is tidal with shallow depths not exceeding 8 m at the entrance. Tides are mostly semidiurnal with a mean tidal height of 3.26 m. Surrounding the bay are intertidal mudflats, up to 4 km wide at low tide, with

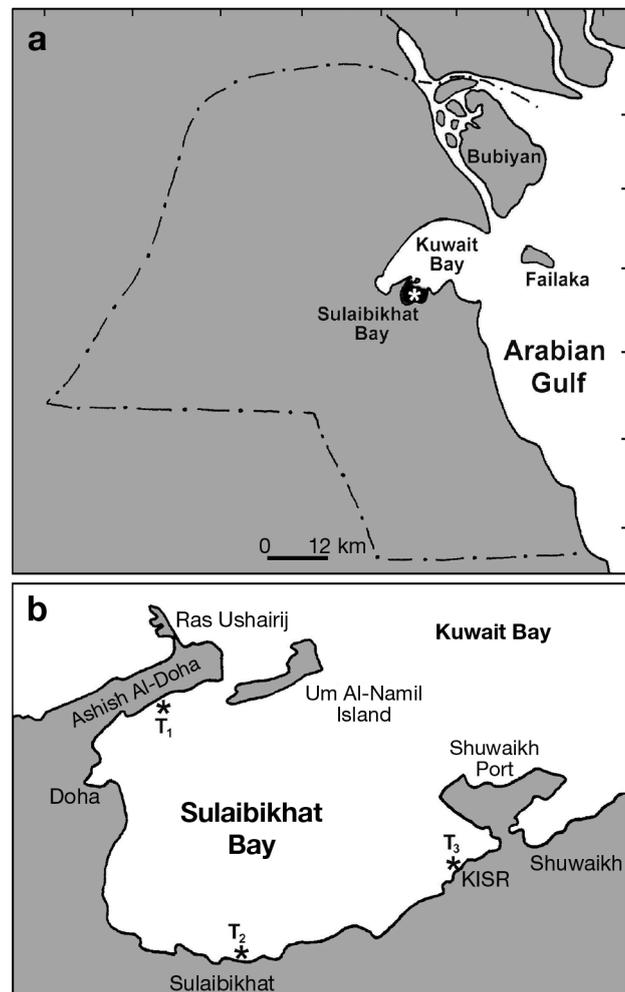


Fig. 1. Map of study area. (a) General location of Kuwait Bay and Sulaibikhat Bay along the Kuwaiti coast. (b) Position of the 3 transects (*) within Sulaibikhat Bay. KISR: Kuwait Institute for Scientific Research

associated salt marsh containing soft mud and clay brought in by rivers via the Shatt-Al-Arab. Salinities at 38 to 40‰ are lower than elsewhere on the Gulf. The Bay is a major nursery ground for many commercial fishery species (Wright et al. 1990, Bishop & Khan, 1999) and harbours endemic species (Al-Khayat & Jones 1996, Apel & Türkay 1999). Despite its ecological and fisheries value many coastal parts of this bay have been subjected to anthropomorphic modification since the mid 1980s, with infilling, reclamation and construction of sewage outlets affecting the ecosystem.

A total of 3 transects were chosen as representative of the study area: a small tidal embayment called Sulaibikhat Bay (approx. 70 km²), sampled during 2000 and 2001 (Fig. 1b). The first transect (T₁) is part of a relatively pristine salt marsh tidal flat located in Ashish Al-Doha area with *Salicornia herbacea* being the dominating intertidal halophyte plants. The second transect is situated opposite the Sulaibikhat residential area (T₂), and has been subjected to infill at the landward edge. Approximately 6 km south from T₂, along the seaward boundary of KISR (Kuwait Institute for Scientific Research) lies T₃ (Fig. 1b). This transect has also been infilled at the landward edge and planted with mangroves *Avicennia marina*.

Sampling collection. Microbial mats: Mat samples were collected from April 2001 to October 2001. Four sampling areas (L 30 cm, W 25 cm) were marked along the intertidal gradient, at each of the 3 transects, from high water spring to highest low water. Four random samples (5 cm²; D 1 cm) were obtained per area using a cube core. The samples were placed separately in each compartment of an ice tray and transferred to the laboratory.

