

# Outwelling from arid mangrove systems is sustained by inwelling of seagrass productivity

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**ABSTRACT:** Mangrove forest productivity is normally sustained by nutrients from terrestrial runoff, with freshwater inputs driving the resulting outwelling of production, but arid mangroves lack this input. The movement of material between seagrass beds and mangroves was examined using the stable C and N isotopic composition of organisms, sediments and suspended matter in 3 seagrass–mangrove transects in the Arabian Gulf. The isotopic signal of suspended particulate material indicated a mixed origin that did not differ over a spring tide. Filter feeders showed significant <sup>13</sup>C enrichment along transects from mangrove forests into seagrass beds, indicating that location within a habitat had a significant effect on isotopic composition. Similarly,  $\delta^{13}\text{C}$  of both sediments and grazers increased sharply outside the mangrove forest, suggesting retention of mangrove carbon, although some outwelling was detected, the strength of which was site specific. The lack of freshwater-mediated nutrient inputs suggests any outwelling of mangrove ecosystem productivity must be balanced by inwelling, and isotopic signatures of both sediment grazers and filter feeders found within the mangrove forest confirmed the inwelling of seagrass production. Significant mangrove isotope signals in the tissue of juveniles of fishes commercially harvested offshore indicate ontogenetic movement of carbon. Additional biological movement of mangrove carbon through ontogenetic migration and ‘trophic relay’ is evidenced by the isotopic signature of juvenile and mature fish captured in waters exiting the mangrove forest, which indicated they fed on mangrove-sustained food webs. This study demonstrates tight coupling between arid mangroves and subtidal seagrass areas and implies that arid mangroves cannot be managed or replanted without consideration of connectivity to downstream systems such as seagrasses.

**KEY WORDS:** Stable isotope · Carbon · Nitrogen · Arabian Gulf · Carbon flux · Trophic guilds

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## INTRODUCTION

Mangrove forests are amongst the most productive tropical ecosystems (Alongi 2012), with distributions mostly limited to areas with a mean winter water temperature above 20°C (Alongi 2002). Mangrove productivity increases with proximity to the equator (Alongi 2002, Kristensen et al. 2008), as benign conditions and a steady supply of nutrients and freshwater from rainfall and runoff feed mangrove pro-

duction. These factors combined with longitude also influence species distribution, with the fewest mangrove species present in Western Africa and South America and the most diverse mangroves found in the equatorial Indo-West Pacific (Duke et al. 1998). Likewise, species numbers also decline with increasing latitude and cooler temperatures, so that at higher latitudes mangroves are reduced to monospecific stands of *Avicennia marina* or *A. germinans*; diversity is also depressed in areas of low rainfall and

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freshwater runoff and, conversely, enhanced where salinity is reduced (Duke et al. 1998).

An estimated 40% of the organic carbon produced by mangroves is surplus to ecosystem requirements (Duarte & Cebrian 1996), and it was similar excessive coastal primary productivity noted in salted marshes that inspired Odum's (1968) hypothesis of outwelling of coastal carbon from primary producers to support the high secondary production in offshore waters. Yet, outwelling is context dependent; it is driven by biological processes that regulate the amount of organic material available for export, such as the amount of litter production and *in situ* consumption by fauna, and the biological and physical processes that enable outward transport. Crabs are particularly important in leaf litter consumption and burial; in East Africa, herbivorous grapsid crabs on the high shore remove all litter fall (Olafsson et al. 2002). In contrast, in Florida (USA), where carnivorous and detritivorous crabs dominated, leaf herbivory appeared to be insignificant (McIvor & Smith 1995). The amount of leaf litter/particulate organic material (POM) available for export is therefore dependent on the species and density of leaf-eating fauna present. Previous studies of mangrove forest in the Arabian Gulf region suggested that litter-processing macrofauna are absent or rare (Cooper 1997, Al-Khayat & Jones 1999), indicating that mangrove POM may be available for export. Physical processes that drive POM outwelling from mangrove forests are related to tidal amplitude, rainfall, hydrology and geomorphology. In northern Australia, where there is a pronounced dry season, the amount of outwelled POM varies throughout the year, with significant reduction in the nutritional contribution of mangroves to penaeid shrimp living in nearby seagrass beds during the dry season (Loneragan et al. 1997).

The present study focused on mangrove systems on the coast of Qatar in the Arabian Gulf with almost no freshwater runoff, as rainfall is restricted to 75 mm yr<sup>-1</sup>, and where tidal amplitude is only 1.6 m (UN 1997), indicating that there is limited opportunity for POM/leaf litter to be exported out of the mangrove forests. Previous studies have shown that these arid mangroves were an insignificant source of nutrition for 2 penaeid species found in adjacent seagrass beds (Al-Maslamani et al. 2012). This apparent lack of outwelling was explained by the arid environment and low productivity of the mangroves due to the combined stresses of extreme winter and summer temperatures and high salinity. This hypothesis is supported by the work of Sheppard et al. (1992), who described these mangrove trees as stunted and of

low density. However, some resident invertebrate fauna within these mangrove systems derive most of their nutrition from mangrove production (Al-Maslamani et al. 2013), which suggests that productivity may be retained within the mangrove forest and that even stressed mangroves are capable of supporting faunal communities. Moreover, isotopic evidence suggested that seagrass production accounted for a significant part (0.2 to 18%) of the diet of the small mangrove-resident crustaceans on which these mangrove-resident palaemonid shrimp feed, suggesting inwelling of seagrass material into the mangrove forests (Al-Maslamani et al. 2013).

Inwelling from other habitats to mangrove forests is not well documented, but isotopic ratios of sediment in *Rhizophora* mangrove in Belize suggested that seagrass was often a significant component (Wooller et al. 2003). Similarly, influx of seagrass and other primary producers was thought to be responsible for the more enriched  $\delta^{13}\text{C}$  signature of sediments in Asian (Kennedy et al. 2004), Indian and Sri Lankan mangrove systems (Bouillon et al. 2003) and for the nitrogen enrichment found in Kenyan (Middelburg et al. 1996) and Mexican mangrove forest sediment (Gonneea et al. 2004). Additionally, Gonneea et al. (2004) suggested that any potential sedimentary contribution from seagrass to mangrove systems is only limited by the available biomass and productivity of the surrounding seagrass beds.

The current health and extent of seagrass in Qatari waters suggests that they could supply a significant portion of the organic matter in sediments within mangrove systems. Using stable isotopes, the contribution of mangrove and seagrass production to sediments and fauna of different trophic guilds (sedentary filter feeders, sediment grazers and mobile predators) along transects through mangrove trees and down into the seagrass beds was used to test the hypothesis that there was limited exchange of material between arid mangrove stands and downstream seagrass beds.

