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Enhanced pore-water nutrient fluxes by the upside-down jellyfish *Cassiopea* sp. in a Red Sea coral reef

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ABSTRACT: The common circum-tropical jellyfish *Cassiopea* sp., unlike other members of the Rhizostomidae (Scyphozoa), exhibits a primarily benthic life. The peculiar orientation of its exumbrella against the sediment is believed to be associated with its mainly autotrophic nutrition, i.e. exposing its zooxanthellae-bearing photosynthetic oral appendages to the sunlight. Here we show that the jellyfish also acts as a nutrient pump, drawing nutrient-rich pore waters from the permeable sediments. Depletion of pore-water ammonium *in situ*, light-enhanced ammonium uptake, and high rates of photosynthesis determined via oxygen flux measurements and underwater fluorometer analysis (rapid light curves) show that *Cassiopea* sp. effectively harnesses pore-water nutrients. At high densities *Cassiopea* sp. may facilitate benthic-pelagic coupling and primary production in oligotrophic coral reefs.

KEY WORDS: *Cassiopea* sp. · Upside-down jellyfish · Advective pore-water transport · Nutrient uptake · Nutrient regeneration · Sediment · Photosynthesis · Zooxanthellae

INTRODUCTION

The upside-down jellyfish *Cassiopea* sp. (Cnidaria, Scyphozoa, Rhizostomidae) leads a benthic life. It is common in coral reefs, lagoons, seagrass beds and mangroves (Fleck & Fitt 1999, Arai 2001, Todd et al. 2006), often attaining high densities of up to 30 ind. m^{-2} (Niggl & Wild 2009) and higher (e.g. 'countless numbers'; Bigelow 1900, p. 190). Another peculiarity of *Cassiopea* sp., shared with few other jellyfish (e.g. *Linuche unguiculata* and *Mastigias* sp.; Kremer et al. 1990, McCloskey et al. 1994), is its association with photosynthetic dinoflagellates (zooxanthellae). These microalgae live as symbionts in the oral appendages and the bell of *Cassiopea* sp. Within the bell they are mainly located beneath the exumbrella and particularly beneath the subumbrellar endodermal epithelia (Bigelow 1900, Blanquet & Riordan 1981), and can reach relatively high densities (1.52×10^6 to 2.68×10^6 cells mg^{-1} protein; Verde & McCloskey 1998).

The zooxanthellae provide a major source of energy to the holobiont, so that *Cassiopea* sp. may act as a functional photoautotroph, depending on light availability (Cates 1975, Verde & McCloskey 1998). *Cassiopea* sp. is able to adapt to high light conditions (e.g. in shallow water) and maintains an effective photosynthetic productivity by protecting itself from an excess of harmful UV radiation via the synthesis of myco-

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sporine acids (Banaszak & Trench 1995), as demonstrated for corals and giant clams (Shick et al. 1995, 1999, Ishikura et al. 1997). Furthermore, *Cassiopea* sp. has a special blue mesogloeal protein that serves as a shield against damaging solar radiation, while simultaneously allowing photosynthetically active wavelengths to reach the zooxanthellae (Blanquet & Phelan 1987).

Cassiopea sp. has an upside-down orientation, with the exumbrella facing the substrate, its beating motion and mucus (Gohar & Eisawy 1960) fixing the animal in place so that 'especially the larger ones would not ordinarily leave the bottom' (Bigelow 1900, p. 191). This unusual modus vivendi of *Cassiopea* sp. has prompted speculations that the jellyfish's activity may represent a mechanism to maintain its position with respect to sunlight, thus enabling prolonged exposure of the zooxanthellae-laden oral appendages and the subumbrella (Gohar & Eisawy 1960). It has also been considered a feeding strategy, whereby autotrophic nutrition is accomplished via the capture of interstitial microorganisms flushed across its oral appendages (Larson 1997), entangled in mucus, and subsequently consumed by the many secondary mouths (Bigelow 1900). Nutrient requirements for photosynthesis may partly be met by this digestion of plankton or suspended organic matter.