Phytoplankton: Phytoplankton was collected from Kuwait Bay during early 1998 using a 20 µm mesh size plankton net (KAHLSICO; model #013WA250) equipped with a calibrated flow meter (KAHLSICO; model #005WB1000), towed for approximately 1 nautical mile (25 to 30 min). Material was placed in a plastic jar kept in a cool box and transported to the laboratory. The sample was passed through different mesh size sieves to remove zooplankton. The clean phytoplankton sample was then placed in a sealed plastic bag and frozen for later analysis.

Macrofauna: The following species were chosen for analysis due to their dominance within the study area.

(1) Intertidal fauna or species: 9 intertidal macrofauna species were collected to determine the gut content. These include the mud snail *Cerithidea cingulata*, mudskipper *Periophthalmus waltoni*, goby *Baleophthalmus boddarti*, mud crab *Leptochryseus kuwaitense*, *Uca sindensis*, *Nasima dotilliformis*, *Tyidoplax indica*, *Macrophthalmus dentipes*, and *Ilyoplax stevensi*. The species were caught by hand (digging) and/or by net

during low tide. The collected intertidal macrofauna were placed in plastic containers filled with filtered seawater and transported to the laboratory.

(2) Subtidal fauna or species: 6 subtidal species visiting the intertidal zone during high tide such as the blue crab *Portunus pelgicus*, jinga shrimp *Metapenaeus affinis*, greenback mullet *Liza subviridis*, Klunzinger mullet *Liza macrolepis*, silver sillago *Sillago sihama*, and seabream *Acanthopagrus* sp. were collected by placing baited fish traps along the transect at low tide and retrieving them after 2 tidal cycles. The fish trap samples were placed in an icebox to be transferred to the laboratory.

At the laboratory, burrowing brachyurans were placed in aquaria containing sterilized sediment from the mudflats which was laid at a 45° angle and covered halfway with filtered seawater. This produced an ebb tide effect, keeping the top end of the sediment exposed but moist, and allowed the organism the choice of immersion. The gastropod *Cerithidea cingulata* and jinga shrimp *Metapenaeus affinis* were also placed in the aquaria but without sediment. An aerator was placed in each aquarium, and during a 24 h period, faeces were collected using a pipette. These were placed in pre-labelled plastic jars with seawater and frozen until examination. The subtidal fish and crabs were dissected and gut contents were extracted. Contents of the gut and faeces of collected samples were then examined under a dissecting and a compound light microscope.

Analysis. Microbial mat composition microscopy: A sub-sample (5 mm²; D 1.5 mm) from each of the original mat samples was removed using a scalpel. Determination of sample depth was related to the fact that beneath 1.5 mm the black anoxic layer occurs. Each sub-sample was placed in 100 ml of filtered seawater, and gently mixed using a whirl homogenizer for duration of 2 to 3 min. A 1 ml sub-sample was extracted from the suspension and equally divided onto 5 glass slides. The number of cells on each slide was counted to give the number of algal cells per ml using a Nikon Microphoto FXA. Taxonomical determination of mat components to genera level was performed using techniques of Al-Hasan & Jones (1989).

Gut analysis: The gut of intertidal and subtidal macrofauna (6 individuals per species) was dissected out using surgical tools and gut content was then removed and placed in a pre-labelled vial containing filtered seawater. The composition of the gut content was examined under a stereo-dissecting microscope as well as under a compound light microscope.

Faeces analysis: Faecal pellets were collected from each aquarium using a pipette during a 24 h period. These were placed in pre-labelled plastic jars with filtered seawater and frozen until examination.

Isotope analysis: Microbial mat samples were collected within a 100 cm² patch to a thickness of 1 cm using a spatula. Only the top 5 mm of the mat, normally occupied by microphytobenthos, was used for the analysis. Where occurring, halophytes and planted mangroves were identified and leaves collected.

For macrofauna the flesh of intertidal gastropods was extracted by crushing the shell and then washing the flesh with distilled water to dislodge small shell remains. Large faunal species were directly dissected and muscle tissue was removed. Small infaunal crabs were too small for dissection, hence the whole animal was used. All samples were washed several times with distilled water, dried at 60°C for 24 h, placed in tightly sealed labelled vials and transferred for isotopic analysis to the School of Ocean Sciences (SOS), University of Wales, Bangor, UK.