## MATERIALS AND METHODS

### Study site and sampling

The study was carried out at 3 sites on the east coast of Qatar in the Arabian Gulf (Fig. 1). Two sites were in the Al Dhakira Bay complex, of which the western site (25°44.880' N, 51°33.498' E) was an embayment with a restricted 200 m wide opening into the rest of the complex and comprised 49.5 ha

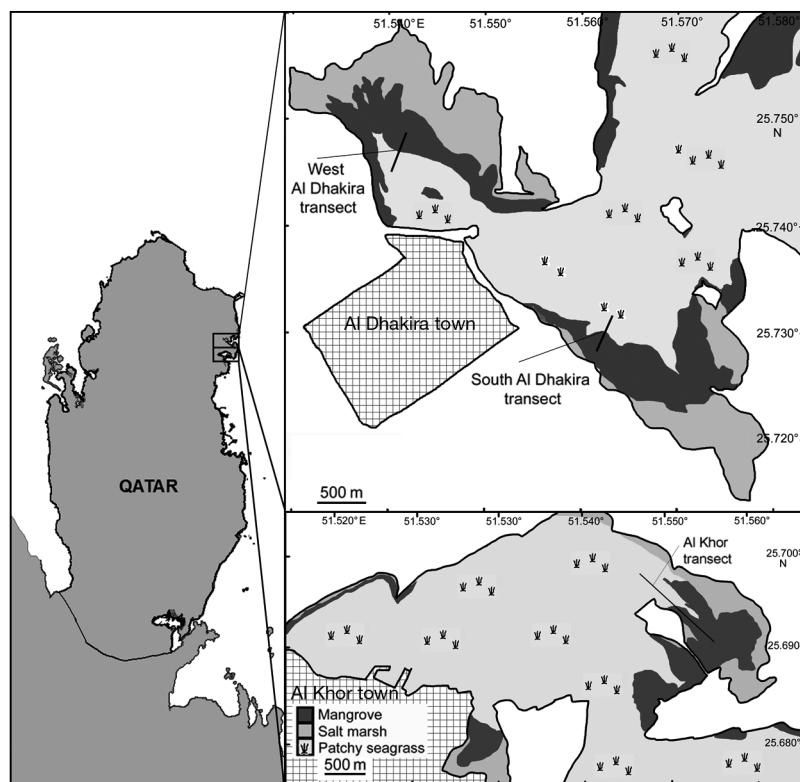


Fig. 1. Mangrove areas and sampled transects in South and West Al Dhakira and Al Khor, Qatar

of *Avicennia marina*, the only mangrove species in Qatar, and 49 ha of seagrass, mainly *Halodule uninervis* with some *Halophila stipulacea*. The more open southern site (25° 43.758' N, 51° 33.738' E), separated by the town of Al Dhakira, supported 81.5 ha of *A. marina* that transitions seaward to sandy sediment and a 205 ha area of seagrass. The third site was in the east of Al Khor Bay (25° 41.643' N, 51° 33.160' E), where a 70 ha *A. marina* stand transitioned seaward through sandy sediment into a 420 ha area of seagrass, also dominated by *H. uninervis* with sparse *H. stipulacea*.

At each of these sites, transects were sampled from dense, subtidal seagrass beds up into the mangrove stands (Fig. 1). The Al Khor transect (~1100 m) was sampled in October 2011 and again in May 2012, the 2 transects in Al Dhakira (~400 m) were sampled only in May 2012. Along each transect, sediment cores were extracted and the top 2 to 3 mm were retained for analysis. Around each sediment station during the 2012 sampling, macrophyte material (seagrass, mangrove and algae) and sedentary faunal species were hand-collected, with special attention paid to sediment grazers and filter feeders. A hand-pulled

seine net (6 m long and 1.5 m high, with internal net mesh size of 0.5 mm and external net mesh size of 5 mm) was also used to catch more mobile fauna in the seagrass. Within the mangrove stands, mobile fauna was caught using fyke-type, funnel-mouthed bag traps of 5 mm mesh size with a single 1.5 m × 0.2 m leader. Fyke nets were placed at least 5 m inside the mangrove forest and angled across drainage channels to catch fauna exiting the forest on the ebbing tide. Sediments, plant and animal samples were stored on ice until arrival at the laboratory.

The tidal re-suspension and exchange of POM was examined in May 2012 by the hourly collection of water samples (from 10 cm below the water surface) over a spring tidal cycle for 12 h starting from low water. Samples were collected from a point over bare sediment between the mangrove stands and seagrass beds in Al Khor and Al Dhakira adjacent to transects. Water samples were immediately prefiltered through a 100 µm sieve to remove zooplankton

prior to onsite vacuum filtration through pre-combusted GF/F Whatman glass fibre filters.

In the laboratory, soft tissue minus guts were removed from the sediment-grazing gastropods, filter-feeding bivalves and barnacles, and muscle tissue was extracted from fish and crustacean samples; the resulting samples were rinsed in distilled water. Plant samples were also rinsed in distilled water to remove sediment, and sand grains were removed with forceps. All samples were oven dried to constant weight at 50°C. Sediments were sequentially acidified with 0.1 M HCl and oven dried repeatedly until addition of HCl resulted in no bubbling, indicating that all carbonates had been removed, after which the sediment was oven dried to constant weight at 50°C. Comparison with 10 unacidified samples indicated that while acidification significantly altered  $\delta^{13}\text{C}$  signatures, no effect was detected on  $\delta^{15}\text{N}$  signatures. All samples were homogenised and weighed into tin cups (Elemental Microanalysis) before being analysed for  $^{13}\text{C}$  and  $^{15}\text{N}$  isotopes using a PDZ Europa ANCA-GSL elemental analyser linked to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon). The POM-loaded GF/F filters were

fumigated for 12 h with concentrated HCl to remove any carbonates, and subsequently re-dried. The GF/F filters and sediments were analysed using an Elementar Vario EL Cube (Elementar Analysensysteme) also connected to a PDZ Europa 20-20 isotope ratio mass spectrometer. Standards were run interspersed with samples, which resulted in standard deviations of  $<0.2\%$  for  $\delta^{13}\text{C}$  and  $<0.3\%$  for  $\delta^{15}\text{N}$ .

### Data processing and analysis

The resulting  $\delta^{13}\text{C}$  values were mathematically corrected for lipid content when C:N ratios of animal tissue were greater than 3.5 (using the equation  $\Delta\delta^{13}\text{C} = -3.32 + 0.99 \times \text{C:N}$ ) following Post et al. (2007). Those authors reported that this mathematical correction removed 91% of the negative impact of lipids on the  $\delta^{13}\text{C}$  values in animals. Literature values, derived from a meta-analysis of predominantly aquatic species, were used for diet–consumer isotopic discrimination; we applied  $\Delta^{13}\text{C}$  values of  $0.3 \pm 1.28\%$  and  $1.3 \pm 1.27\%$  for animals analysed whole and excised muscle tissue, respectively, and likewise  $\Delta^{15}\text{N}$  values of  $2.1 \pm 1.6\%$  and  $2.9 \pm 1.24\%$  were used (McCutchan et al. 2003). Recently fallen *A. marina* leaves, *H. uninervis* leaves and phytoplankton sampled using 52  $\mu\text{m}$  mesh net in the open sea to minimise contamination by sediment were used as primary producers in the Bayesian isotopic mixing model SIAR (Parnell et al. 2008) to examine their relative contributions to the sediments, POM and to the nutrition of fauna in different trophic guilds. SIAR was selected as it allows uncertainty about the meta-analysis discrimination factors to be incorporated into the model (Parnell et al. 2010). Modal contributions are given, as this represents the most likely contribution (Parnell et al. 2008), in combination with the 95% credible intervals of the mean, with the exception of the sediment grazers where the mixSIAR model (Stock & Semmens 2013) was used to give the combined dietary contribution to the sediment grazers at each of the sample sites. Isotopic compositions of sedentary filter feeders and sediment grazers were used to examine the physical movement of C and N between habitats, while the isotopic composition of mobile fauna caught inside mangrove forests was used to determine the contribution of mangrove primary production to their nutrition and hence potential for export by trophic relay and ontogenetic migration.

