Faunal mediated carbon export from mangroves in an arid area

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HIGHLIGHTS

- The unquantified role of migratory fauna in the fate of carbon, means that mangrove carbon budgets are unresolved.
- We quantified the faunal biomass exiting mangroves and used energy budgets and isotopic dietary tracers.
- We found that less than 1% of mangrove litter production is actually faunally outwelled.
- We predict that the proportion of faunally-outwelled carbon is likely to be similar in other mangroves
- Our results support the current hypothesis that 40–50% of mangrove production is exported as dissolved inorganic carbon.

GRAPHICAL ABSTRACT
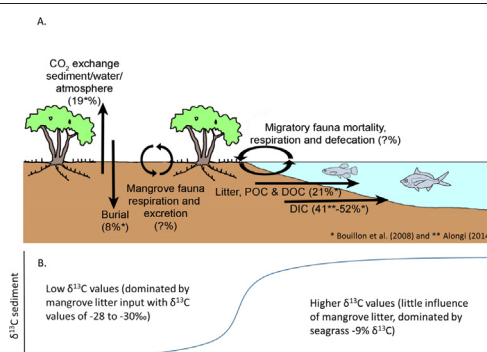
ABSTRACT

The outwelling paradigm argues that mangrove and saltmarsh wetlands export much excess production to downstream marine systems. However, outwelling is difficult to quantify and currently 40–50% of fixed carbon is unaccounted for. Some carbon is thought outwelled through mobile fauna, including fish, which visit and feed on mangrove produce during tidal inundation or early life stages before moving offshore, yet this pathway for carbon outwelling has never been quantified. We studied faunal carbon outwelling in three arid mangroves, where sharp isotopic gradients across the boundary between mangroves and down-stream systems permitted spatial differentiation of source of carbon in animal tissue. Stable isotope analysis (C, N, S) revealed 22–56% of the tissue of tidally migrating fauna was mangrove derived. Estimated consumption rates showed that 1.4% ($38 \text{ kg C ha}^{-1} \text{ yr}^{-1}$) of annual mangrove litter production was directly consumed by migratory fauna, with <1% potentially exported. We predict that the amount of faunally-outwelled carbon is likely to be highly correlated with biomass of migratory fauna. While this may vary globally, the measured migratory fauna biomass in these arid mangroves was within the range of observations for mangroves across diverse biogeographic ranges and environmental settings. Hence, this study provides a generalized prediction of the relatively weak contribution of faunal migration to carbon outwelling from mangroves and the current proposition, that the unaccounted-for 40–50% of mangrove C is exported as dissolved inorganic carbon, remains plausible.

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1. Introduction

Mangrove forests are amongst the world's most productive marine ecosystems (Alongi, 2014), with net primary productivity (NPP) in the order of 208 Tg C yr^{-1} (Bouillon et al., 2008a). Mangrove forests achieve a steady state once the forest reaches maximum biomass at around 20–30 years through a constant process of mortality and renewal (Lugo, 1980) so, assuming the living biomass is not becoming more carbon dense, then carbon has to be lost at a rate equal to the amount of carbon fixed as NPP. Hence this productivity is either retained within the mangrove forest, as a standing stock of live material such as wood, buried in sediments, or exported to neighbouring habitats as litter, particulate and dissolved organic carbon (POC and DOC) and dissolved inorganic carbon (DIC), or lost to the atmosphere (Bouillon et al., 2008a; Maher et al., 2013; Alongi, 2014). The out-welling hypothesis argues that export of locally-derived POC and DOC is an important ecosystem function of mangroves, which drives detrital based food webs in adjacent coastal habitats (Odum, 1968; Odum and Heald, 1972). Export of mangrove carbon has been estimated to make a significant trophic contribution to adjacent ecosystems (Lee, 1995; Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006; Abrantes et al., 2015). The theory of outwelling is supported by mass balance evaluations that show the amount of carbon fixed by mangroves normally greatly exceeds the amount stored within the forest (Alongi, 2014; Twilley et al., 2017), although the scale of outwelling varies considerably between forests (Guest and Connolly, 2004), due to differences in coastal geomorphology, tidal regimes, freshwater flow and productivity (Granek et al., 2009; Vaslet et al., 2012). In the 1990s, global estimates could account for 48% of the total global mangrove primary production (Fig. 1) of 218 ± 72 million tons C yr^{-1}, by incorporating information on carbon burial, CO_2 efflux and carbon outwelled as leaf litter, POC and DOC; the remaining 52% was thought outwelled as DIC, albeit there was insufficient data to confirm this (Bouillon et al., 2008a). More recent assessments of DIC export at two sites in Australia (Maher et al., 2013; Santos et al., 2019) supported the estimates of Bouillon et al. (2008a), although Alongi (2014) suggested that only 40% of NPP was exported as DIC.

Here, we explore the extent to which faunal outwelling accounts for some of the un-explained losses in mangrove NPP.

While the outwelling of mangrove carbon as POC, DOC and DIC may represent an important tropic subsidy to other coastal habitats (Dittmar et al., 2006), the movement of fauna out of the mangrove, and their subsequent capture or predation, is an additional plausible direct mechanism for export of mangrove carbon, as well as a route for mangrove contribution to coastal food webs and fisheries. Fauna that feed in the mangrove during high tides and then move offshore to defecate and respire during low tide should also contribute to carbon outwelling (Fig. 1). At present, however, there is little evidence to clarify what proportion of fauna-mediated export may benefit fisheries production (Saenger et al., 2013).

Adult and juvenile fauna use mangroves as spawning and feeding grounds and as a refuge from predation (Saenger et al., 2013). Faunal outwelling occurs when mangrove carbon that has been ingested by animals within the mangrove either directly, through eating mangrove leaves or indirectly through eating fauna containing mangrove C, is then transferred out of the mangrove into downstream/subtidal habitats. Two forms of direct faunal mediated mangrove outwelling have been proposed, although we do not differentiate between them in the current study: ontogenetic outwelling, where juveniles/larvae that have been sustained on mangrove production migrate out of the mangroves as they mature; and trophic relay, where predators transfer mangrove carbon out of the forest after feeding on mangrove-sustained prey (Kneib, 1997; Connolly and Lee, 2007). Indirect faunal outwelling includes the mangrove carbon assimilated by fauna feeding at the base of the food web transforming the refractory mangrove material into more labile carbon that may then be exported by transfer up the food chain or water mediated tidal export after mineralization.

Tree litter (leaves, fruits, etc.) on average represents 31% of mangrove production (Bouillon et al., 2008a) and its fate is central to unravelling mass-balance budgets. Some litter is exported directly on the tide (Boto and Bunt, 1981) and the contribution of litter export to coastal food webs has been questioned, as mangrove litter has low nutritional value (high C:N ratios) and is highly refractory (Rodelli et al.,

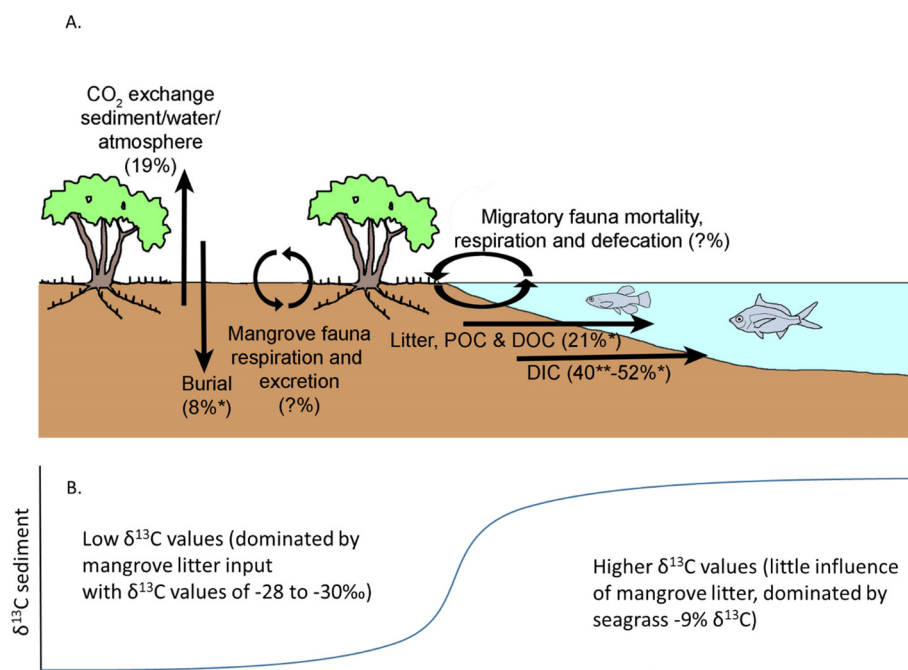**Fig. 1.** A.) Fate of mangrove primary production and importance of each component, as a percentage of net mangrove primary productivity. Percentages are based on data in * Bouillon et al. (2008a) and ** Alongi (2014). B.) Isotopic profile of sediments across the transition from mangrove to intertidal mudflats and seagrass beds, illustrating the retention of mangrove productivity within the forest.