Thoroughly dried samples were individually crushed and homogenised with a pestle and mortar. A sub-sample was weighed into precombusted silver boats (500°C, 3 h), and carbonate material was removed through a combination of HCl (10%) additions and drying at 40°C. The $\delta^{13}\text{C}_{\text{POC}}$ was determined from CO₂ generated by vacuum combustion in quartz tubes (Kennedy & Kennedy 1994) containing copper and pre-combusted copper oxide (910°C, 3 h). The CO₂ was collected by vacuum distillation and was measured on a PDZ-EUROPA GEO 20/20 mass spectrometer. Results are reported in the δ notation, i.e.:

$$\delta^{13}\text{C}_{\text{sample}} = 1000 \left(\frac{R_{\text{sample}}}{R_{\text{VPDB}}} - 1 \right) \quad (1)$$

where

$$R = \frac{^{13}\text{C}}{^{12}\text{C}} \times \text{VPDB}$$

Vienna Pee Dee Belemnite (VPDB) was the reference standard. The external measurement precision was better than $\pm 0.1\%$ based on analyses of an internal laboratory standard run concurrently with all the samples.

The fractional contribution of organic matter to the animal's diet can be explored using a simple mixing equation:

$$\delta^{13}\text{C}_{\text{animal}} = f_1 \delta^{13}\text{C}_{\text{source-1}} + f_2 \delta^{13}\text{C}_{\text{source-2}} \quad (2)$$

where f_1 to f_2 is the fractional contribution of each potential source and $\delta^{13}\text{C}_{\text{source-1}}$ to $\delta^{13}\text{C}_{\text{source-n}}$ is the isotopic composition of each of the sources.

RESULTS

Microbial mat composition

At both T₂ and T₃, *Microcoleus* spp. dominated the top shore where the sediment is almost dry, particu-

larly at the sand and boulder infill interface. At the fine mud interface where the actual mudflat starts and sediment is relatively moist, the abundance of *Microcoleus* spp. in the mat decreased until it was virtually absent and bundles of *Oscillatoria* spp. filaments dominated, appearing as a dark band at the mud interface. Below this level and lower across the mudflats extending towards the horizon, mats had a golden brown appearance and were dominated by benthic diatoms. At T₁, *Microcoleus* spp. dominated at the top of the shore, but *Oscillatoria* spp. was absent. Diatom-dominated mats occurred across the whole mudflat surface at the 3 transects, increasing in abundance within water-retaining depressions, and particularly between clay crevices at T₂.

Macrofaunal species migrate along the intertidal gradient. Therefore in order to determine their overall potential diet, the abundances of microbial mat composite at the 3 transects were compiled to obtain the average composition. Twenty genera belonging to 4 algal groups contribute to the mat assemblage (Table 1). Bacillariophyceae (diatoms) showed a high mean contribution of 61% followed by Cyanophyceae (blue-green algae) with 30.6%. Chlorophyceae (green algae) represented 6.9% of the mats sampled, while

Table 1. List of microphytobenthos genera contributing to the composition of microbial mats (top 1.5 to 2 mm) within 3 transects in Sulaibikhat Bay, as % of total cell count

Components	Mean %
Bacillariophyceae	
<i>Bacillaria</i> spp.	25.0
<i>Nitzschia</i> spp.	15.0
<i>Navicula</i> spp.	8.1
<i>Rhizosolenia</i> spp.	5.2
<i>Coscinodiscus</i> spp.	2.6
<i>Pleurosigma</i> spp.	2.6
<i>Gyrosigma</i> spp.	2.5
Total	61.0
Chlorophyceae	
<i>Cladophora</i> spp.	2.2
<i>Enteromorpha</i> spp.	2.2
<i>Chaetomorpha</i> spp.	1.6
<i>Chlamydomonas</i> spp.	0.6
<i>Urospora</i> spp.	0.3
<i>Acrosiphonia</i> spp.	0.1
Total	6.9
Cyanophyceae	
<i>Microcoleus</i> spp.	14.2
<i>Oscillatoria</i> spp.	8.5
<i>Chroococcus</i> spp.	3.7
<i>Lyngbya</i> spp.	3.0
<i>Calothrix</i> spp.	0.8
<i>Spirulina</i> spp.	0.3
Total	30.6
Rhodophyceae	
<i>Porphyra</i> spp.	0.3

Rhodophyceae (red algae) had the lowest contribution (0.3%). Since the abundance of chlorophytes and rhodophytes within the mat was low, the mat composition is described by its dominating constituents. Accordingly, diatoms make up 69.4% of the mat while blue-green algae form 30.6%. In general, the pennate diatoms *Bacillaria* spp. formed 28.6% of the mean total mat composition, followed by *Nitzschia* spp. and the filamentous cyanophytes *Microcoleus* spp. and *Oscillatoria* spp. The pennate diatoms *Navicula* spp. contributed 8.3%.