The contributions of phytoplankton, mangrove and seagrass to the sediment samples and POM were

analysed assuming that source isotopic compositions remained unchanged after their incorporation in POM and sediment (Gonneea et al. 2004), while a single level of discrimination was used for estimating the dietary contribution of the grazers and filter feeding bivalves in seagrass and mangrove habitats, omitting data from the sandy transition zone. For other fauna, trophic level was estimated using 2.1% for the first trophic step above the mean  $\delta^{15}\text{N}$  values of the primary producers and an additional 2.9% for each higher trophic level (Shang et al. 2008, Al-Maslamani et al. 2012). Prior to isotopic modelling, differences in isotopic signals between habitats were examined using analysis of variance (ANOVA). General linear modelling (GLM) analysis was used to compare isotopic composition between the 3 sediment grazers and the sediments in seagrass and mangrove habitats. All data complied with ANOVA test assumptions with no need for data transformation. Isotopic values are presented as mean  $\pm$  SD.

## RESULTS

### Trophic resolution

The isotopic values for the primary producers and consumers used in the mixing models are shown in Table 1. The C and N signatures of primary producers were isotopically well separated from each other, allowing good resolution in determining their contribution to the sediment, POM and fauna.

The trophic hierarchy of organisms feeding within the 3 sampling sites was determined by their mean  $\delta^{15}\text{N}$  signature according to the procedure of Minagawa & Wada (1984) (Fig. 2). The divisions between primary consumption, omnivory and carnivory are isotopically based on the average enrichment (discrimination – see ‘Materials and methods’) in  $^{15}\text{N}$  at each trophic step and supported by dietary literature (e.g. Sukumaran & Neelakantan 1997, Ward & Shumway 2004). Filter feeders ranged from almost pure primary consumers, such as *Brachidontes variabilis*, through to the omnivorous *Balanus amphitrite* that feed almost 1 trophic level higher. The trophic range of sediment grazers was more conservative, with  $<1\%$   $\delta^{15}\text{N}$  separating *Osilinus kotschyi*, *Cerithidea cingulata* and *Clypeomorus bifasciata*. From the traps that caught mobile species exiting the mangrove stands on the ebbing tide, *Aphanius dispar* (trophic level, TL = 3.0), *Gerres longirostris* (TL = 3.74) and *Terapon puta* (TL = 3.94) were the most frequently caught fish species.

Table 1. Mean  $\pm$  SD of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of samples from the 3 sample locations in each habitat (M: mangrove, SG: seagrass) and number of samples collected (n). The extended table is available in the Supplement at [www.int-res.com/articles/suppl/m507p125\\_supp.pdf](http://www.int-res.com/articles/suppl/m507p125_supp.pdf). POM: particulate organic material

Sample	Habitat	Al Khor			South Al Dhakira			West Al Dhakira		
		Mean $\delta^{13}\text{C}$ $\pm$ SD	Mean $\delta^{15}\text{N}$ $\pm$ SD	n	Mean $\delta^{13}\text{C}$ $\pm$ SD	Mean $\delta^{15}\text{N}$ $\pm$ SD	n	Mean $\delta^{13}\text{C}$ $\pm$ SD	Mean $\delta^{15}\text{N}$ $\pm$ SD	n
<i>Avicennia marina</i> leaf (brown)	M	-29.2 $\pm$ 0.2	-2 $\pm$ 0.5	4	-28.2 $\pm$ 0.9	-2.4 $\pm$ 1.1	7	-30.1 $\pm$ 0.6	-2.8 $\pm$ 0.5	4
<i>Halodule uninervis</i> leaf	SG	-9 $\pm$ 1.2	-3.9 $\pm$ 3.2	129	-9.3 $\pm$ 0.8	-5.2 $\pm$ 2.1	5	-8.6 $\pm$ 1	-0.8 $\pm$ 1.3	5
Phytoplankton		-19.1 $\pm$ 1.4	4.1 $\pm$ 0.8	3	-19.1 $\pm$ 1.4	4.1 $\pm$ 0.8	3	-19.1 $\pm$ 1.4	4.1 $\pm$ 0.8	3
Sediment Oct	SG	-15.4 $\pm$ 0.4	1.6 $\pm$ 0.6	5						
	M	-26.1 $\pm$ 0.4	-1.2 $\pm$ 0.2	8						
Sediment May	SG	-15.2 $\pm$ 0.5	1.4 $\pm$ 0.3	5	-18.8 $\pm$ 1.4	-2.3 $\pm$ 1.3	7	-21.5 $\pm$ 1.2	-2.7 $\pm$ 1.7	4
	M	-24.1 $\pm$ 1.6	-0.3 $\pm$ 1.3	6	-23.4 $\pm$ 0.2	-2.4 $\pm$ 0.5	3	-26.4 $\pm$ 0.5	-1.7 $\pm$ 0.3	6
POM (suspended)		-21 $\pm$ 1	-0.2 $\pm$ 1	9				-14.6 $\pm$ 3.2	1 $\pm$ 0.6	10
<i>Cerithidea cingulata</i>	SG	-14.5 $\pm$ 0.7	1.2 $\pm$ 0.4	4	-12 $\pm$ 0.6	2.4 $\pm$ 0.2	4	-16.6 $\pm$ 0.6	2.1 $\pm$ 0.1	4
	M	-21.5 $\pm$ 0.3	2.3 $\pm$ 0.1	3	-16.2 $\pm$ 0.4	0.9 $\pm$ 0.2	4	-21.3 $\pm$ 1	1.5 $\pm$ 0.6	3
<i>Brachidontes variabilis</i>	SG	-16.5 $\pm$ 1.1	2.6 $\pm$ 0.5	15				-18.5 $\pm$ 0.6	1.1 $\pm$ 0.4	7
	M	-17.9 $\pm$ 1.5	1.6 $\pm$ 0.3	6				-19.6 $\pm$ 0.4	1.8 $\pm$ 0.2	4
<i>Clypeomorus bifasciata</i>	SG	-11.5 $\pm$ 1.4	3.9 $\pm$ 0.4	8	-13.4 $\pm$ 1.6	2.8 $\pm$ 0.3	4	-15.8 $\pm$ 0.9	2.4 $\pm$ 0.7	5
	M	-20.6 $\pm$ 1.4	2 $\pm$ 0.5	4	-16.4 $\pm$ 0.4	1.9 $\pm$ 0.2	4	-21.2 $\pm$ 0.9	1 $\pm$ 1.1	4
<i>Osilinus kotschy</i>	SG	-10.7 $\pm$ 1.4	3.8 $\pm$ 0.3	14	-14.1 $\pm$ 0.3	2.8 $\pm$ 0.2	4	-16.7 $\pm$ 2.3	2.7 $\pm$ 0.4	5
	M	-20.4 $\pm$ 1.9	2.7 $\pm$ 0.2	4	-19.2 $\pm$ 0.8	2.2 $\pm$ 0.3	3	-22.1 $\pm$ 0.3	1.6 $\pm$ 0.4	3
<i>Balanus amphitrite</i>	SG	-14.2 $\pm$ 1.3	4 $\pm$ 0.8	4				-16.7 $\pm$ 0.5	4.9 $\pm$ 0.4	4
	M	-16.7 $\pm$ 0.9	4.3 $\pm$ 0.8	6				-17.5 $\pm$ 1.8	5.1 $\pm$ 0.5	4
<i>Aphanius dispar</i>	M	-15.2 $\pm$ 1.1	4.5 $\pm$ 0.2	6	-15.9 $\pm$ 1.2	5.2 $\pm$ 0.4	3	-16.8 $\pm$ 0.5	5.5 $\pm$ 0.4	3
<i>Gerres longirostris</i>	M	-14.3 $\pm$ 3.3	7.1 $\pm$ 0.4	7	-15.4 $\pm$ 0.2	6.6 $\pm$ 0.1	4	-18.3 $\pm$ 0.8	6.5 $\pm$ 0.4	3
<i>Terapon puta</i>	M	-15.2 $\pm$ 0.3	7.7 $\pm$ 0.3	3	-14.2 $\pm$ 0.3	6.7 $\pm$ 0.4	3	-17.3 $\pm$ 1.1	7.4 $\pm$ 0.3	3