1984; Loneragan et al., 1997; Bouillon et al., 2002; Skov and Hartnoll, 2002; Connolly et al., 2005). Much litter is retained in the mangrove through herbivory, as many invertebrates are highly dependent on mangrove produce as a food source (eg. Rodelli et al., 1984; Chong et al., 2001; Walton et al., 2014). This is especially true of the old world mangroves in Indo-West Pacific biogeographic region (McIvor and Smith, 1995; Lee, 1998). Litter feeders and microbes process and nutritionally enrich litter transforming it to detritus, making it available for uptake by deposit and filter feeders (Poovachiranon et al., 1986; Skov and Hartnoll, 2002). In turn, litter, detritus and filter feeders are consumed by tidal predators and thus litter may be indirectly exported through trophic relay (Lee, 1995), although this outwelling mechanism is rarely considered and has never been quantified.

The idea of faunal outwelling has been around for 50 years (Heald and Odum (1970), yet its significance to mangrove carbon budgets remains untested, probably because generating the evidential data is technically challenging. First, the abundance of migratory fauna per unit area of mangrove has to be estimated. This can be achieved catching fauna at the mangrove edge during the ebbing tide in water draining from a known area of mangrove (Thayer et al., 1987; Blaber and Milton, 1990; Barletta et al., 2003; Castellanos-Galindo and Krumme, 2013; Shahraki and Fry, 2016), although estimating the size of the catchment area can be difficult if the mangrove has complex drainage/creek morphology (Huxham et al., 2008). Secondly, the proportion of mangrove carbon in the tissues of migratory fauna needs quantification. This step has been facilitated by the development of chemical tracers, such as stable isotopes and fatty acids, which utilize the principle of "you are what you eat" (eg. Rodelli et al., 1984; Meziane and Tsuchiya, 2000). Thirdly, the tracers used to account for mangrove carbon should only be present inside the mangrove to ensure that the mangrove carbon in the fauna was acquired within the mangrove forest. Fourthly, the NPP of the site needs to be known. Typically, litter production is used as a proxy for NPP as this is simple to measure and typically accounts for 31% of NPP (Bouillon et al., 2008a).

We undertook the first empirical study of the role of aquatic faunal-mediated outwelling to mangrove carbon budgets and tested the hypothesis that outwelling by marine migratory faunal represents a significant component of mangrove productivity. Two estimates of outwelling were considered: (1) direct outwelling, that is mediated by feeding in mangrove forests at high tide by non-mangrove resident species, and their subsequent excretion or mortality in adjacent subtidal; and (2) indirect outwelling, represented by the proportion of the mangrove carbon food web that supports fauna migrating between the mangrove and down-stream habitats.

2. Methods

2.1. Study sites

We used arid mangroves in Qatar as an ideal system for studying faunal outwelling. Firstly, Qatar mangroves have gently sloping shorelines with relatively simplified systems of creeks and drainage channels that enables positioning of the traps and estimation of their catchment area. In arid mangroves outwelling to adjacent food webs is limited (Walton et al., 2014; Ray and Weigt, 2018), as lack of rainfall greatly restricts flushing and the resulting outwelling of particulate organic material (POM) that is otherwise characteristic in wetter, tropical climates (Loneragan et al., 1997; Al-Maslamani et al., 2012; Al-Maslamani et al., 2013). The high retention of productivity within Qatar mangrove forests leads to a sharp isotopic boundary in sediments and sedentary fauna at the seaward edge of forests, between a mangrove area which is depleted in ^{13}C, and down-stream tidal flats and subtidal seagrass habitats, which are more enriched in ^{13}C (Fig. 1: B) (Walton et al., 2014). The low export of litter, and associated sharp isotopic boundary, makes Qatar mangroves ideal sites for investigating faunal mediated carbon export, as any mangrove carbon incorporated into the tissue of migratory

fauna has to have been consumed within the mangrove area; it is unlikely to have been outwelled and consumed down-stream.

The study sampled the three largest mangrove forests in Qatar: Al Khor, West Al Dhakira and South Al Dhakira (Fig. 2). These had 2 m tidal ranges, silty sediments and mono-specific *Avicenna marina* stands. Trees ranged from ~5 m tall at the seaward fringe to stunted <1 m mature trees at landward fringes (Chatting et al., 2020). Sites had a central tidal channel, but on either side were dominated by a flat substrate that drained evenly across the surface, except, where the gradient was slightly steeper and small channels (2–5 cm deep, <50 cm wide) formed. These flatter areas were selected for sampling, in order to represent the majority of the mangrove area. A broad, gently sloping mudflat exists to the west of the mangroves in Al Khor, with sediments similar to the mangrove. Non-mangrove intertidal areas at Al Dhakira sites were steep and relatively narrow. Subtidally, sites had patchy seagrass beds, mainly *Halodule uninervis*, with some *Halophila stipulacea* occasionally reaching intertidal areas close to the mangrove fringe (Walton et al., 2016). Anthropogenic impacts from fishing, tourism and sewage input is limited in these mangroves (Walton et al., 2016), they are protected with no fishing permitted under the Protected Area Management Plan 2008–2013 (SCENR, 2007).

2.2. Sampling design

At each mangrove site three fyke nets (3 mm mesh) were placed along the seaward mangrove fringe (Figs. 3, S1. Table 1). Previous trials indicated 1 mm was easily blocked and 5 mm mesh permitted smaller shrimp and fish to escape. All traps were at the same tidal elevation. Nets were 1 m tall (well above high tide level) and with 5 m wings, resulting in a 5.8–9.2 m trapping gape per trap, with gape variation due to wing placement. Bottom edges of nets were buried in the sediment. In West Al Dhakira and Al Khor fyke nets were set over small drainage channels (Fig. 3). South Al Dhakira had no clear drainage channels and traps were randomly positioned along the mangrove edge. To simplify the estimation of the area from which water drained through each fyke net, nets were placed where the ebbing water flowed perpendicular to the mangrove edge. Prior trapping trials conducted in 2013–2016 indicated that small channels perpendicular to the shore line produced the least variable estimates of faunal density. Sampling took place on one spring-tide day in spring (29 April–1 May 2017) and in the autumn (8–10 October 2017), to represent the spawning season and the appearance of juveniles in coastal habitats, respectively. These periods were selected to capture the maximum migratory biomass and was informed by the previous campaigns to traps fish detailed in Walton et al. (2014) and the trial use of larger nets (30 m) to block the larger mangrove channels, in addition to field observations of fish migratory pattern during our extended presence in the mangroves over a two year period. As the major spring tides occurred at night, fyke nets were set in the afternoon at low water and emptied the next morning at the following low water. Thus, sampling quantified mobile fauna using the mangrove during the nocturnal spring tide. During the second sampling, a mudflat site at Al Khor was also sampled, to evaluate whether migratory fauna were specific to mangroves or generalist fauna present in other intertidal habitats. Only Al Khor had a suitable mudflat site for sampling, with intertidal flats of the same intertidal height, slope and sediment characteristics as the mangrove.