Gut and faecal analysis

Of the 9 macrofaunal species analysed for gut contents, 3 were intertidal species while the remainder were subtidal.

The intertidal faunal species included the common mud snail *Cerithidea cingulata*, the carnivorous mud-skipper *Periophthalmus waltoni*, and the herbivorous goby *Boleophthalmus boddarti*. In the gut of *C. cingulata* benthic algae consisting of diatoms and cyanobacteria filaments plus inorganic debris occurred. Fully intact crabs of the species *Tyloidiplax indica* and some other flesh were found in the gut of *P. waltoni*. Diatoms and sediment particles were present in the gut of *B. boddarti*.

The 6 subtidal species consisted of 2 invertebrates (crustaceans) and 4 vertebrates (osteichthyes). The edible blue crab *Portunus pelagicus* had flesh and skeleton remains of the small brachyuran *Tyloidiplax indica* in its gut. A green coloured organic residue occurred in the gut of the shrimp *Metapenaeus affinis*. In the gut of the mullet *Liza subviridis* algal material, foraminifera and organic residues were seen, while mullet *Liza macrolepis* appeared to feed on phytoplankton and a variety of microalgae represented mainly by benthic diatoms. Brachyurans and bivalves were found in the gut of *Sillago sihama*. In the gut of seabream *Acanthopagrus cuvieri* algae (*Ulva* sp. and *Enteromorpha* sp.), gastropods and other organic residues were found.

The faeces of 6 intertidal macrofaunal species were investigated (Table 2) for mat components. It was evident that the xanthid crab *Eurycarcinus orientalis* does not feed on mats; however, the remaining species all contained mat residues in their faeces. The endemic crab *Leptochryseus kuwaitense* and the fiddler *Uca sindensis*, both occupying the upper intertidal, contained a significant amount of non-digested benthic diatoms in their faeces. Fully intact cyanobacteria

Table 2. Presence and absence (–) of microbial mat components (diatoms, cyanobacteria filaments 'CBF') in the faecal product of some faunal species found along the intertidal mudflats of Sulaibikhat Bay. *shell only; **empty and full shells; ***full diatoms; +: sheath only, ++: empty and full sheaths, +++: full sheaths

No.	Species list	Location	Mat component	
			Diatoms	CBF
1	<i>Leptochryseus kuwaitense</i>	High intertidal	**	+
2	<i>Uca sindensis</i>	High	***	+
3	<i>Eurycarcinus orientalis</i>	Low	–	–
4	<i>Macrophthalmus dentipes</i>	Low	*	++
5	<i>Cerithidea cingulata</i>	Low	*	++
6	<i>Metapenaeus affinis</i>	Subtidal	*	+++

filaments outnumbered diatoms in the faeces of *Cerithidea cingulata* and that of the largest mud crab *Macrophthalmus dentipes*. Both species inhabit the mid-lower intertidal. A significant amount of intact blue-green algal filaments occurred in the faeces of the subtidal jinga shrimp *Metapenaeus affinis*.

Isotope analysis

The stable carbon isotopic ratios ($\delta^{13}\text{C}$) of major primary producers and dominating consumers (Jones 1986, Wright et al. 1990, Bishop & Khan 1999) on Sulaibikhat Bay mudflats are displayed in Table 3. The major primary producers on the mudflat are phytoplankton, the microbial mat/diatom complex (70% benthic diatoms, 30% cyanobacteria), the halophyte *Salicornia herbacea*, and the mangrove *Avicennia marina*. The introduced *A. marina* has the lightest isotope signature, while the microbial mat/diatom complex has the heaviest $\delta^{13}\text{C}$ value. The annual glasswort *S. herbacea* and phytoplankton had values slightly heavier than *A. marina*.

All consumers were relatively enriched with ^{13}C by comparison with the major primary producers. The $\delta^{13}\text{C}$ values of consumers were enriched by 6.3 to 12.3‰ relative to phytoplankton, enriched by 9.4 to 15.4‰ relative to *Salicornia herbacea*, and by 12.8 to 18.8‰ relative to *Avicennia marina*, but showed least enrichment (0.5 to 4‰) relative to the microbial mat/diatom complex (Fig. 2). This indicates that phytoplankton *S. herbacea* and *A. marina* cannot be important food sources for these consumers. Hence, almost 53% of all isotopically analysed consumers had $\delta^{13}\text{C}$ signatures close to that of microbial mats, with slight enrichment of 0.5 to 2‰. The remaining 47% were slightly more enriched by 2.6 to 6‰ relative to microbial mats.