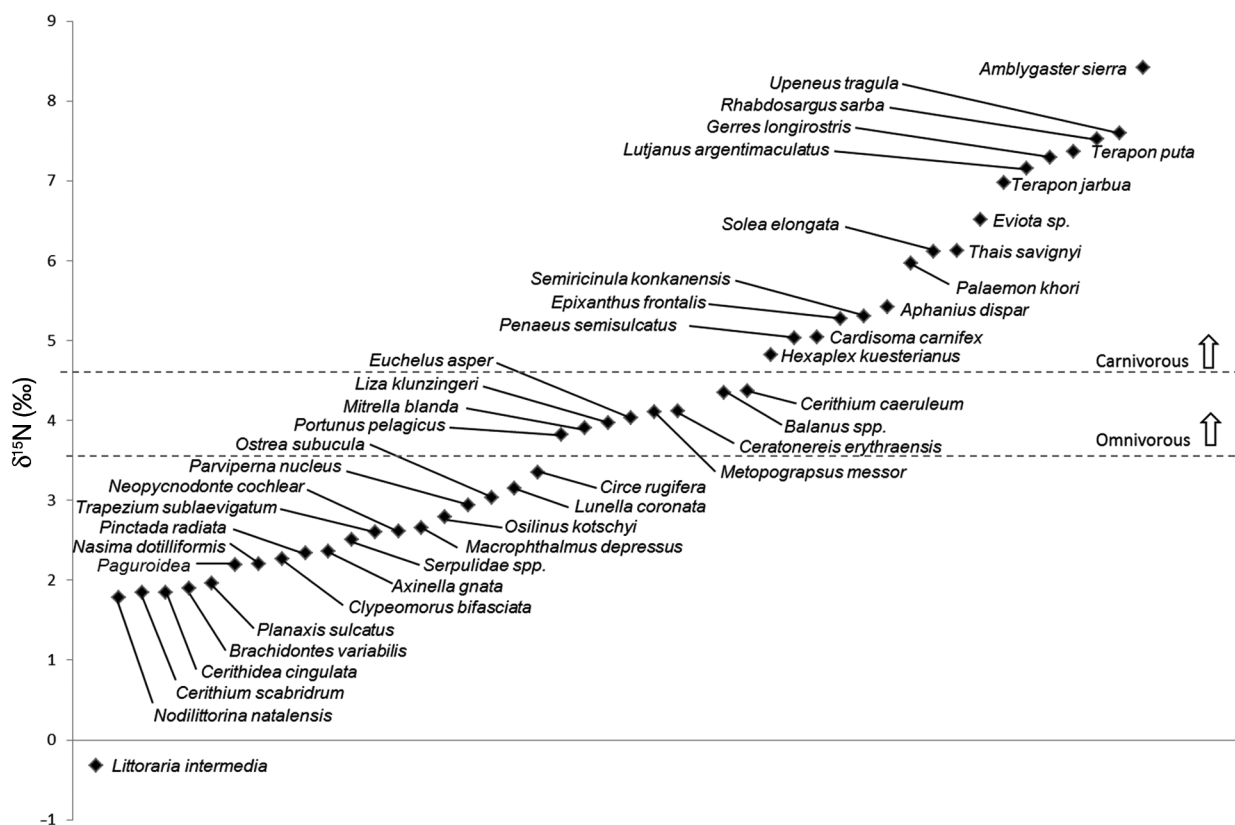


Fig. 2. Trophic hierarchy in the mangrove/seagrass food webs at 3 locations as determined by mean  $\delta^{15}\text{N}$  signatures. Average  $\delta^{15}\text{N}$  signature is  $-0.84\text{‰}$  for all primary producers (mangrove, seagrass and phytoplankton) and  $-1.59\text{‰}$  for sediment (not indicated)