The catch, mainly fish and shrimp, was stored on ice until sorting. All species other than *Aphanius dispar* and *Gerres longirostris*, were separated out, counted and the total length and wet weight noted. The remaining catch of *A. dispar* and *G. longirostris* which formed 94% of the biomass was subsampled and each species weighed, measured and counted, and scaled up by the total biomass from that species to determine population structure. Fish biomass estimates from mangrove areas in October (n = 9) were compared with those from mudflat areas (n = 3) using a two sample *t*-test on normally distributed data. More detailed analysis of catch composition data is presented in Supplementary material 1.
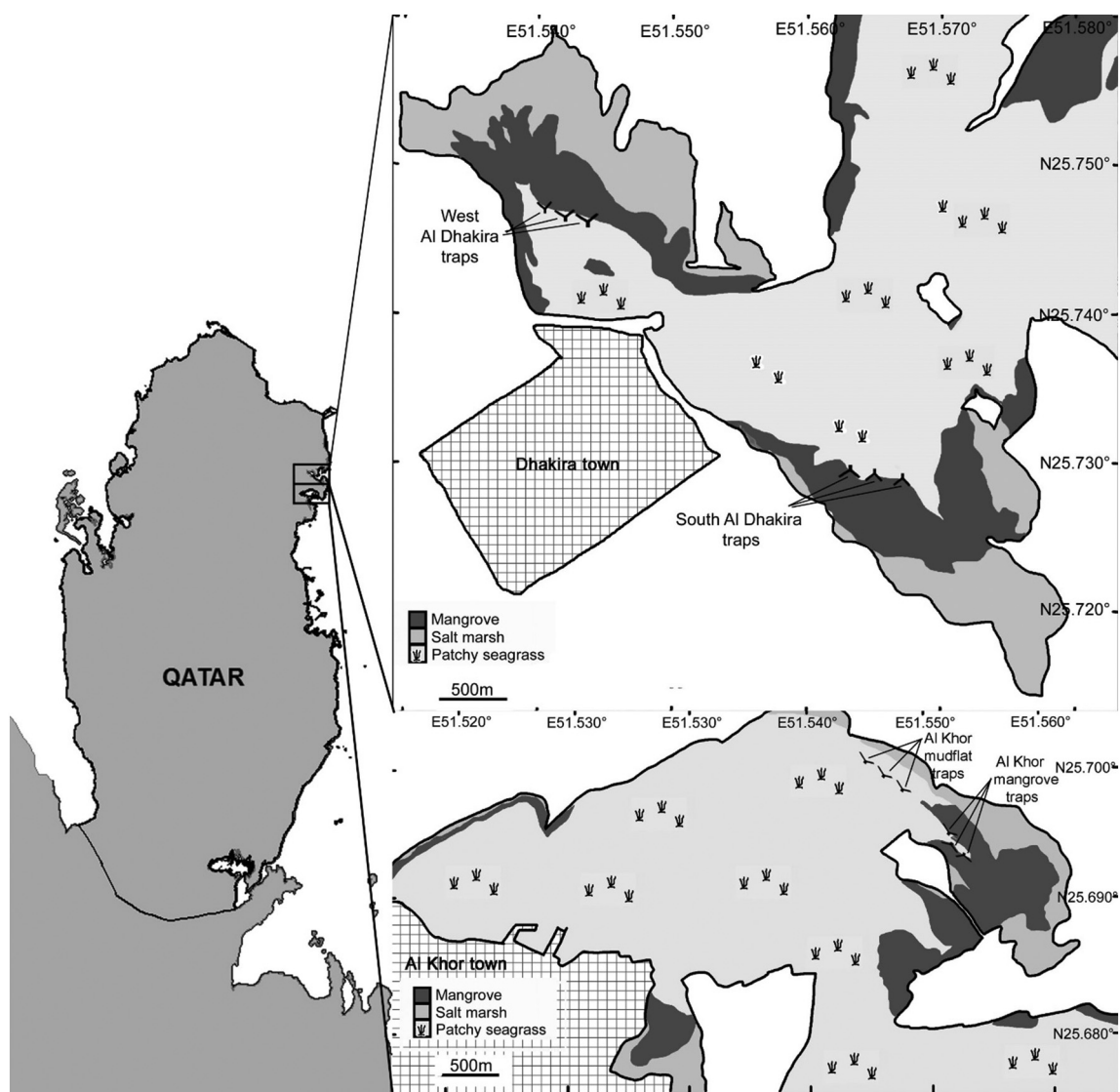
Fig. 2. Location of traps in the mangrove forests of Al Khor, West and South Al Dhakira.

2.3. Tracing the food source of fauna (trophic linkage)

Stable isotopes of C, N and S were used to assess the contribution of mangroves and alternative dietary sources to the tissues of migratory fauna. Muscle tissue was extracted (~1 g dw/specimen) from 5 specimens per species per trapping event. Three potential food sources were sampled. Mangrove leaves were collected from 5 stations along seaward to landward transects through each of the 3 mangrove forests (For transect details see Chatting et al., 2020), seagrass leaves were collected from 12 stations across Al Khor and Al Dhakira bays. Yellow
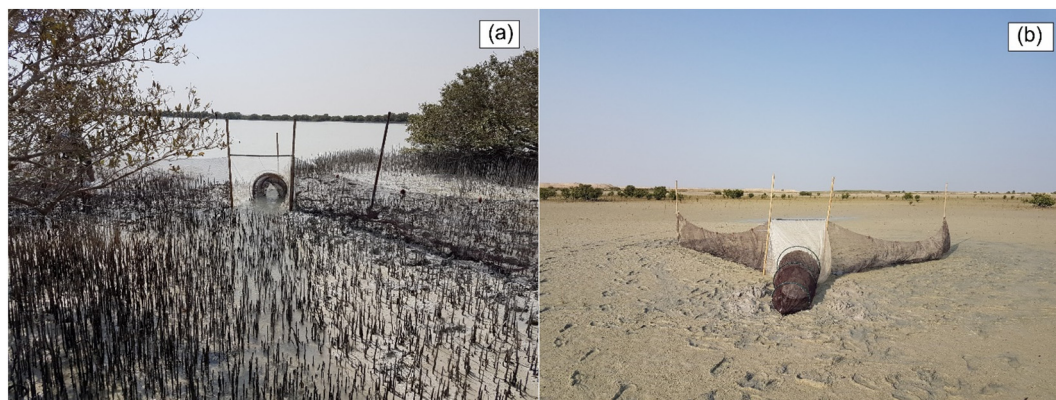

Fig. 3. Fyke nets placed across (a) a small mangrove drainage channel and (b) on the un-vegetated mudflat at Al Khor.

Table 1
Faunal biomass (kg ha^{-1}) caught at mangrove and mudflat sites (mean $\pm$ SD, n = 3 fyke nets/site).

Site	May	October
Al Khor mangrove (n = 3)	12.26 ± 6.40	16.21 ± 17.98
South Al Dhakira mangrove (n = 3)	12.16 ± 6.78	10.23 ± 9.33
West Al Dhakira mangrove (n = 3)	17.14 ± 1.35	16.50 ± 2.19
Al Khor mudflat (n = 3)		4.49 ± 1.15
Combined average of all mangrove areas (n = 9)	13.85 ± 5.32	14.32 ± 10.64

leaves (n = 5 per site) of the mangrove *Avicenna marina* and leaves of the seagrass *Halodule uninervis* were cleaned under distilled water to remove encrusting organisms and sediment. Phytoplankton (n = 3 samples) were collected at the bay mouths using a 50 μm phytoplankton net; the sample were sieved and particles >100um were excluded to minimise contamination by zooplankton. Samples were dried (50 °C, 48 h), homogenised and weighed into tin cups (Elemental Microanalysis Ltd.), before elemental analysis and isotope ratio mass spectrometry (EA–IRMS) by a Europa Hydra 20/20 stable-isotope mass spectrometer were performed by Iso-Analytical Ltd. Isotopic results are reported as δ values, where $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ are equal to $1000 \times [(R_{sample} - R_{standard}/ R_{standard}) - 1]$, in which R_{sample} and $R_{standard}$ equal the $^{13}C/^{12}C$, $^{15}N/^{14}N$ and $^{34}S/^{32}S$ ratios of samples and standards, respectively. Laboratory standards, traceable to inter-laboratory comparison standards distributed by the International Atomic Energy Agency (for further detail see http://www.iso-analytical.co.uk/standards.html), were run interspersed with samples which resulted in standard deviations of <0.4‰ for δ^{13}C, <0.3‰ for δ^{15}N and <0.3‰ for δ^{34}S.

2.4. Construction of carbon outwelling budget

The amount of mangrove carbon consumed by migratory aquatic fauna (MC_F, Kg C ha^{-1} yr^{-1}) was derived by Eq. (1) (broadly based on consumption models in Scheiffarth and Nehls (1997) and Walton et al. (2015)), which includes five main parameters, the estimation of which are outlined in sections further down:

$$MC_F = \sum B \times Q/B \times pM \times DWt : WWt \times pMC_c \qquad (1)$$

where B (kg ha^{-1}) was the mean biomass of migratory aquatic species per catchment area of mangrove forest; Q/B was the consumption rate per year by that biomass of fauna; pM was the proportion of that food that was mangrove-derived; and MC_F estimates were converted to leaf

dry weight using 0.342 (the mean dry weight to wet weight ratio (DWt:WWt) of yellow mangrove leaves (Fourqurean and Schrlau, 2003)) as Q/B is a WWt:WWt ratio; and pMC is the proportion of C in yellow mangrove leaves (Mean C% ± SE = 39.7 ± 0.47, n = 11). The amount of carbon outwelled by fauna (FCO) was estimated for each species using our Eq. (2) and is formed of two parts excretion and mortality:

$$FCO = MC_F \times 0.9 \times T_{RE} + \sum (B \times Mort_{yr} \times DWt:WWt \times pM \times pFC) \qquad (2)$$

Excretion   Mortality

where T_{RE} was the proportion of the time migratory fauna spent outside the mangrove respiring and excreting (estimated at 60% - see below Section 2.4.5) and 0.9 the trophic transfer efficiency (Pauly and Christensen, 1995); while pFC is the proportion of C in the fauna from the isotopic analysis, DWt:WWt is the wet to dry weight ratio of 0.226 (unpublished data) and $Mort_{yr}$ was the annual mortality rate, as estimated using literature values for instantaneous mortality for each species. We assumed that mortality of fauna was predominantly outside the mangrove, as mangroves are considered a refuge from predation.