Approximately 73% of analysed intertidal consumers were slightly more enriched (2.6 to 6‰) relative to

Table 3. $\delta^{13}\text{C}$ values of producers and consumers inhabiting the tidal mudflats of Sulaibikhat Bay. U: upper intertidal; M: middle intertidal; L: lower intertidal; S: subtidal; P: pelagic

Sample	Zonation	$\delta^{13}\text{C}$ (‰) Range	Mean (\pm SE)
Primary producers			
Phytoplankton	P	-21.64	-
Microbial mat/diatom complex	U	-14.55 to -16.17	-15.28 (0.35) ^(b)
<i>Salicornia herbacea</i>	U	-24.74	-
<i>Avicennia marina</i>	U	-28.09	-
Consumers			
<i>Leptochryseus kuwaitense</i>	U	-9.35	-
<i>Uca sindensis</i>	U	-10.82	-
<i>Uca annulipes albimana</i>	U	-9.26	-
<i>Nasima dotilliformis</i>	U	-12.63	-
<i>Tylodiplax indica</i>	U/M/L	-15.32	-
<i>Macrophthalmus dentipes</i>	M/L	-9.67	-
<i>Eurycarcinus orientalis</i>	M/L	-13.43, -13.48	-13.46 ^c
<i>Metaplex indica</i>	M/L	-14.70, -15.14	-14.92 ^c
<i>Portunus pelagicus</i>	S	-12.06 to -15.19	-13.66 (0.50) ^d
<i>Metapenaeus affinis</i>	S	-14.65, -14.79	-14.72 ^c
<i>Cerithidea cingulata</i>	M/L	-10.74, -13.61	-12.18 ^c
<i>Periophthalmus waltoni</i>	U/M/L	-10.76 to -13.06	-12.05 (0.44) ^d
<i>Boleophthalmus boddarti</i>	M/L	-8.79 to -11.73	-10.49 (0.51) ^d
<i>Acentrogobius ornatus</i>	S	-12.48 to -12.78	-12.64 (0.09) ^a
<i>Rhonicus stridens</i>	S	-13.65	-
<i>Sillago sihama</i>	S	-13.18	-
<i>Acanthopagrus cuvieri</i>	S	-13.52	-
<i>Synaptura orientalis</i>	S	-14.15	-
<i>Liza macrolepis</i>	S	-14.45	-

Sample number: ^a3; ^b4; ^c2; ^d5

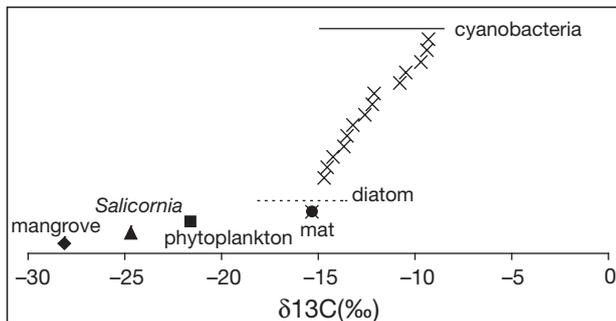


Fig 2. $\delta^{13}\text{C}$ signatures of intertidal and subtidal primary and secondary consumers, and $\delta^{13}\text{C}$ of primary producers that may contribute to their diet on mudflats of Sulaibikhat Bay (Table 3). X: $\delta^{13}\text{C}$ for macrofaunal species (Table 3) dotted line and thin bar: $\delta^{13}\text{C}$ of diatoms and cyanobacteria, respectively, from literature (Table 4)

microbial mats, while the remaining 27% had $\delta^{13}\text{C}$ values corresponding to those of the mats (0.5 to 2‰ enrichment). The dominating mud snail *Cerithidea cingulata* showed an approximate 3‰ enrichment. The endemic crab *Leptochryseus kuwaitense*, the fiddler crab *Uca annulipes albimana*, and *Macrophthalmus dentipes* all showed ~6‰ enrichment relative to the microbial mats. The fiddler crab *Uca sindensis*, which occupies the upper