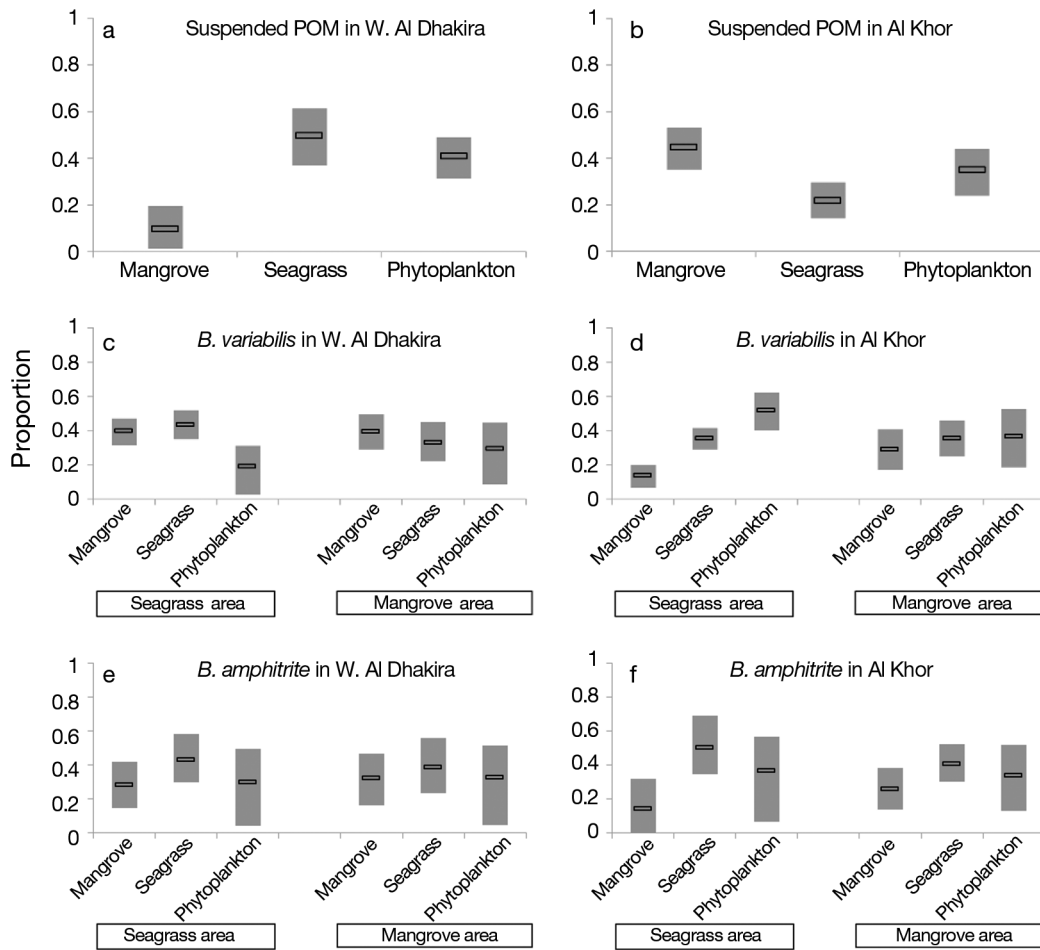


Fig. 3. Modal proportion and 95 % credible intervals of the contribution of mangrove, seagrass and phytoplankton to the suspended particulate organic material (POM) sampled between *Avicennia marina* stands and *Halodule uninervis* beds at (a) West Al Dhakira and (b) Al Khor, to the filter feeder *Brachidontes variabilis* sampled in mangrove and seagrass areas in (c) West Al Dhakira and (d) Al Khor, and to *Balanus amphitrite* sampled in mangrove and seagrass areas in (e) West Al Dhakira and (f) Al Khor

### Physical mixing of carbon

Across both sites there was no significant difference in  $\delta^{13}\text{C}$  values for POM in samples from the rising tide inflowing across the seagrass beds and that sampled from the ebbing tide outflowing from the mangroves (2-way ANOVA,  $F = 2.95$ ,  $p = 0.107$ ), although the mean  $\delta^{13}\text{C}$  for POM at Al Khor was significantly more depleted ( $-20.95 \pm 1.03\text{‰}$ ) than that of West Al Dhakira ( $-14.57 \pm 3.18\text{‰}$ ,  $F = 37.04$ ,  $p < 0.001$ ; Table 1). SIAR analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated that mangrove material made up 45% of POM in Al Khor and only 10% in West Al Dhakira (Fig. 3a,b). The C:N ratio of POM samples was  $6.5 \pm 0.5$  in Al Khor and  $7.4 \pm 2.0$  in Al Dhakira. The colour of the POM deposited on the filter paper suggested that suspended sediment, not phytoplankton, was

the dominant fraction present in the water column, and C:N ratios of POM were closer to those of sediment ( $13.3 \pm 2.4$ ) than to those of phytoplankton ( $17.8 \pm 4.7$ ).

The influence of mangrove and seagrass  $\delta^{13}\text{C}$  values on filter feeding molluscs along the tidal elevation gradient was confined to *B. variabilis*, being the only filter feeding mollusc present in both habitats at 2 sites (not at the South Al Dhakira site). Two-way ANOVA showed that both site ( $F = 29.3$ ,  $p < 0.001$ ) and habitat ( $F = 10.72$ ,  $p = 0.004$ ) significantly influenced  $\delta^{13}\text{C}$  values, with individuals collected from West Al Dhakira being more  $\delta^{13}\text{C}$  depleted than those from Al Khor, and those from mangrove habitats having more negative  $\delta^{13}\text{C}$  values than those from seagrass habitats. SIAR analysis confirmed these differences, suggesting that mangrove-derived organic

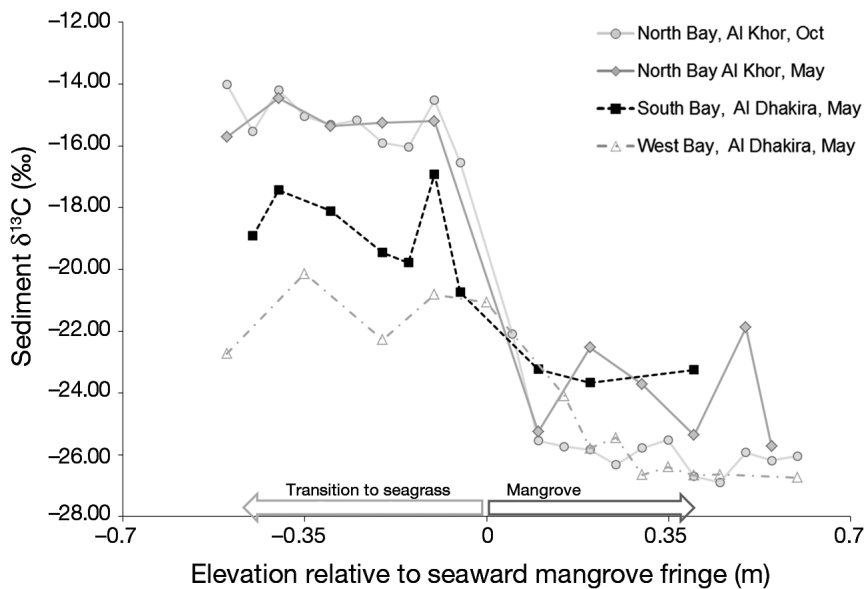


Fig. 4. Carbon isotope signatures of surface sediments along 4 transects running from subtidal seagrass beds up into intertidal mangrove stands at 3 different sites. Sample points are joined to aid identification only

material was equally important in both habitats in West Al Dhakira, contributing 40% of tissue in *B. variabilis*, with lower contributions at Al Khor of 29% in animals from mangrove areas and 13% in those from seagrass beds (Fig. 3c,d). Interestingly, seagrass accounts for about 30% of *B. variabilis* diet even for those found inside the mangrove areas at both sites.

The barnacle *B. amphitrite* was feeding at a TL of 2.50 above the mean value for the primary producers. South Al Dhakira was omitted from the analysis due to insufficient samples, but in both West Al Dhakira and Al Khor, the contributions from mangrove and seagrass to barnacle tissue were not as marked as for *B. variabilis*, although the model suggested that mangrove was still likely to be an important source in both habitats in West Al Dhakira and in mangrove stands in Al Khor (Fig. 3e,f). The dietary contribution of seagrass appeared to be equally as important as that of mangrove even within the mangrove habitat.

The carbon isotopic profiles of the sediment sampled along transects showed a clear transition from seagrass beds up into mangrove stands. At Al Khor,  $\delta^{13}\text{C}$  was 10‰ lower inside the mangrove forest than in the seagrass beds, with similar but less pronounced differences in West and South Al Dhakira (Fig. 4). Mangrove sediments were significantly more negative, by 2‰  $\delta^{13}\text{C}$ , in October than in May (*t*-test,  $t = 3.02$ ,  $p = 0.029$ ), while seagrass sediments showed no significant temporal differences at Al Khor. The tran-

sition in sediment  $\delta^{13}\text{C}$  values reflects the mean isotopic  $\delta^{13}\text{C}$  signature of seagrass leaves (−9‰) and mangrove leaves (−28‰). SIAR analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of sediment indicates that at Al Khor, there was very little movement of organic material, between habitats, regardless of season, so that sediment in seagrass contained almost no mangrove-derived organic material, and likewise sediment from the mangrove forest contained little seagrass material (Fig. 5). In West and South Al Dhakira, there was limited contribution of seagrass material to the mangrove sediments, but outwelling of mangrove organic material formed 56% and 39% of seagrass sediments, respectively. C:N ratios were not significantly different between habitats within site or between sites (seagrass  $12.3 \pm 2.6$ , mangrove  $13.6 \pm 2.2$ ), but were significantly different from both green and

brown *Avicennia marina* leaves, which had values of  $28.9 \pm 4.4$  ( $n = 8$ ) and  $73.8 \pm 15.8$  ( $n = 12$ ), respectively.