2.4.1. Faunal biomass per catchment area, B (kg ha^{-1})

Faunal biomass values from fyke-net catches (kg wet weight), were expressed relative to an estimate of the catchment area. In Qatar the relatively homogenous mangrove surface and simple drainage facilitates estimates of catchment area. The method for calculation of the catchment area for each fyke net depended on the presence or absence of drainage channels in the sampling area. Where no drainage channels were present (South Al Dhakira), the catchment area equalled the gape width of the fyke net multiplied by the mangrove depth (the distance between the seaward and landward mangrove forest boundaries) (Fig. 4a). Where the net straddled a channel, the catchment area equalled the mangrove depth multiplied by half the distance between the trapped drainage channel and the adjacent drainage channels on each side (ie. x/2 + y/2. Fig. 4b). The logic of the latter was that adjacent channels had similar sizes (confirmed by visual inspection) and thus were likely to have equal shares in the catchment area between them.
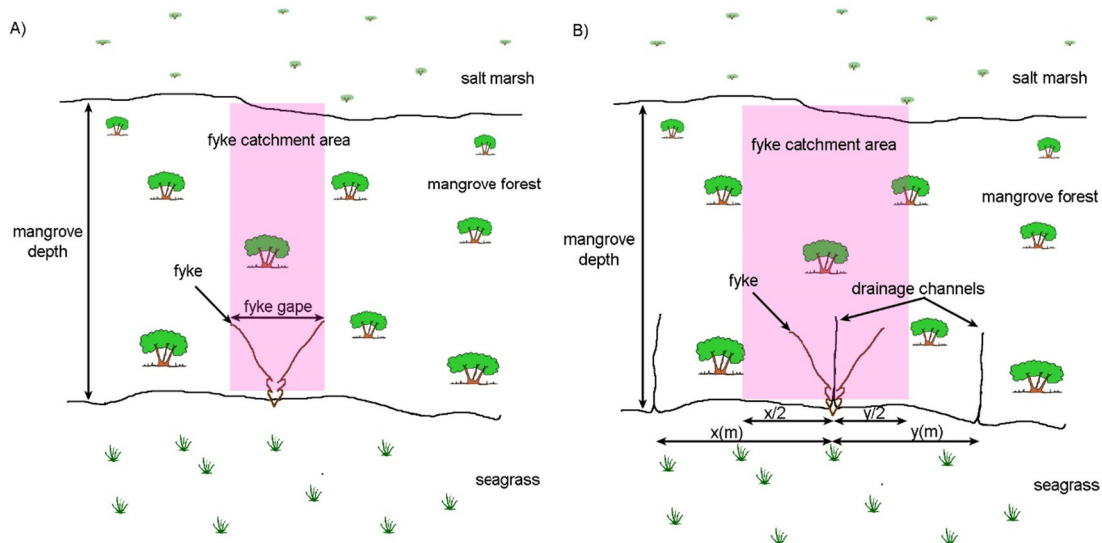

Fig. 4. Diagrammatic representation of the catchment area (shaded) for fyke-nets placed without (a) and with (b) a drainage channel.

2.4.2. Food consumption rate, Q/B (yr^{-1})

Body weight has been used to estimate daily energy expenditure in birds and animals (eg. Nagy, 1987). Here, the amount of food ingested, expressed as a proportion of the consumer's biomass (Q/B), was estimated using a combination of body weight and the aspect ratio of the caudal fin (following Palomares and Pauly, 1998), in the equation

$$log Q/B = 7.964 - 0.204 log W^\infty - 1.965\, T\prime + 0.083A + 0.532\, h + 0.398d \tag{3}$$

where W^∞ was the asymptotic weight (g), $T\prime$ was the mean annual water temperature (27.05 °C) expressed as 1000/Kelvin (Kelvin = °C + 273.15), A was the caudal fin aspect ratio, h and d represented the type of food consumed (if herbivore h = 1, d = 0; if detritivore h = 0, d = 1; and if carnivore h and d = 0), with fish dietary habits derived from $\delta^{15}N$ values (see trophic level estimates below). Caudal fin aspect ratio was estimated with Image J (version 1.51j8) to measure the caudal fin area and height, on images obtained from FishBase (2019). Q/B values of 21.9 and 10.75 yr^{-1} were used for crustaceans and other rare fish species (<1% of the total biomass), respectively, with values derived from the mangrove studies of Wolff et al. (2000) and Vega-Cendejas and Arreguın-Sánchez (2001).

2.4.3. Proportion of faunal diet that was mangrove derived, pM

The source of carbon assimilated in faunal tissues was derived from stable isotopes of ^{13}C, ^{15}N and ^{34}S. For the four species that individually represented >1% of the caught biomass (combined they composed 98% of the biomass), the contribution of primary producers to faunal tissues was estimated using the Bayesian isotopic mixing model mixSIAR (Stock and Semmens, 2013). For the remaining 16 species, which individually formed <1% of the trapped biomass, the combined average dietary contribution of mangroves, as estimated by the mixing model, was used. The MixSIAR model was selected as it is incorporates the isotopic variability in the sources and consumers, as well as the uncertainty of the trophic discrimination factor (Stock and Semmens, 2013). MixSIAR was run in JAGS and called through R (R Core Development Team, 2016) and the 'MixSIAR' package (Stock and Semmens, 2013). The models were run with no informative priors and specified both residual and process error. Mangrove site was entered as a random effect. The longest Markov Chain Monte Carlo settings were used: chains = 3, chain length = 1,000,000, burn-in rate = 500,000 and thinning rate = 500, as this produces the best convergence on the true posterior distribution for each variable (Stock and Semmens, 2013). Convergence was evaluated by Gelman-Rubin diagnostics (Gelman and Rubin, 1992). The trophic level of a consumer was estimated using 2.3‰ for the first trophic step above the mean $\delta^{15}N$ values of the primary producers and an additional 2.9‰ for each higher trophic level (McCutchan et al., 2003; Shang et al., 2008; Walton et al., 2014). To account for the isotopic discrimination that occurs between primary producers and primary consumers trophic enrichment factors (±1SD) of 0.5 ± 1.32‰, 2.3 ± 1.54‰ and 0.5 ± 0.52‰ were applied and for subsequent trophic steps values of 1.3 ± 0.85‰, 2.9 ± 1.24‰ and 0.5 ± 0.52‰ were used for C, N and S respectively (McCutchan et al., 2003). MIcrophytobenthos (MPB) was not included in isotopic mixing models, as it was present in very low concentrations (~0.1% of sediment carbon, Chatting unpublished data) and as MPB δ^{13}C values of 29–26‰ indicated that mineralised mangrove carbon was incorporated into MPB (David et al., 2019).

2.4.4. Estimation of mangrove-derived biomass consumed, MC$_F$

The amount of mangrove biomass that was consumed either directly by the migratory fauna, or indirectly by all the organisms that form the base of the food web on which the migratory fauna feed.

a) **Direct consumption:** The annual consumption of mangrove derived carbon (Direct MC$_F$ estimated using Eq. (1)) eaten by the migratory fauna feeding either on mangrove biomass or fauna that contain mangrove carbon (part of indirect consumption).
b) **Indirect consumption:** The annual mangrove carbon consumed by herbivores and detritivores at the base of the food web that supports the migratory fauna. It is an estimate of the biomass of mangrove primary production supporting each of mobile faunal species, assuming 10% transfer between trophic steps (Pauly and Christensen, 1995) using the equation.

$$\text{Indirect MC}_F = \text{Direct MC}_F \times 10^{(TL-2)}$$

where TL equates to trophic level. A proportion of the indirect consumption will end up being ingested by the migratory fauna.

An average mangrove litter production estimate for these three mangrove sites of 6847 kg ha^{-1} yr^{-1} (Chatting pers. comm.), the equivalent of 2718 kg C ha^{-1} yr^{-1} (using the below yellow leaf carbon content estimate), was used to covert dry wieght consumption estimates to percentage of mangrove litter production. All estimates were converted to C using the C to dry weight ratio of 0.397 derived from the carbon content of oven dried yellow *A. marina* leaves.