intertidal, and the endemic crab *Nasima dotilliformis*, which is present along the upper intertidal extending slightly into the mid-intertidal zone, were both less enriched (2.7‰) relative to the microbial mat compared to the above mentioned brachyuran species. An enrichment of 1.8‰ was seen for *Eurycarcinus orientalis*, while the least enrichment within the brachyuran group was for *Metaplex indica* (~0.4‰), also a carnivore occurring towards low tide. On the other hand, the tiny ocyropid crab *Tylodiplax indica*, had a $\delta^{13}\text{C}$ signature of -15.32‰ almost equal to that of the mat. The intertidal gobies *Periophthalmus waltoni*, and *Boleophthalmus boddarti*, had mean $\delta^{13}\text{C}$ values relatively more enriched than the mat (3.2‰ and 4.8‰ enrichment respectively).

Almost all subtidal consumers feeding intertidally at high tide that were analysed were 1 to 2‰ enriched relative to the $\delta^{13}\text{C}$ signature of the microbial mat/diatom complex except the goby *Acentrogobius ornatus* which was enriched by ~3‰ relative to the mat. The edible blue crab *Portunus pelagicus*, showed 1.6‰ enrichment.

A low enrichment (0.6‰) was seen for juveniles of the shrimp *Metapenaeus affinis*, relative to the mat. The fish species *Liza macrolepis*, had the least enrichment relative to the mats (0.8‰) when compared with other fish species (Table 3), while silver sillago fish *Sillago sihama* had the highest enrichment of 2‰.

DISCUSSION

Microbial mat composition

In Sulaibikhat Bay, cyanobacteria dominate the coarser grained top shore sediments which are subject to desiccation, but are increasingly replaced by diatoms lower on the shore where fine sediments retain water at low tide. This is similar to European temperate shores where epipellic (motile) diatoms dominate the microbial mat complexes (Colijn & Dijkema 1981, Lucas & Holligan 1999). Madsen et al. (1993) found that benthic diatoms made up 75% of the biomass with cyanobacteria contributing the remainder. Watermann et al. (1999) also found that cyanobacteria favour high temperatures and coarser sediments as found in Kuwait.

Gut and faecal analysis

Results confirm that microbial mats are utilised by a range of intertidal and subtidal macrobenthic grazers. The results of the faecal analyses indicate that top shore species contained more benthic diatoms than cyanobacteria filaments, while the faecal pellets of lower shore species were dominated by cyanobacteria. This appears to be in contrast to the distribution of these mat components on the shore. As feeding selection between diatoms and cyanobacteria was not observed, it is likely that differential assimilation occurs after ingestion (Fenchel & Kofoed 1976).

Isotopic analysis

The stable isotope ratio has been shown to be particularly useful in identifying the origin of plant carbon sources supporting food webs of organisms at higher trophic levels (Fry & Sherr 1984). Table 3 shows the major sources of primary production in Sulaibikhat

Bay are isotopically distinct, and that their values agree with $\delta^{13}\text{C}$ measurements for similar plants sampled over a wide geographical range (Table 4).

Present measures of the stable carbon of microbial mats from Kuwait overlap values reported by others (Table 4). This variation in the stable isotope composition for benthic microbial mats is to be expected (Fry & Sherr 1984). Based on values of heavier $\delta^{13}\text{C}$ values for pelagic cyanobacteria (Calder & Parker 1973, Fry & Sherr 1984) and benthic cyanobacteria (Calder & Parker 1973, Pulich & Scalan 1987, Des Marais et al. 1989), $\delta^{13}\text{C}$ values heavier than -17‰ may be particularly prevalent in environments where cyanobacteria dominate in benthic microalgal biomass. In the present study benthic diatoms and cyanobacteria were the major components of the mats with a 70 and 30% contribution by each respectively to the mat. Hence, the isotopic value of these mats reflects the proportions of these components.