Common sediment-grazing molluscs that were found in both mangrove forests and seagrass beds at all 3 sites showed a very similar pattern in  $\delta^{13}\text{C}$  to sediments sampled along the same transects (Fig. 6, cf. Fig. 4). GLM analysis indicated a significant relationship between tidal elevation and the  $\delta^{13}\text{C}$  isotopic signature ( $p < 0.004$ ) of sediments, *C. cingulata*, *C. bifasciata* and *O. kotschy*. The interaction term indicated that the  $^{13}\text{C}$  content of sediment and grazers decreased at a similar rate as tidal elevation increased ( $p = 0.054\text{--}0.75$ ). However, we did find significant differences in the mean  $\delta^{13}\text{C}$  values of the grazers and sediment once tidal elevation was accounted for ( $p < 0.003$ ). Subsequent post hoc Tukey's pairwise comparisons indicated a significant difference of approximately +3‰ between the  $\delta^{13}\text{C}$  signatures of all 3 grazers and sediments in Al Khor; in South Al Dhakira the difference was more variable, with only *C. cingulata* (+5‰) and *C. bifasciata* (+3‰) being significantly enriched compared to the sediment values, and in West Al Dhakira the difference was +5‰ for *C. cingulata* and *C. bifasciata* and +4‰ for *O. kotschy*. However, the isotopic C signatures of the grazers compared across species and sample sites, taking into account tidal elevation, showed no significant difference—with the exception of *O. kotschy* in South Al Dhakira.

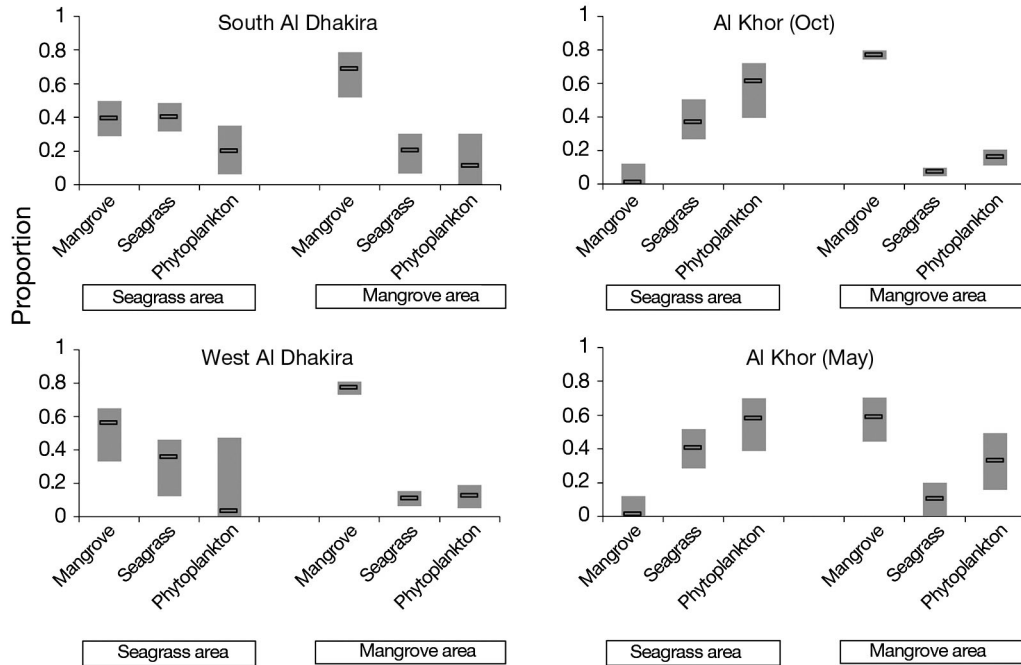


Fig. 5. Modal proportion and 95 % credible intervals of the contribution of mangrove, seagrass and phytoplankton to the sediments sampled within the *Avicennia marina* stands and *Halodule uninervis* beds

The mixSIAR model indicates that the contribution of the primary producers to the diet of grazers broadly reflects that estimated for the sediment, although with reduced mangrove contributions in

the grazers. Mangrove organic material forms an almost negligible proportion of the diet of sediment grazers in the seagrass beds and a much larger contribution within the mangrove forest. The reverse is true of the seagrass contribution only within the Al Khor mangrove stands, and not in South and West Al Dhakira mangrove forests, where mangrove and seagrass contributions appeared to be equally important. Overall, the seagrass contribution to sediment grazers appears to be enhanced compared with that found in the sediments, and in the mangrove stands, seagrass median contribution to grazers ranged between 18 and 47 % (Fig. 7).

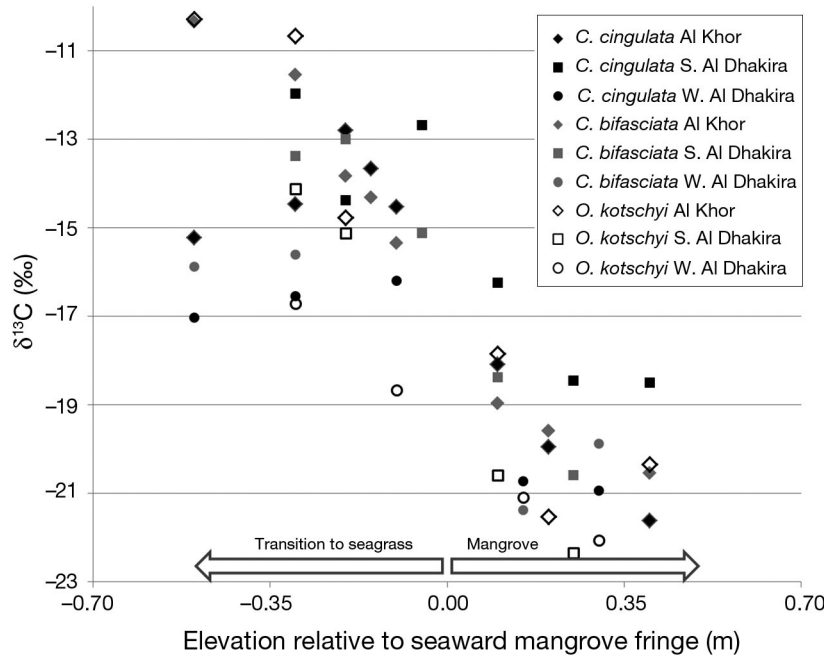


Fig. 6. Carbon isotopic signatures of sediment grazers sampled along transects from subtidal seagrass beds up into intertidal mangrove stands

### Biological mixing of carbon

A TL of 3.1 indicated that the adult Arabian killifish *Aphanius dispar* was feeding mostly on primary consumers (TL = 2), and the isotopic model indicates that killifish are most likely obtaining between 23 and 32% of their nutrition from mangrove productivity (Fig. 8), with