Cassiopea sp. usually occurs on sandy patches in coral reefs, seagrass beds or mangroves characterised by calm waters. These permeable sandy sediments function as large-scale filter systems (e.g. Hansen et al. 1992, Holguin et al. 2001), where accumulated organic material is effectively decomposed by high abundances of heterotrophic microbes (Wild et al. 2006) and regenerated nutrients are stored interstitially (Rasheed et al. 2002, Wild et al. 2005). Sedimentary nutrient recycling is mainly achieved by anaerobic microbes below a rather thin aerobic layer (Holguin et al. 2001). Under undisturbed conditions few nutrients are released from the sandy sediment to the overlying water column, while the pore water beneath the aerobic layer contains high concentrations of inorganic nutrients. Nutrients are slowly distributed through diffusion and are primarily consumed by microbes within the thin aerobic layer typical for coral reef sands (Wild et al. 2004, Werner et al. 2006), thereby preventing nutrient release in the overlying water column. However, advective transport, e.g. caused by animal activities (Huettel et al. 2003) or bottom water currents, may cause intense release of water with high concentrations of inorganic nutrients from the permeable sediments (Huettel et al. 1998). Nutrients released from coral reef regenerative spaces (crevices and sediments) may play an important role in sustaining primary production in coral reefs (Richter et al. 2001, Rasheed et al. 2002). It is likely that also *Cassiopea* sp. may utilise regenerated nutrients for the photosynthesis of its zooxanthellae (Hoegh-Guldberg & Smith 1989, Rahav et al. 1989, Dubinsky et al. 1990).

The present study explored the so-far untested hypothesis that the jellyfish acts as a nutrient pump releasing sediment-locked nutrients into the overlying water, and then perhaps assimilating them, thus supporting the holobiont's photosynthesis in oligotrophic waters. We studied the jellyfish's pumping performance, nutrient uptake and metabolism (photosynthesis and respiration), as well as the impact of *Cassiopea* sp. on pore-water nutrient content and its mobility behaviour *in situ*.

MATERIALS AND METHODS

Study site. The present study was carried out in the Marine Reserve of the Marine Science Station (MSS), Aqaba, Jordan. Although the *Cassiopea* species investigated resembles *C. andromeda*, Holland et al. (2004) point out the difficulty of identifying the species in this genus in the absence of molecular data. Therefore, the generic notation *Cassiopea* sp. will be used. All investigated specimens revealed similar morphological characteristics and were collected within the same area (100 m^2). Similarly sized specimens of *Cassiopea* sp. were sampled by SCUBA divers, whereby plastic bags rather than nets were used for transportation in order to prevent any harm to the fragile oral appendages. All subsequent experiments were conducted with freshly collected individuals in the outdoor flow-through system at the MSS using small glass or plastic tanks (8 to 10 l). The average diameter of *Cassiopea* sp. in the experiments was 7.8 ± 2.7 cm (mean ± SE; n = 57). All investigations were conducted from November 2007 until April 2008.

Pumping and vertical pore-water flows. Pumping activity of *Cassiopea* sp. was explored in a series of experiments. The catchment area of pore waters below actively pumping *Cassiopea* sp. was observed in open tanks (8 l, n = 3) lined with three, 2 cm thick, different-coloured layers of natural, washed sediment: the top layer was un-coloured sediment, the middle layer was dyed with fluorescein (yellow-green) and the bottom layer was dyed with food colour (red). It should be noted that washing and mixing of sediment altered its characteristics in comparison to naturally occurring sediments (e.g. regarding microbial and oxygen vertical distribution). Careful filling of the experimental tanks with natural seawater kept the sediment layers intact. For incubations with fluorescein-dyed sediment, no photosynthetically active radiation (PAR) was measured, as the beat frequency of the bells was inde-

pendent of the light intensity (unpubl. data). Incubations were performed under a roof without direct sunlight, as fluorescein is degraded by UV (M. Huettel pers. comm.). The movement of the pore waters was monitored photographically in the course of the 14 h observation period.