A compilation of estuarine benthic microalgal stable isotopic values from the literature (Table 4) produces a mean value of -16.2‰ for benthic diatoms and -10.93‰ for cyanobacteria, giving an average of

Table 4. $\delta^{13}\text{C}$ values of primary producers obtained from published literature on salt marsh-estuarine systems in different geographical locations, and present values from the present study

Sample	Location	$\delta^{13}\text{C}$ (‰)	Source
Phytoplankton	Malaysia	-19.6	Rodelli et al. (1984)
	Auke Bay, Alaska	-21.5, -20.6	Goering et al. (1990)
	S. California, USA	-22.4, -20.8	Kwak & Zedler (1997)
	Delaware Bay, USA	-22	Dittel et al. (2000)
	Mean \pm SE	-21.15 \pm 0.42	
		-21.64	Present study
<i>Salicornia virginica</i>	Georgia, USA	-26	Haines (1976a,b)
	S. California, USA	-27.6, -26.7	Kwak & Zedler (1997)
	Santa Barbara, USA	-29.2, -25.9	Page (1997)
Mean \pm SE	-26.08 \pm 0.61		
<i>Salicornia herbacea</i>		-24.74	Present study
Benthic flora			
Microalgae	Malaysia	-18.7	Rodelli et al. (1984)
	S. Carolina, USA	-13.5, -12.1	Couch (1989)
	N. Carolina, USA	-17.5, -13	Currin et al. (1995)
	Mallorca, Spain	-16.5, -16, -14.9	Jennings et al. (1997)
	Mean \pm SE	-15.28 \pm 0.82	
		-15.28 \pm 0.35	Present study
Cyanobacteria	Arabia	-8.5	Calder & Parker (1973)
	Bahamas	-8.5	Barghoorn et al. (1977)
	Crane Key, Florida	-11.1	Barghoorn et al. (1977)
	Shark Bay, Australia	-12.7	Barghoorn et al. (1977)
	Virgin Islands	-9.4	Fry et al. (1982)
	Texas	-11.5	Pulich & Scalan (1987)
	Texas	-14.9	Pulich & Scalan (1987)
	Mean \pm SE	-10.93 \pm 0.90	
Diatom			
<i>Gyrosigma</i> sp.	Georgia, USA	-17.9	Haines (1976a,b)
	Nova Scotia, Canada	-18.1, -13.6	Schwinghamer et al. (1983)
<i>Navicula</i> sp.	Malaysia	-14.8	Rodelli et al. (1984)
Mean \pm SE		-16.24 \pm 0.91	

–13.6‰, assuming an equal contribution by each. Using these cited $\delta^{13}\text{C}$ values for the calculated contributions of both mat components dominating mats found during the present study produces a $\delta^{13}\text{C}$ value of –15.4‰, which is close to the mean of $\delta^{13}\text{C}$ signatures actually measured for microbial mats in the present study ($-15.3 \pm 0.35\text{‰}$) and the mean cited $\delta^{13}\text{C}$ values for benthic microalgae ($-15.3 \pm 0.82\text{‰}$). This demonstrates that the $\delta^{13}\text{C}$ signature of the microbial mats in Sulaibikhat Bay is an aggregate of the $\delta^{13}\text{C}$ signals for benthic diatoms and cyanobacteria.

$\delta^{13}\text{C}$ measurements primarily act as a trace of sources of primary production. Animal tissues are built with atoms of the food they assimilate thus retaining the stable isotope signature of the food. However enrichment/depletion occurs reflecting either mixing of nutrition sources or selective excretion or respiration (Fry & Sherr 1984). Virtually all benthic and pelagic consumers sampled during this study have $\delta^{13}\text{C}$ signatures falling within a narrow range of –15.3 to –9.3‰, showing least enrichment (0.5 to 4‰) relative to the signature of the microbial mat/diatom complex, rather than any of the other sources of primary production (Fig. 2). This is in agreement with McConaughy & McRoy (1979), Fry & Sherr (1984) and Rau et al. (1992) who found $\delta^{13}\text{C}$ enrichment values of 0.7 to 2.2‰ per trophic level. However, some primary consumers show increased enrichment relative to the signature for microbial mats and closer to cited values obtained for cyanobacteria alone (Tables 3 & 4). According to the zonation of mat components along the intertidal gradient, in conjunction with the faecal results, it would only be logical to expect the $\delta^{13}\text{C}$ value of primary

consumers to reflect a greater fraction of diatoms as we move down the shore (more negative; lighter $\delta^{13}\text{C}$ value). However, this was not the case when applying the '2-source mixing model' of diets for this study (Eq. 2 & Table 5). It was apparent that some of the primary consumers occurring along the mid- to low intertidal zone exhibited a more positive signature indicating a larger contribution of cyanobacteria to the diet. However, diet mixing between microbial mat complex and other sources of primary production (phytoplankton *Salicornia*) is unlikely since upon applying the mixing model of diets, the microbial mat complex contributes the highest fraction to the diet.