2.4.5. Proportion of time fauna spend outside the mangrove, T$_{RE}$

The mean tidal height of the lower mangrove fringe was measured using DGPS during spring tides in February 2016 and found to be 0.2 m above mean tide. Tidal charts were used to estimate the proportion of the day when the tidal level was below this mean tidal level of 0.2 m, this was regarded as the time when fauna are all clear of the mangrove.

3. Results

The catchment area that drained through each of the traps varied from just over 1 ha for the traps in West Al Dhakira to under a tenth of hectare for one of the traps in Al Khor. Species compositions and biomass varied markedly between mangrove and the mudflat, but not between mangrove sites: Area-adjusted catches indicted that ~3 times more fish (by biomass) used the mangroves than the mudflat area, with pooled mangrove catches significantly higher than mudflat catches (*t*-test, on October data only: $T = -2.72$, $P = 0.026$, $DF = 8$) (Table 1). Mangrove traps caught in total 74.49 kg (74,420 individuals) in May and 76.42 kg (79,290 individuals) in October and 1.19 kg (340 individuals) on the mudflat (see Supplementary information Table 2 for further information). Sampled individuals ranged in size from ~1 cm for the smallest *Paleamon khori* to 34 cm for a garfish (*Belone belone*) with the majority of the catch 2-7 cm in length. On average (±SE), mangrove forests were visited by ~14 kg ha^{-1} of fish and crustaceans during a single tide; 97 ± 2% of that was fish, and 78 ± 3% was the Arabian pupfish *A. dispar*. The other major contributors were the strongspine silverbiddy *Gerres longirostris* (16 ± 3%), the milkfish *Chanos chanos* (2 ± 1%) and the shrimp *Palaemon khorii* (3 ± 2%). In contrast crustaceans formed 70 ± 19% of the smaller mudflat catches, with the blue swimming crab *Portunus pelagicus* forming 69 ± 19% of the biomass. For details on areas trapped, catch biomass, biodiversity and non-parametric statistical tests used to detect differences, see Supplementary material S1.

3.1. Consumption rate (Q/B, yr^{-1})

The three major fish species, *A. dispar*, *G. longirostris,* and *C. chanos*, consumed 52.2, 16.8 and 27.8 times their body mass per year, respectively, estimated using the body mass and caudal fin ratios. Literature derived values of Q/B of 21.9 and 10.75 were used for *P. khori* and the less frequently occurring (<1% of biomass) species (Vega-Cendejas and Arreguın-Sánchez, 2001).

3.2. Mangrove derived dietary proportion and trophic level

Primary producers had distinct $\delta^{13}C$ and $\delta^{34}S$ values, averaging −28.6‰ and 0.3‰ for mangrove (yellow leaves), −16.4‰ and 19.2‰ for phytoplankton and −9.1‰ and 8.6‰ for seagrass, respectively (Fig. 5). However, only seagrass $\delta^{15}N$ values of −4.9‰ were well separated from the other two primary producers: mangroves (1.1‰) and phytoplankton (0.7‰). Of the consumers *P. khori* was the most depleted in ^{13}C at −18.4‰, *C. chanos* the most depleted in ^{34}S at −2.7‰, while *G. longirostris* was the most enriched in ^{15}N at 7.2‰. The δN values of the main consumers, relative to those of the primary producers, showed the trophic level (TL) of the dominant species ranged from omnivores to carnivores (*C. chanos* – TL 2.6, *A. dispar* - TL 3.3, *P. khori* - TL 3.5, *G. longirostris* – TL 4.0). The higher the trophic level, the larger the amount of primary production required to support the consumer (Pauly and Christensen, 1995).

G. longirostris and *A. dispar* used different sources of primary productivity, with the latter much more reliant on phytoplankton-derived productivity than the former (Fig. 6). The Bayesian mixing models indicate that the mean (±1SD) mangrove contribution to animal tissue was 40‰ (±13) for *A. dispar*, 43‰ (±13) for *G. longirostris*, 51‰ (±18) for *C. chanos*, 57‰ (±9) for *P. khori* and 22‰ (±7) for the pooled remaining species (Fig. 6).

3.3. Biomass consumed

Direct consumption (Direct MC$_F$): On average (±1SD) 35 ± 33 and 2 ± 3 kg (C) ha^{-1} yr^{-1} of mangrove carbon were consumed by the two main species *A. dispar* and *G. longirostris* (Table 2). Table 2 shows the steps by which the annual consumption of mangrove material by migratory fauna is estimated. Faunal biomass is derived from fyke net catches, daily consumption rates of the biomass are based on the Q/B estimated from Eq. (3). To reiterate, the proportion of the consumption that originated from mangrove production was estimated from the proportion of mangrove derived carbon in the sampled fauna (from the isotopic modelling and assumed assimilation and ingestion rates were similar) and extrapolated to a yearly rate. These estimates of mangrove consumption as wet weight were then converted to dry weight using a value of 0.342, the dry to wet weight ratio of yellow mangrove leaves determined by Fourquean and Schrlau (2003), and finally to carbon using our value of 39.7% as carbon content of yellow mangrove leaves.

In total, 37.7 ± 32.8 kg C ha^{-1} yr^{-1} of mangrove material or 1.4 ± 1.2% of the annual (C) litter production was directly consumed by the migratory fauna and, thus, available for export (Table 2).

Indirect consumption (Indirect MC$_F$): Significantly more, 928 ± 698 kg C ha^{-1} yr^{-1} of mangrove production, was on average (±SD) processed by the food web that supported the migratory fauna (indirect consumption). Thus, 34.1% (=0.928 ∗ 100/2.72 t C ha^{-1} yr^{-1}) of the leaf litter produced in these mangroves passed through the food web that supported the migratory fauna, assuming a mean annual litter production of 2.72 t C ha^{-1} yr^{-1} for Qatar mangroves. Of this only 4% (Direct consumption = 37.7 kg C ha^{-1} yr^{-1}) were passed on to the migratory fauna.

Litter production has been estimated to account for 31% of mangrove net primary production (MNNP) (Bouillon et al., 2008a), and these consumption values therefore represent 0.4% (=1.4% × 0.31) and 10.6% of mangrove net primary production, for direct and indirect consumption respectively.