Vertical fluxes of pore waters across the sediment-water interface were quantified by short-term incubations in open tanks (10 l). Again, natural, washed sediment was used, whereby a layer of dyed sediment (fluorescein) was covered with an un-coloured layer. During short-term incubations, water motion was only provided by the jellyfishes' body movement (not by stirring) to prevent distortion of pore-water release. In one set of incubations, the un-dyed top layer had a constant 1 cm thickness (n = 13, control: n = 2). In a second set of incubations, the thickness of the top layer varied: 0.5, 1, 1.5 or 2 cm (each n = 6). For all incubations, water samples were taken in time series after introducing 1 specimen to each tank (first set: at 0, 0.5, 1 and 2 h; second set: at 0.5, 1, 2, 3 and 4 h). Fluorescein concentrations of water samples were analysed with a spectral fluorometer (Turner 10-AU-005-CE, excitation 470 nm, emission 514 nm). Accumulating fluorescein concentrations in the tank waters over time were used to calculate pore-water release rates, as fluorescein release across the sediment-water interface (nmol min^{-1}). For each *Cassiopea* sp. specimen the bell beat rate (min^{-1}) was determined 4 times during each incubation. Area pulse rate was calculated by bell beat rate × bell area of each specimen (cm^{-2} min^{-1}). After completing the experiments, the bell diameter (central exumbrellar area including bell margins) of each specimen was measured by placing the live specimen on a measuring tape fixed to the bottom of the holding tank. Bell diameter (D) was recorded between beats, with the relaxed bell lining the bottom. Bell area (A) was calculated according to: $A = \pi \times (0.5 \times D)^2$.

Pore water was collected *in situ* by taking 'minicores', using truncated 100 ml syringes. Minicores (n = 10) were sampled in close vicinity (<2 cm) of pumping *Cassiopea* sp. specimens. Control minicores (n = 10) were taken in reference areas unaffected by the jellyfishes (>1 m away from *Cassiopea* sp.). Pore water was extracted after the methods of Rasheed et al. (2002) and pore-water ammonium and phosphate concentrations were analysed according to Grasshoff et al. (1999).

Nutrient uptake. The jellyfishes were incubated in open tanks (as above, 10 l), with (n = 16) and without (control, n = 8) nutrient solution (ammonium and phosphate). Initial concentrations were 15 µM ammonium and 6 µM phosphate. Controls showed no detectable nutrient uptake (data not shown). PAR (µmol quanta m^{-2} s^{-1}) was measured with the PAR sensor of a Diving-PAM (see below). Half of the incubations were performed under sunlight (856 ± 129 PAR [µmol quanta m^{-2} s^{-1}]), the other half under dark conditions (0 PAR [µmol quanta m^{-2} s^{-1}]), respectively. Water samples were taken in time series after 0, 1, 2, 3 and 5 h and filtered through precombusted (450°C for 6 h) GF/F filters (Whatman, 25 mm in diameter). Ammonium and phosphate concentrations were analysed according to Grasshoff et al. (1999). Uptake rates (nmol cm^{-2} h^{-1}) were calculated by dividing the product of the concentration differences (nmol l^{-1}) and chamber volumes (l) with the bell surface area (cm^2) for the respective specimen.

Photosynthetic performance and respiration. Closed-chamber incubations (3 l) were carried out to quantify photosynthesis and respiration via O_2 fluxes (e.g. Schneider & Erez 2006, Borell et al. 2008). Incubations were conducted in gas-tight acrylic chambers at 2 light intensities (see below) and 0.5 h after sunset (as the Diving-PAM measurements, see below) in a flow-through water bath with ambient seawater. The chambers were not stirred, as *Cassiopea* sp. was assumed to mix the water column enclosed in the chambers by its own body movements (which could be observed throughout the incubations). Oxygen concentrations were determined with an Optode (Q 40, Hach-Lange) at the start and end of each chamber incubation. Oxygen fluxes, i.e. rates of oxygen evolution and consumption (net photosynthesis and respiration rates), were calculated as the difference between start and end amounts of oxygen of each incubation (n = 4). Rates were normalised to bell area (cm^2), to obtain a reference for the size of each specimen, yielding µg O_2 cm^{-2} min^{-1}. Net photosynthesis was determined via light-chamber incubations carried out under direct sunlight at 12:19 to 13:17 h and 13:40 to 14:50 h. For light measurements, the PAR sensor was placed next to the specimens, and showed mean PAR intensities of 506 ± 150 and 269 ± 19 µmol quanta m^{-2} s^{-1}, equivalent to maximum *in situ* light intensities at 3 to 5 m and 8 to 12 m depth (Jantzen et al. 2008) for each incubation, respectively. Respiration was determined via dark chamber incubations (0 PAR [µmol quanta m^{-2} s^{-1}]).