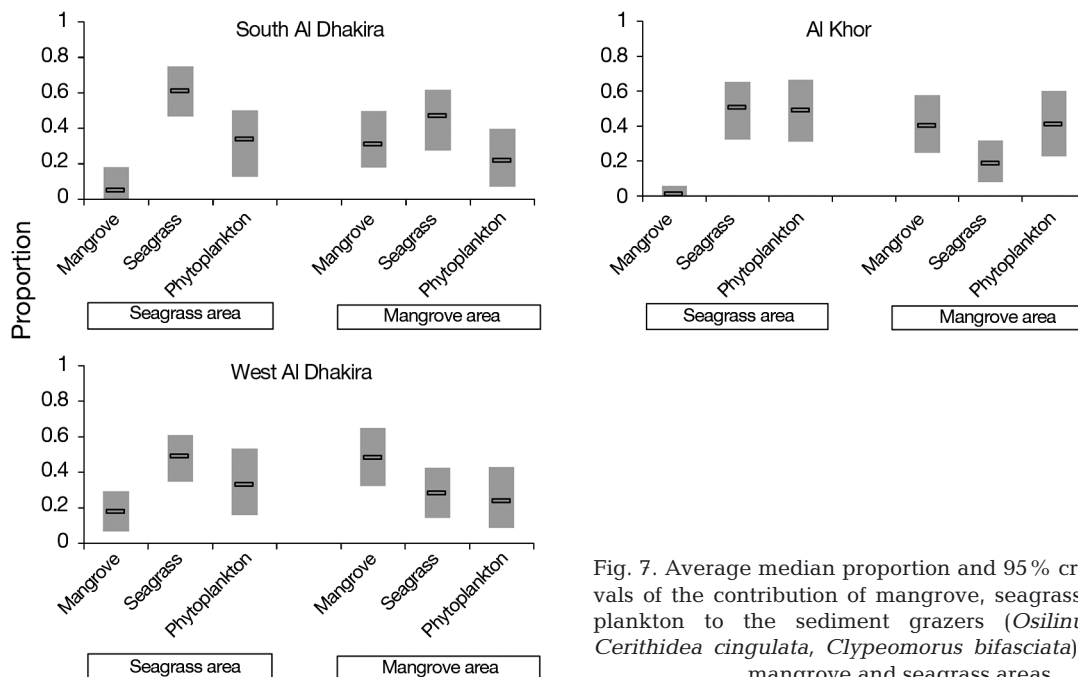


Fig. 7. Average median proportion and 95 % credible intervals of the contribution of mangrove, seagrass and phytoplankton to the sediment grazers (*Osilinus kotschy*, *Cerithidea cingulata*, *Clypeomorus bifasciata*) sampled in mangrove and seagrass areas

seagrass and phytoplankton playing a slightly more important role (35–42 %). The  $\delta^{15}\text{N}$  signature indicated a TL of 3.74 for the juvenile (7–10 cm total length) strongspine silver-biddy *Gerres longirostris*, with a similar pattern of indirect contribution from mangrove, seagrass and phytoplankton of 29–38 %, 28–38 % and 33–35 %, respectively, in the 3 different mangrove areas. The nitrogen isotopic signature of juvenile (6–11 cm total length) *Terapon puta* indicates a TL of 3.84, with a similar contribution from mangrove of 25–36 %, with seagrass contributing 32–43 % and phytoplankton 33–35 %.

## DISCUSSION

### Outwelling of mangrove carbon

Arid mangrove stands in Qatar were effective retainers of most of their production. However, we found significant variation in the contribution of mangroves to downstream systems at the 3 mangrove sites sampled. This is the first study to document this sharp increase in  $\delta^{13}\text{C}$  values using continuous transects between mangrove and seagrass habitats, although similar gradients can be inferred from studies in other intertidal habitats (see Hemminga et al. 1994, Guest & Connolly 2004, Kennedy et al. 2004). Within the mangrove forests, away from the transition zone, sediments were predominantly of

mangrove origin, with an insignificant contribution from seagrass, except in South Al Dhakira where seagrass detritus was visibly trapped amongst the pneumatophores. Likewise, seagrass sediments were mostly of seagrass origin in Al Khor, but mangrove still formed a significant proportion in West and South Al Dhakira. The more enriched isotopic signal in the Al Dhakira systems is unlikely to be related to effluent, as coastal towns in both areas have tertiary treatment of all sewerage, with the resulting waste water used for agricultural irrigation (Qatar Public Works Authority 'Ashgal' pers. comm.). The sedimentary sediment grazers also showed a very similar  $\delta^{13}\text{C}$  gradient but with a mean enrichment of 3 to 5 ‰  $\delta^{13}\text{C}$  above that of the sediment, suggesting that the grazers are selectively feeding on seagrass detritus as reported by Vohra (1970) and Houbrick (1985) and/or that grazers reflect the integrated sediment composition over a longer time period than the one-time sediment sample. Using the discrimination values of McCutchan et al. (2003), the mixing model suggested that this isotopic difference was due to an enhanced dietary contribution from seagrass with a corresponding decrease in the role of mangrove. Thus, for example, even though there was some export of mangrove material, as indicated by the isotopic signature of the sediment in West and South Al Dhakira, its incorporation into body tissue of the sediment grazers was limited. The lower nitrogen content, higher refractory content and slower decomposition

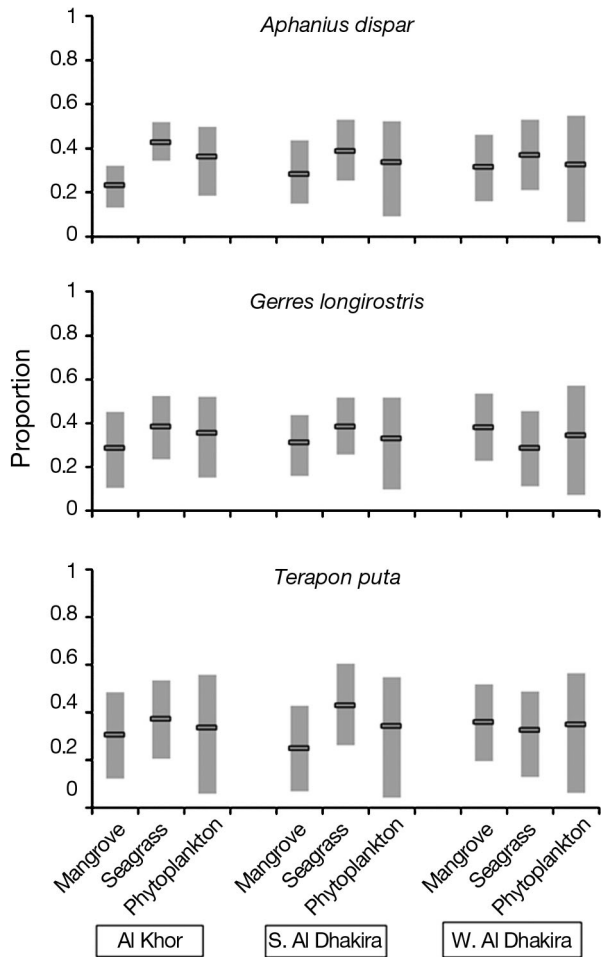


Fig. 8. Modal proportion and 95% credible intervals of the indirect contribution of mangrove, seagrass and phytoplankton to *Aphanius dispar*, *Gerres longirostris* and *Terapon puta* sampled in mangrove and seagrass areas in West Al Dhakira, South Al Dhakira and Al Khor

rate of mangrove leaves compared with seagrass (Rodelli et al. 1984, Kristensen 1994) means that mangrove organic material is less easily assimilated compared to seagrass or phytoplankton detritus.