3.4. Proportion of time fauna spend outside the mangrove T_{RE}

The mean height of the mangrove fringe was 0.2 m above mean tide level with the water level high enough to enter the mangroves on average 40% of the time, so conversely the mangrove was dry 60% of the time forcing the fauna into subtidal habitats. A T_{RE} of 60% of the time was used to calculate the amount of respiration/excretion that occurred outside the mangroves.
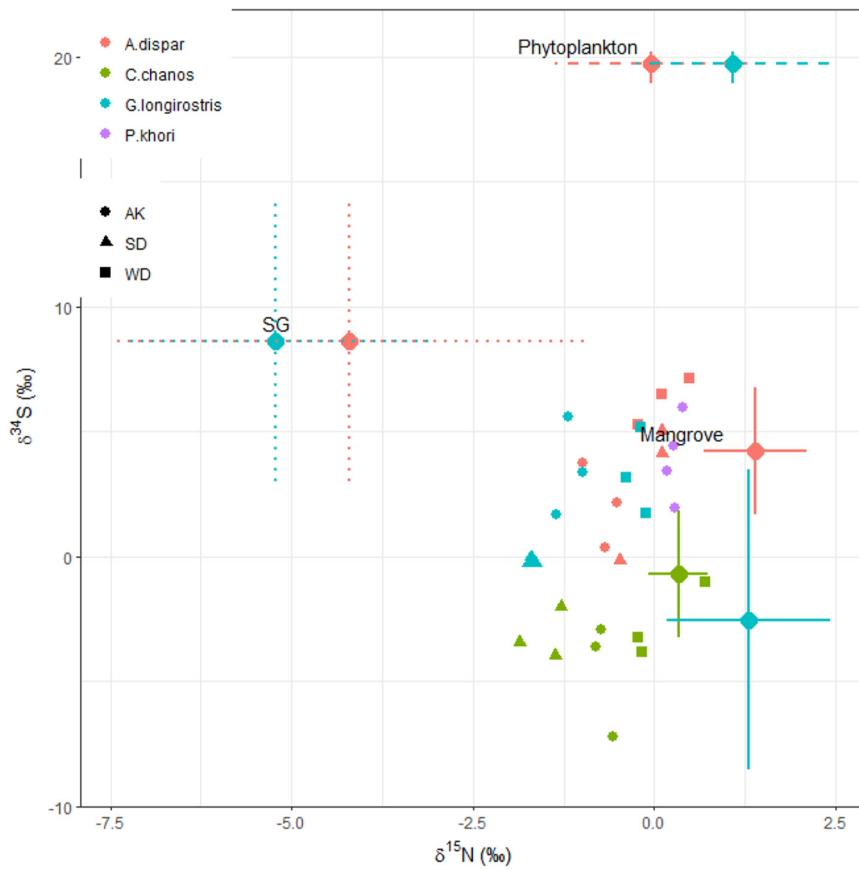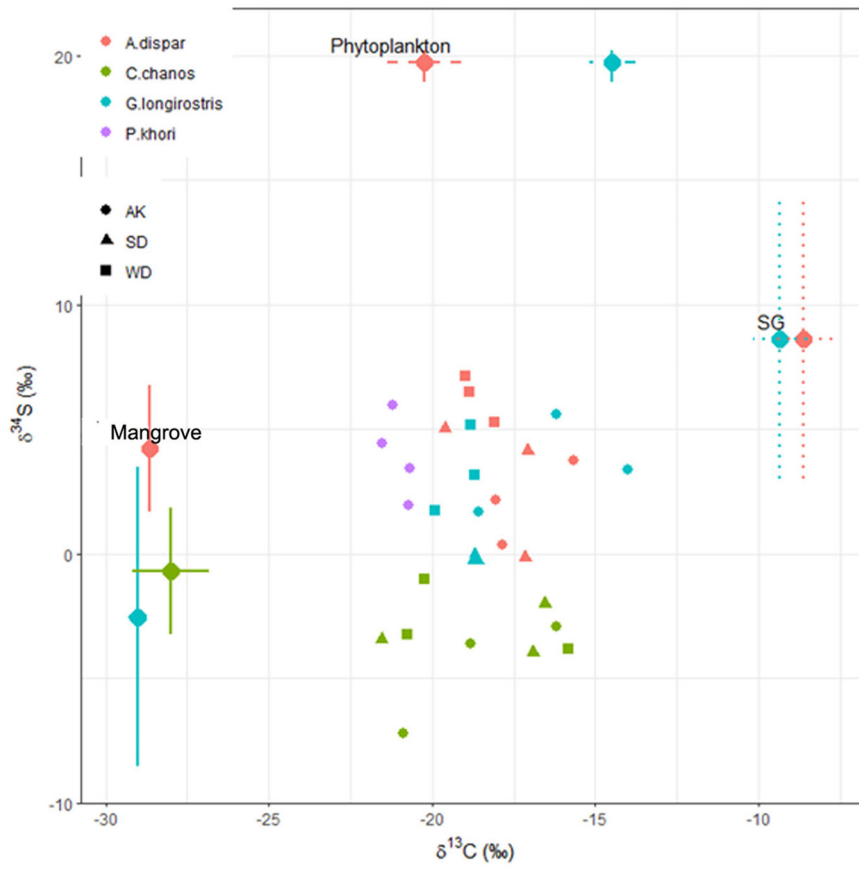
3.5. Faunal carbon outwelling (FCO)

The amount of faunally outwelled carbon (FCO) estimated from Eq. (2) is composed of two parts, excretion/respiration and mortality. Outwelling due to carbon excretion/respiration was estimated assuming that 90% of the food ingested is later respired or excreted, based on the 10% assimilation rate of Pauly and Christensen (1995). Therefore of the 38 kg C ha^{-1} yr^{-1} of mangrove material directly consumed, 34 kg C ha^{-1} yr^{-1} is lost through excretion/respiration but only 60% is lost outside the mangrove while the tide is out and is thus estimated to be 20.8 ± 18.0 kg C ha^{-1} yr^{-1} or 0.8% of leaf litter production. Mean outwelling of mangrove biomass from mortality of migratory species, is estimated at 0.48 ± 27 kg C ha^{-1} yr^{-1} or 0.02% of leaf litter production. This was based on annual mortality rates (derived from instantaneous mortality rates) that ranged from >90% for *A. dispar* and *P. khori* to 40% for larger-sized minor species and C percentages with a range of 44–46% obtained from the isotope analysis.

4. Discussion

This study provides a first estimate of the proportion of mangrove productivity that is outwelled by migratory fauna. The idea that fauna are a significant pathway for the movement of carbon out of mangroves was first suggested by Beever et al. (1979) after describing the outwelling of larvae from mangrove resident crabs. Later, Lee (1995) hypothesised that faunal outwelling of mangrove-derived carbon maybe an important and neglected pathway of mangrove C export, and the idea has since been reiterated (eg. Connolly and Lee, 2007; Bouillon and Connolly, 2009; Saenger et al., 2013), but its significance has never been quantified until now.

For Qatari mangroves direct consumption of mangrove carbon by all fauna that move in and out of the mangroves with the tides was very minor, at 37.7 ± 32.8 kg (C) ha^{-1} yr^{-1} or 1.4% of mangrove litter production, suggesting mobile fauna have a relatively insignificant role in the consumption of mangrove production. Estimates of faunally induced outwelling of that consumed mangrove material resulting from Eq. (2) were only 20.8 kg C ha^{-1} yr^{-1} (equivalent to 0.77 ± 0.66% of mangrove litter production or 0.26% of mangrove NPP). This faunal carbon export had two modes: the excretion and respiration of fauna during the period when the mangrove forest was dry; and from the mortality of migratory fauna, that we assumed occurred outside the mangrove. Our estimates of the mangrove carbon both consumed and outwelled by migratory fauna are 30 to 50 times smaller than estimates for C outwelled to neighbouring habitats as POC (1312 and 1187 kg C ha^{-1} yr^{-1}) and DOC (1500 and 2029 kg C ha^{-1} yr^{-1}) (Bouillon et al., 2008a, Alongi, 2014, respectively).

Our estimate for indirect consumption, that part of the mangrove productivity that is consumed by the food web supporting the migratory fauna, is much more significant, accounting for 34.1% of the mangrove litter production or 10.6% of NPP, however it is unclear how much is outwelled. Other studies have shown the importance of fauna in processing mangrove carbon, in a review Lee (1998) reported high densities of grapsid crabs could process all the litter in some Indo-Pacific mangroves resulting in the retention of mangrove material within the forest. Similarly in Northern Australia isopod densities of >7000 individuals m^{-2} producing faecal pellets at a maximal rate of 4 g C m^{-2} d^{-1} and was equivalent to litter production rates (Poovachiranon et al., 1986). In Qatar only 4.1% of this indirect consumption is passed up the food web to the migratory fauna and just 2.2% faunally outwelled, with the rest likely recycled or ending in the DIC, DOC or POC pathways. Previous studies of the same systems have found evidence of only limited biogeochemical outwelling (Walton et al., 2014), yet present results show that a significant proportion of
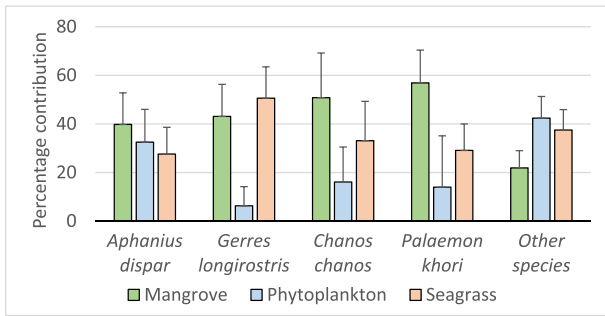
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Fig. 6. Mean percentage of diets originating from the primary producers (mangrove, seagrass (SG) and phytoplankton) in the 3 sampled habitats for *A. dispar*, *G. longirostris*, *C. chanos*, and *P. khori* and the other 14 minor species that formed <2% of the total biomass, estimated using the Bayesian model mixSIAR. Error bars represent 1 standard deviation from the mean.

migratory faunal biomass is derived from mangrove production and in agreement with findings across a wide range of mangroves (Hemminga et al., 1994; Primavera, 1996; Abrantes and Sheaves, 2009; Al-Maslamani et al., 2012; Al-Maslamani et al., 2013; Walton et al., 2014).