The photosynthetic performance of *Cassiopea* sp. was further investigated using a submersible pulse amplitude modulated fluorometer (Diving-PAM, Heinz Walz; for details see Schreiber 1986). Three rapid light curves (RLC) were conducted on each of 6 dark-adapted *Cassiopea* sp. specimens 0.5 h after sunset, when PAR was no longer detectable and the adaptation of the zooxanthellae to dark conditions was likely completed (Durako et al. 2003, Iglesias-Prieto et al. 2004). Eight increasing PAR intensities up to ~3000 µmol quanta m^{-2} s^{-1} were applied for each RLC using the internal settings of the Diving PAM; the electron transport rate (ETR [µmol e^- m^{-2} s^{-1}]) was recorded. The ETR is defined as: PAR × ([Fm – F°]/ Fm) × 0.5,

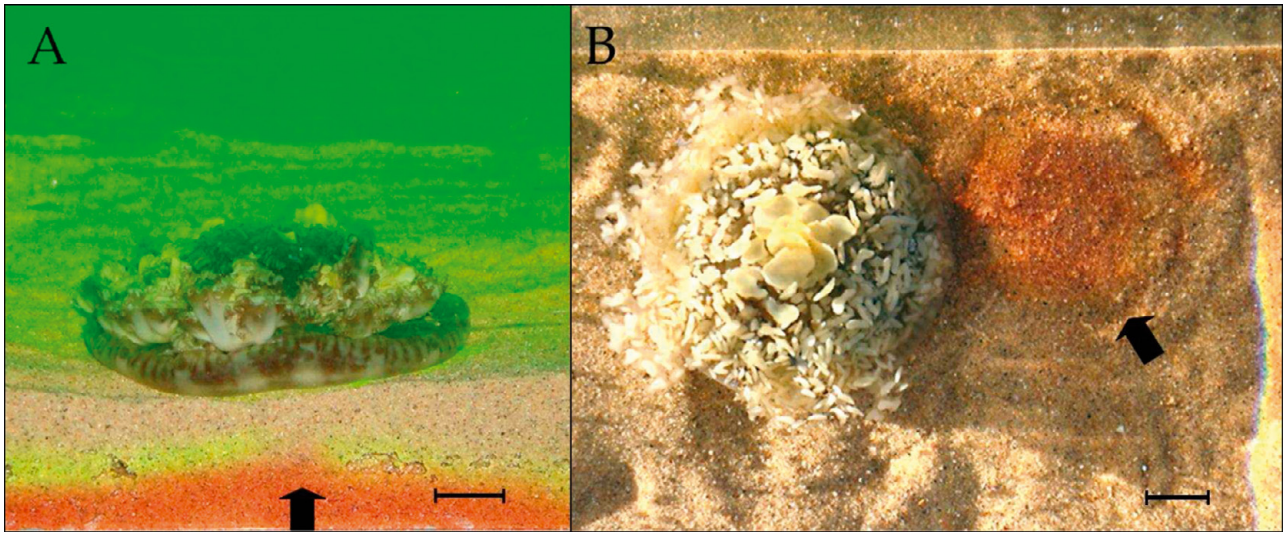

Fig. 1. *Cassiopea* sp. Pumping activity on coloured sediment. (A) Lateral view of an individual entraining pore water (black arrow) from deeper sediment layers into the water column (greenish hue), as indicated by the doming of yellow and red bands. (B) Red-coloured mould of the concave bell in the sediment (arrow) shows that pore waters from the bottom layer have reached the surface (removed *Cassiopea* sp. on the left). Red: food colour; yellow: fluorescein, covered by an un-dyed sediment layer. Scale bars ≈ 1 cm

where PAR is the corresponding PAR intensity, ([Fm – F°]/ Fm) is the potential photosystem II quantum yield and 0.5 represents the assumed uniform distribution of electrons between the 2 photosystems. As no absorption coefficient was defined, this rate is a widely accepted 'relative ETR' (e.g. Glud et al. 2002, Ralph et al. 2002).