Although further validation is required, the progressive ^{13}C -enrichment observed for these species may be due to selective herbivory (Dittel et al. 2000), selective digestion (Caswell & Reed 1976), or preferential assimilation (Ponsard & Ardit 2000) of the heavier mat component (cyanobacteria). Table 6 compares $\delta^{13}\text{C}$ values for

Table 6. $\delta^{13}\text{C}$ signatures for a selection of consumers from present study, and those ecologically similar in a Malaysian mangrove/mudflat system (Rodelli et al. 1984). ^hherbivore; ^ccarnivore; ^oomnivore; ^ddeposit feeder

Consumer genera	$\delta^{13}\text{C}$ (‰)	
	Unvegetated mudflats (present study)	Mangrove-associated mudflats
<i>Cerithidea</i> ^d	–12.05	–24.05
<i>Metaplex</i> ^c	–14.92	–22.35
<i>Uca</i> ^o	–10.04	–19.28
<i>Metapeneus</i> ^o	–14.72	–20.35
<i>Boleophthalmus</i> ^h	–10.49	–15.70
<i>Periophthalmus</i> ^c	–12.05	–22.60
<i>Liza</i> ^d	–14.45	–22.50
Primary producer		
Microbial mat/ diatom complex	–15.28	–17.82
Mangrove plants	–	–27.10

Table 5. Fraction (%) of mat component using Eq. (2), in the $\delta^{13}\text{C}$ values of macrofaunal species of Sulaibikhat Bay mudflats, in comparison to other primary production sources. U: upper intertidal; U/M: upper to middle intertidal; M/L: middle to lower intertidal; S: subtidal

Species	Zonation	Cyanobacteria vs. Diatoms	Cyanobacteria vs. Phytoplankton	Cyanobacteria vs. <i>Salicornia</i>
<i>Leptochryseus kuwaitense</i>	U	100	100	100
<i>Uca sindensis</i>	U	100	100	100
<i>Uca albimana</i>	U	100	100	100
<i>Nasima dotilliformis</i>	U/M	68	84	88
<i>Tyloidiplax indica</i>	M/L	18	59	68
<i>Cerithidea cingulata</i>	M/L	75	88	91
<i>Boleophthalmus boddarti</i>	M/L	100	100	100
<i>Macrophthalmus dentipes</i>	M/L	100	100	100
<i>Metapeneus affinis</i>	S	29	65	73
<i>Liza macrolepis</i>	S	34	67	75

some of the consumers in Sulaibikhat Bay with ecologically similar genera that derive their nutrition from a Malaysian mangal system (Rodelli et al. 1984). Despite the presence of microbial mats on the Malaysian mudflats where mangroves dominate, the contribution by microbial mats to food webs appears to be insignificant. Page (1997) stated that $\delta^{13}\text{C}$ enrichment of 1.5 to 3‰ in deposit-feeding bivalves inhabiting a Californian salt marsh relative to other fauna occurred due to selective assimilation of carbon from benthic microalgae enriched in $\delta^{13}\text{C}$ rather than grazing on the detritus of vascular salt marsh plants. Kwak & Zedler (1997) used stable isotopes to characterise food webs in California wetlands. Their results indicated that macroalgae, marsh microalgae and *Spartina* all support consumers in these ecosystems. However, in the absence of *Spartina* from salt marsh, organic input of macroalgae and microalgae formed the base of the food web.

Results of the present study indicate that Kuwait food webs appear to rely almost entirely upon microbial mats as their source of nutrition, simply because they are the most abundant source of nutrition. Nevertheless, the macrofaunal biodiversities, abundances and biomasses in Kuwait mudflats (Al-Zaidan 2002) are higher than or as high as similar habitats elsewhere in the Gulf (Apel & Türkay 1999) and the world (Swennen et al. 1982, Govindan et al. 1983). And as Table 3 and Fig. 2 indicate, not only do many of the intertidal macrofauna depend upon microbial mats, but also there are food links to commercial shellfish (e.g. *Metapenaeus affinis*, *Portunus pelagicus*) and fish species (e.g. *Liza macrolepis*, *Sillago sihama*, *Acanthopagrus* sp.). Recent research (Al-Zaidan et al. 2003) suggests that the biodiversity is declining due to presence of urbanisation and industrialisation. Present findings indicate a direct link to the support of key local fisheries underlining the necessity for conservation of these mudflats.

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