The propagation of errors through our model has resulted in large standard deviations about the mean values, most of which come from variation in catches and the uncertainty around the estimates for mangrove dietary proportion from the isotope modelling. Biomass estimates were especially varied between traps in the autumn sampling of the Al Khor and South Al Dhakira mangroves, in contrast to the traps in West Al Dhakira where estimates of biomass were remarkably consistent, this was likely due to changes in drainage patterns or the presence of a larger more mobile predator eliciting an evasion response from the smaller species. Invariably, traps will underestimate fish abundance. However, when compared to other studies (Table 3) our study showed some of the tightest estimates of biomass variation including those conducted in the mangroves of neighbouring Iran (Shahraki and Fry, 2016). Sampling seasons were selected based on observations of when the highest numbers of fish are seen at the mangrove fringe, these coincide with spring spawning season in the Gulf (Sivasubramaniam and Ibrahim, 1982) and the appearance of juveniles in the autumn. These sampling times were similar to those of Shahraki and Fry (2016) although our second sampling was performed later in the year as our aim was to estimate peak fish abundance so as to be able to estimate the maximum amount of carbon outwelling due to faunal movement. Our estimates do not attempt to include other methods of faunally induced outwelling resulting from sedentary or resident mangrove fauna such as the release of eggs/larvae or the outwelling of excretory products as detailed in Beever et al. (1979) although some of this is cap-

tured through our indirection consumption estimates. These traps with 3 mm mesh were selected as mesh size is a balance between capturing relevant sized organisms and the allowing the free passage of water to prevent net avoidance by the target species. Trap size was based on previous trapping trials using both non quantitative smaller fyke nets reported in (Walton et al., 2014) and large larger nets employed across major drainage channels, where water pressure caused sub-net erosion regardless of measures taken. We did not try to assess organisms smaller than the 3 mm mesh size, which may have included both larval stages and zooplankton. Zooplankton has been found to feed mostly on phytoplankton in mangrove areas (Bouillon et al., 2000; Chew et al., 2012) indicating a limited role in the outwelling of mangrove material. Our biomass estimates are from fairly pristine arid mangroves that have been protected under the Protected Area Action Plan 2008–2013 (SCENR, 2007). Nutrient inputs to our sites are also limited, as water from waste water treatment plants are used for inland irrigation and only a small amount of nutrient enrichment was detected in the west of Al Khor bay, furthest from the studied mangroves (Walton et al., 2016). While the mangroves are currently surrounded by substantial amounts of sabkha/salt marshes in which to expand as climate change causes sea level to rise, this situation could be jeopardised by future coastal developments.

Our estimates of Q/B of 10 to 52 fall within the range estimated for marine fish of 1–115 and are close to the only mangrove associated species *Signus canalicutatus* that has a Q/B of 61.7 (Palomares and Pauly, 1998). The highest consumption rates were calculated for *A. dispar* which would have significant positive impact on the resulting mangrove consumption estimates and hence faunal outwelling. We reran the analysis using a Q/B of 23.7, which assumes *A. dispar* to be a carnivore, and not an omnivore as indicated by the isotope data, and this led to a fall in the proportion of mangrove litter production consumed by the migratory fauna from 1.4% to 0.7%.

We used isotopes rather than stomach contents to determine contribution of mangrove carbon to the diet, as the carbon present in tissues of mobile fauna represent food that has been assimilated over a period of weeks and hence will include periods where access to the mangrove might be limited. Isotopic values of primary producers (mangrove, seagrass and phytoplankton) were similar to those of other studies with the exception of the depleted $\delta^{15}N$ values of *H. uninervis* (Newell et al., 1995; Bouillon et al., 2008b; Walton et al., 2014), however previous research has shown these values widespread in these bays (Walton et al., 2016). We included sulphur isotopes to increase the isotopic distance between primary producers as recommended by Connolly et al. (2004). Mangrove and phytoplankton have similar $\delta^{15}N$ and only differ by ~10‰ $\delta^{13}C$, but phytoplankton is enriched in ^{34}S by 17‰. Isotopic Bayesian mixing models showed the 4 species with the highest biomass were much more reliant on mangrove production for their nutrition 40–57% compared with 20% for the less abundant "minor" species.

Table 2
Estimation of the mean (±SD) proportion of mangrove litter production consumed and potentially outwelled by migratory fauna.

	A. dispar	G. longirostris	C. chanos	P. khori	Minor sp.
Fish biomass (kg wet wt ha^{-1})	11.92 ± 7.1	1.98 ± 1.4	0.28 ± 0.52	0.24 ± 0.59	0.27 ± 0.06
Consumption by fish (kg ha^{-1}d^{-1})	1.73 ± 1.1	0.09 ± 0.1	0.02 ± 0.04	0.01 ± 0.04	0.01 ± 0.002
Annual mangrove consumed (kg wet t ha^{-1} yr^{-1})	254.22 ± 240.5	15.83 ± 19.3	3.95 ± 8.7	2.78 ± 7.2	0.64 ± 0.3
Annual mangrove consumed (kg dry wt ha^{-1} yr^{-1})	86.94 ± 82.3	5.41 ± 6.6	1.35 ± 3.0	0.95 ± 2.5	0.22 ± 0.1
Annual mangrove consumed (kg (C) ha^{-1} yr^{-1})	34.52 ± 32.6	2.15 ± 2.6	0.54 ± 1.2	0.38 ± 0.98	0.09 ± 0.05
Percentage of mangrove litter directly consumed by migratory fauna (%)	1.27 ± 1.2	0.08 ± 0.1	0.02 ± 0.04	0.01 ± 0.04	0.003 ± 0.002
Indirect annual consumption of mangrove biomass (kg (C) ha^{-1} yr^{-1})	672.56 ± 636.4	234.41 ± 285.3	2.24 ± 5.0	13.04 ± 33.9	5.37 ± 2.9

Fig. 5. Stable isotope values (‰) of carbon and sulphur ($\delta^{13}C$, $\delta^{34}S$) (above) and nitrogen and sulphur ($\delta^{15}N$, $\delta^{34}S$) (below) for *A. dispar*, *G. longirostris*, *C. chanos*, *P. khori* (corrected for isotopic discrimination) and primary producers (mangrove, seagrass (SG) and phytoplankton) in the sampled mangrove areas of Al Khor (AK in red), West Al Dhakira (WD in blue) and South Al Dhakira (SD in green), Qatar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Estimates of fish biomass and number of species reported in mangrove forests around the world with estimates of total mangrove area, sampled mangrove area and annual rainfall. Sampling gears both measure density though by catching fauna from a known area of mangrove. Block nets by blocking the seaward migration of fauna during the ebbing tide, and enclosure nets are nets raised at high tide that enclose an area of mangrove.

Location and habitat	Total mangrove area (ha)	Annual rainfall (mm)	Trap catchment area (m²)	Sampling gear	No. spp.	Biomass mean ± SD (g m⁻²)	Source
Bahía Málaga, Pacific Columbia	4400	7399	6245	Block net	50	0.851 ± 1.194	Castellanos-Galindo and Krumme (2013)
Caeté Estuary, North Brazil	9900[a]	2545	5896	Block net	49	2.1	Barletta et al. (2003)
Everglades National Park, USA	144,447[b]	1520	42	Block net and rotenone	63	14	Thayer et al. (1987)
Solomon Islands, Pacific Ocean	64,200[c]	3541[d]	83.6	Block net and rotenone	85	11.6 ± 12.4	Blaber and Milton (1990)
Moreton Bay, Eastern Australia	15,200[e]	1008	3340	Enclosure net	41	25.3 ± 20.4	Morton (1990)
Embley River, Northern Australia	8300	1787	585	Enclosure net	55	3.9	Vance et al. (1996)
Pagbilao Bay, Philippines	110·7	2242	161	Enclosure net	46	10.4 ± 13.2	Ronnback et al. (1999)
Gazi Bay, Kenya	661	1074	9	Enclosure net	49	0.9 ± 1.5	Crona and Ronnback (2007)
Qeshm Island, Iran	6750	200	6837	Block net	26	0.0085 ± 0.02	Shahraki and Fry (2016)
Al Khor & Al Dhakira, Qatar	234.5	75	5400	Block net	20	1.4 ± 0.8	This study

[a] Wolff et al. (2000).
[b] Simard et al. (2006).
[c] Gilman et al. (2006).
[d] SOPAC (2007).
[e] Accad et al. (2016).

Moreover these 4 species showed strong attachment to the mangroves having a biomass at least 10 fold higher in the October mangrove than mudflat catches perhaps indicating that the higher biomass is related to feeding activity Whereas many of the minor species such as *Portunus pelagicus*, *Terapon jarbua*, *Platycephalus indicus*, and *Sillago sihama* were also found in mudflat catches suggesting more widespread use of coastal habitats. Further evidence of the distinct and significant differences in the species composition of catches from mangroves and mudflats are provided by PCoA and PERMANOVA analysis (S1.). We modelled the source contribution of mangroves to the tissue of migratory fauna, based on using yellow mangrove leaves but omitted MPB from the analysis to simplify the otherwise complicated isotopic influences between mangrove litter, MPB and sediment. We feel justified in this approach, because the biomass and productivity of MPB is very low in Qatar and the carbon incorporated into the MPB is of mangrove in origin (Davis et al., 2009; Walton et al., 2014). Further discussion of the interpretation of the isotopic evidence related to MPB is presented in the Supplementary material (S2). The isotope Bayesian mixing models suggested that the contribution of mangrove carbon to the tissue of the migratory fauna ranged from 21 to 58%, with *P. khori* most reliant on the mangroves as a carbon source. The high reliance of *P. khori* on mangrove material as a dietary source is likely due to its strong attachment to the mangroves, it is a mangrove resident that has never been found in catches over the surrounding mudflat/seagass beds (Al-Maslamani et al., 2013).