Mobility. The mobility of *Cassiopea* sp. was monitored *in situ* in an area with high *Cassiopea* sp. abundance (n_{total} = 22; 9 m water depth) using a 3 × 3 m square subdivided into smaller squares (1 m^2). Photographs were taken daily over a 6 d period (17 to 22 May 2008) and the positions of each individual (identified on the basis of colouring and size) determined. Trajectories of individuals were plotted as progressive vector diagrams and average occupation time (d^{-1} m^{-2}) was determined.

RESULTS

Pumping and vertical pore-water flows

Tank experiments with fluorescein-dyed sediment showed an increase in fluorescein visible as a greenish hue in the tank water (Fig. 1A). The release of fluorescein into the water was accompanied by a doming of the coloured bands in the sediment below the jellyfish (Fig. 1A, black arrow). After ~6 h, pore water from deeper sediment layers reached the surface, as evidenced by the red dye emerging from the circular imprint of the bell on the sediment (Fig. 1B, black arrow shows imprint of bell).

Short-term incubations with *Cassiopea* sp. revealed linearly increasing fluorescein concentrations with time (2.7 ± 1.7 nM min^{-1}, R^2 = 0.4), in contrast to undetectable levels of fluorescein increase in the controls (Fig. 2). The jellyfishes pumped at a rate of 31 ± 7 beats min^{-1}, but no correlation between calculated release rates (nmol min^{-1}) and area pulse rate (cm^2 min^{-1}) was found (R^2 = 0.0007). A 2 cm thick layer of un-coloured sediment delayed dye release by almost 1 h (52 ± 47 min; Fig. S1A,B

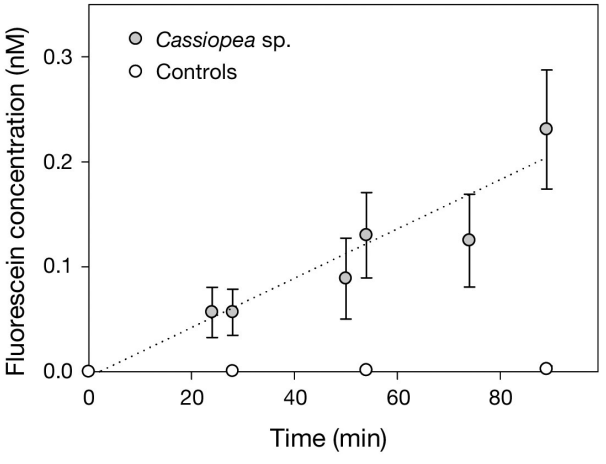

Fig. 2. *Cassiopea* sp. Pumping activity. Sediment-layer fluorescein accumulates in the water column over time in tanks with *Cassiopea* sp. (●; 2.7 ± 1.7 nmol min^{-1}, R^2 = 0.4), but not in controls (○). Data are mean ± SE

in Supplement 1, available at www.int-res.com/articles/suppl/m411p117_supp.pdf). Consequently *Cassiopea* sp. needed ~1 h to draw pore water from this depth (Fig. S1B in Supplement 1).

Pore-water sampling *in situ* revealed significantly lower pore-water ammonium concentrations by ~2 µM, equal to a reduction of 15%, in the direct vicinity of a pumping jellyfish (11.99 ± 1.46 µM) compared to the adjacent, but undisturbed, sediments (14.07 ± 1.45 µM; Fig. S2 in Supplement 1; $p = 0.005$, 2-sided *t*-test, heterogeneity of variances). However, no corresponding differences in phosphate concentrations were detectable.