Similarly, while POM isotopic signatures provided limited evidence of tidally driven outwelling of mangrove organic material, the filter feeder *Brachidontes variabilis*, which represents a more integrated signal of the long-term movement of suspended POM, suggested that in West Al Dhakira mangrove material contributes 42% (95% CI: 33–50%) to *B. variabilis* in seagrass areas, while confirming restricted outwelling from Al Khor mangroves. This appears to support the first half of the outwelling hypothesis of Odum (1968) that at least in the Al Dhakira mangrove sites there is some export of nutrients and organic material to seagrass areas. Odum's theories

were developed in Florida (USA), where absence of leaf-eating crabs meant that most leaf litter was exported intact; however, in Indo-Pacific mangrove forests, leaf-litter processing by crabs may significantly reduce the amount of mangrove material available for export (Robertson et al. 1992, Olafsson et al. 2002). In our arid mangrove stands, none of the observed crabs were leaf eaters, and the lack of species able to process leaf litter (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m507p125\\_supp.pdf](http://www.int-res.com/articles/suppl/m507p125_supp.pdf)) suggests a large potential reservoir of litter and particulate organic carbon available for export. However, absence of rainfall appears to significantly reduce outwelling from mangrove ecosystems (Loneragan et al. 1997) and may partly explain carbon retention. The differences in the amount of outwelling between West Al Dhakira and Al Khor, evidenced from the sediment isotopic signatures, may be due to variations in geomorphology and hydrodynamics that enable larger tidally driven export of mangrove material at the latter site (Kristensen et al. 2008).

Mangrove primary production may also be exported by ontogenetic migration (where carbon assimilated during nursery stages in the mangrove forests is exported as animals migrate during development) and by trophic relay (where mangrove carbon is transferred offshore by a series of predator-prey interactions) (Kneib 1997). Ontogenetic migration has been demonstrated in fish (Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2003, Jones et al. 2010), prawns (Staples & Vance 1986, Kenyon et al. 2004) and crabs (Walton et al. 2006). However, recently, these arid mangrove stands were found to have no nursery function nor do they contribute to the diet of 2 commercial shrimp species, *Metapenaeus affinis* and *Penaeus semisulcatus*, even though they are found in the seagrass beds immediately outside the mangrove area (Al-Maslmani et al. 2012). Elsewhere, juveniles of both penaeid species are found within mangrove forest (Sasekumar et al. 1992, Primavera 1998, Rajendran & Kathiresan 2004, Crona & Ronnback 2005).

Evidence of ontogenetic migration of mangrove carbon is provided by the trapping of juveniles of 2 fish species (*Gerres longirostris* and *Terapon puta*) within the mangrove forest (Table 1) that contained a significant portion of mangrove carbon. Adults of these species are targeted in commercial coastal fisheries in the region (Carpenter et al. 1997, Grandcourt et al. 2006), suggesting that mangrove carbon is exported when adults move to deeper waters. Other juvenile fishes with similar isotopic signatures were

also caught in the traps (see the Supplement). These include *Liza klunzingeri*, *Rhabdosargus sarba*, *Lutjanus argentimaculatus*, *Platycephalus indicus* and *T. jarbua*, which suggests a nursery function for a range of different fish species that contribute to the outwelled carbon (Carpenter et al. 1997). The small euryhaline species *Aphanius dispar* (Skadhauge 1974) was observed moving in large shoals into the mangrove forests on the flooding tide. Their capture in the mangrove traps and their isotopic signatures indicate that they carry a significant amount of mangrove carbon out into the seagrass beds. Similarly, the abundant shrimp species *Palaemon khori*, which is found only within these mangrove systems, obtains 27 to 48 % of its nutrition from mangrove productivity (Al-Maslamani et al. 2013). The abundance and density of both species suggests that they are a likely part of the trophic relay transferring carbon from mangroves to deeper waters.

### Inwelling of seagrass carbon

Evidence of seagrass inwelling into mangrove areas was present at all sites. Duarte & Cebrian (1996) pointed out that systems that export significant amounts of organic material into neighbouring systems are likely to be losing valuable nutrients by the same processes. Assuming that these systems are in equilibrium and in order to maintain production, these lost nutrients have to be replenished from adjacent systems. Therefore, in arid systems, where there is little terrestrial nutrient input, mangroves can only exist where the outwelling of organic material is balanced by inwelling from, in this case, seagrasses in order to maintain adequate nutrient balance.

In one of the mangrove areas, South Al Dhakira, a significant amount of seagrass detritus was trapped in the pneumatophores of *Avicennia marina*, and SIAR suggested that 21 % (95 % CI: 8–32 %) of the sediment organic matter in the mangrove stands was of seagrass origin. In contrast, seagrass-derived carbon only accounted for 5 % (95 % CI: 0.1–11 %) of the sediment in West Al Dhakira and was insignificant in Al Khor mangrove forests. However, the median contribution of 18 to 47 % from seagrass to the diet of sediment grazers sampled within the mangrove areas suggested that a significant amount of seagrass material had inwelled at some stage but may no longer be detectable due to ingestion by the grazers. The filter feeding bivalve *B. variabilis* also appears to be feeding on the inwelled seagrass material within the mangrove forest. Isotopic signatures indicate a

similar contribution of seagrass to the tissue of *B. variabilis* and the magnitude, 34 % (95 % CI: 24–44 %) and 30 % (95 % CI: 18–42 %), is very similar in both Al Khor and West Al Dhakira, respectively. SIAR analysis of the zooplankton-feeding barnacle *B. amphitrite* also indicated that 38 % (95 % CI: 21–53 %) of the diet was dependent on seagrass-derived production in both Al Khor and West Al Dhakira. This dependence on seagrass-derived organic material, despite the constant supply of mangrove particulate material, suggests that seagrass is an important source of C and N, being more bioavailable than the more refractory detritus derived from mangroves. It is not clear how widespread this phenomenon of inwelling is in tropical mangroves, as very few studies have mentioned it. However, in mangroves with no strong freshwater flushing, inwelling may be widespread and important where nutrient supply is limited. A few authors have recently suggested that there may be significant retention of organic matter under certain tidal regimes and topographic settings within mangrove stands, enabling some degree of inwelling (Bouillon et al. 2003, Bouillon & Connolly 2009, Kruitwagen et al. 2010).

Our study confirms that even in the absence of freshwater inputs, there is coupling between the seagrass and mangroves, although the degree and direction of exchange of organic material may vary between locations, and export may in some cases be absent. While the lack of macrofauna able to directly process litter within these arid mangrove stands means that it is available for export, outwelling of litter and detritus is dependent on the geomorphology and hydrodynamics of the area, as suggested by Kristensen et al. (2008). Thus, physical factors are most probably causing significant differences in the amount of tidally driven export of mangrove organic matter in the Arabian Gulf and other arid regions. Inwelling of seagrass material is a feature of all 3 sites studied here, and was consistently detected in the sedentary fauna within the sampled mangrove forests, although its presence was not always detectable in the mangrove sediments, suggesting that there may be some preferential selection or assimilation of organic material of seagrass origin.

The close coupling of seagrass and arid mangrove forests has potential management implications for future replanting schemes that are used to compensate for mangrove loss due to coastal development. This possible reliance on inwelling as a source of nutrients enabling the persistence of mangroves in the Gulf region needs further investigation.

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