Mangroves are found intertidally between mean sea level and high water, although these vary with location (Ellison, 2009). In Qatar, mangroves are found 0.2 m above mean sea level, and from tidal charts we estimated that the mangroves were dry for 60% of the time when migratory fauna are forced out of the mangrove, where they continue to respire and excrete mangrove-sourced nutrients. We found that of the mangrove material consumed, 34 kg C ha⁻¹ yr⁻¹ (i.e. 90% from Pauly and Christensen, 1995) is lost through excretion/respiration but only 60% is lost outside the mangrove while the tide is out and is thus estimated to be 20.8 ± 18.0 kg C ha⁻¹ yr⁻¹ or 0.8% of leaf litter production. We assumed that this carbon loss was lost in proportions equal to that of the carbon composition of the migratory fauna, so that the tissue and excretion of *A. dispar* had a carbon content of 40% mangrove, 32% phytoplankton and 28% seagrass. The increase in metabolism after eating, known as specific dynamic action, indicates that respiration rates are not uniform (Jobling, 1981). Similarly digestion times and assimilation efficiency, as mangrove carbon is regarded as especially refractory

(Rodelli et al., 1984) may result in the unequal release of consumed material in neighbouring habitats. The impact of this could be explored further however it is unlikely to significantly increase the proportion mangrove carbon outwelled by fauna.

The values reported for outwelled POC and DOC of around 30% each of leaf litter production (Bouillon et al., 2008a), are much larger than our estimates of outwelled C in fish biomass (mortality estimates). However mangrove carbon outwelled as fish tissue, may be of much greater importance to coastal food webs than DOC or POC, as it directly enters at a high trophic level through predation; fish biomass in the present study had an average trophic level of ~3. Hence, while faunal-mediated direct export of mangrove matter might be a small fraction of primary productivity, it may be much more significant to coastal fisheries than carbon outwelled as DIC, POC and DOC that has to pass through various trophic levels, before being incorporated into an exploitable species, with the potential associated trophic transfer loss by two orders of magnitude (Pauly and Christensen, 1995). Moreover, while mangrove POC is highly refractory with high C:N ratios of 20–30 (Canfield et al., 2005) but enriched compared to recently fallen leaf litter (Mean C:N ± 1SD = 93.7 ± 9.8 unpublished data), mangrove carbon outwelled as mortality of fish biomass has a C:N of 4.2 to 5.1 that is more easily assimilated by consumers. In the studied mangroves (201 ha), the total outwelling associated with the mortality of the migratory fauna is equivalent to 96 kg of mangrove C yr⁻¹ or 947 kg yr⁻¹ of mangrove derived fish biomass wet weight. If commercial species were preying directly on the this outwelled mangrove fish biomass, this small area of mangrove may support commercial fish catches of 95 kg yr⁻¹, using the 10:1 trophic efficiency ratios of Pauly and Christensen (1995). However this does not consider the greater quantities of carbon outwelled through respiration and excretion by the mobile fauna.

The amount of the mangrove litter that is consumed is related to the biomass of the migratory fauna. *A. dispar* formed 80% of the biomass and is responsible for 91% of the mangrove carbon consumed (Table 3), the proportions are not equal as this species also had the highest consumption rate. We highlighted earlier, the impact of reducing consumption rates of *A. dispar* from 52 to 24, on the decreased mangrove consumption by the migratory fauna. The other important factor influencing mangrove consumption is the dietary reliance on mangrove as estimated by isotopic modelling, the biomass and consumption rates of *P. khori* and minor species are similar but isotopic values of *P. khori* suggest 57% of its diet is mangrove derived compared to the 22% of minor

species resulting in consumption rates of mangrove that are much greater (Table 3). Our faunal biomass sampling indicates that arid mangroves support similar richness of migratory fauna to other mangroves (Table 3). The differences in species composition and biomass found between the Al Khor mudflat and our experimental mangrove forest sites suggests that the faunal outwelling is specific to mangrove sites and not generalized coastal outwelling. To determine if the lack of rainfall at the current sites might have some influence on the biomass of migratory fauna, and hence one of the most important factors in faunal consumption and outwelling of mangrove carbon, we compiled data from other studies that estimated mobile faunal biomass from around the world (Table 3). We used Pearson's correlation analysis to examine strength and direction of any relationship between logged biomass of mobile mangrove fauna with annual rainfall, logged total mangrove area, logged mean trap catchment area, and species numbers using the values given in Table 3. We found no relationships between faunal biomass and annual rainfall, nor with mangrove area, nor mean trapped area, nor the number of species ($p > 0.05$). Of course it is likely that other factors such as mangrove productivity, retention of productivity within the mangrove, and the amount bioprocessed within the mangrove, as well as faunal biomass in surrounding habitats will be important in influencing the biomass of mobile faunal that feeds in the mangrove forests. Hence, there may well be differences between old and new world mangrove due to the feeding traits of the mangrove fauna that can impact energy flow (McIvor and Smith, 1995; Lee, 1998). As the biomass of migratory faunal does not relate to aridity, we cautiously suggest that the results of the current study ought to be applicable to other higher rainfall areas. Rainfall-generated wash out of particulate mangrove carbon can lead to less defined isotopic boundaries, so that it becomes impossible, using stable isotopes, to determine whether mangrove carbon in mobile fauna is outwelled or derives from the ingestion of previously outwelled mangrove material. However in old world mangroves where the leaf litter is highly processed (McIvor and Smith, 1995; Lee, 1998) and there is a large biomass of migratory fauna a correspondingly great proportion of the mangrove carbon may be faunally outwelled. However we suggest that migratory faunal biomass and amount (not proportion) of mangrove C exported by this faunal group are likely to be correlated.

5. Conclusions

This study presents a first estimate of the proportion of the primary productivity that may be outwelled by mobile aquatic species through the phenomenon known as trophic relay. The study indicates that only small amounts (1.4%) of mangrove leaf litter produced is consumed and only 0.8% outwelled by fauna via two modes: through the excretion and respiration of the ingested mangrove matter by migratory fauna during low water periods when the mangroves are dry; and through the mortality of migratory fauna. Our trapping studies produced biomass estimates with lower statistical variation than other studies, and our isotopic evidence supports the dietary reliance of migratory fauna on mangrove production. Our sites were flooded just 40% of the time, meaning that these water-dependent fauna were spending at least 60% of the time in habitats subtidal to the mangrove. We suggest arid mangroves are ideal sites for studying the faunal movement of carbon due to the lack of rainfall driven outwash of mangrove carbon that increases the certainty that the mangrove carbon in the tissues of mobile fauna originated from feeding within the mangrove forest. We suggest that the biomass of migratory fauna moving between mangrove and subtidal habitats and the amount of faunally outwelled mangrove carbon is likely to be highly correlated. However the proportion of NPP that is faunally outwelled may vary according to the difference in mangrove leaf litter processing and retention in old and new world mangrove. The differences in biomass estimates from mangrove forests in some other regions of the world suggest that migratory faunal biomass has the potential to contribute correspondingly more to the outwelling of carbon. Finally, although the proportion of faunal outwelled carbon is small, that carbon is more readily bioavailable to coastal foodwebs than other forms of outwelled carbon (DIC, DOC & POC), given the value of fauna to higher consumers in the coastal foodweb. Thus, faunal-mediated carbon export may be of much greater significance, for example in support of commercial fish biomass, than its relatively small proportion of the total mangrove carbon budget suggests. The small proportion of carbon outwelled by migratory fauna supports the current mass-balance models that suggest 40–50% of mangrove production is indeed outwelled as DIC.

CRediT authorship contribution statement

M.E.M. Walton: Conceptualization, Methodology, Writing - original draft. **I. Al-Maslamani:** Investigation, Writing - review & editing. **M. Chatting:** Investigation, Writing - review & editing. **D. Smyth:** Investigation, Writing - review & editing. **A. Castillo:** Investigation, Writing - review & editing. **M.W. Skov:** Methodology, Investigation, Writing - review & editing. **L. Le Vay:** Methodology, Investigation, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.142677.

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