Nutrient uptake

Open-chamber incubations with added nutrient solutions revealed highest uptake rates for ammonium in the light with 5.88 ± 2.17 nmol cm^{-2} min^{-1} (Fig. S3 in Supplement 1). In contrast, during dark conditions, ammonium uptake was more than 4 times smaller, yielding only 1.29 ± 0.81 nmol cm^{-2} min^{-1}. This difference was highly significant, with $p << 0.001$ (2-sided *t*-test, heterogeneity of variances).

Photosynthetic performance and respiration

Closed-chamber incubations with *Cassiopea* sp. (Fig. 3) revealed maximum net oxygen production rates of 1.66 ± 0.4 µg O_2 cm^{-2} min^{-1} at high PAR intensities (506 ± 150 µmol quanta m^{-2} s^{-1}). Corresponding values at moderate PAR levels (269 ± 19 µmol quanta m^{-2} s^{-1}) were 0.94 ± 0.2 µg O_2 cm^{-2}. Respiration rates were low (0.37 ± 0.08 µg O_2 cm^{-2}), resulting in a high quotient of net photosynthesis to respiration (Q) of 2.6 to 4.5, depending on light conditions.

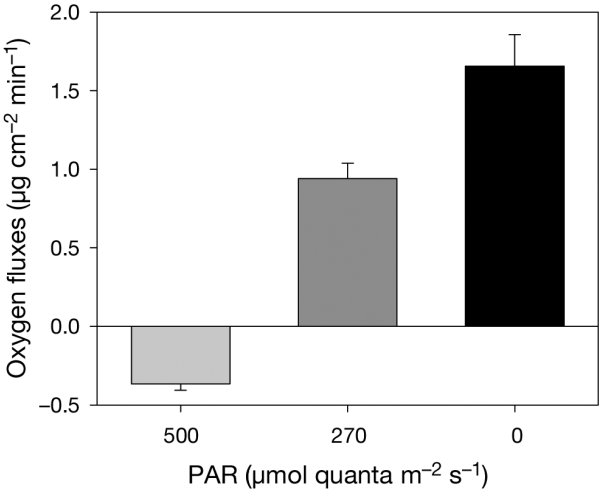

Fig. 3. *Cassiopea* sp. Net photosynthesis and respiration rates. Oxygen fluxes (normalised per bell area) determined under 2 light intensities (506 ± 150 and 269 ± 19 µmol quanta m^{-2} s^{-1}) and in the dark. PAR: photosynthetically active radiation. Data are mean ± SE

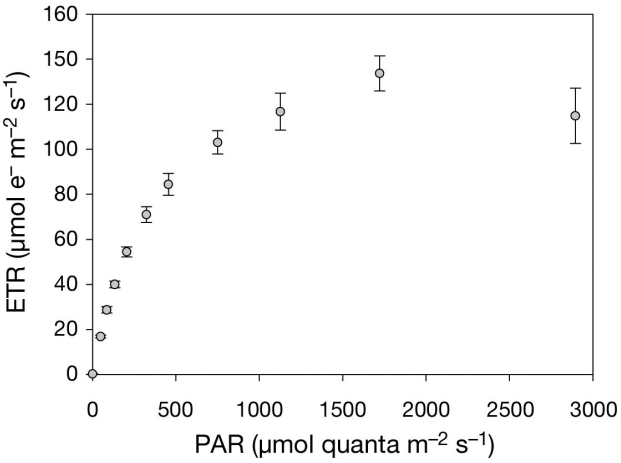

Fig. 4. *Cassiopea* sp. Dark-adapted rapid light curves (RLC). Electron transport rate (ETR) with increasing light intensities (photosynthetically active radiation [PAR]) shows no saturation up to 2-fold maximum ambient light conditions. Data are mean ± SE

RLCs of dark-adapted *Cassiopea* sp. showed no saturation in ETR at up to 2-fold maximum ambient light intensities, revealing *Cassiopea* sp. capable of maintaining an efficient photosynthesis even under very high light intensities (Fig. 4). Maximum photosynthesis was on average 130 ETR (µmol e^- m^{-2} s^{-1}) and individually up to 178 ETR (µmol e^- m^{-2} s^{-1}).

Mobility

Photographic documentation on a scaled area revealed a relatively long residence time of conservatively 2.8 ± 1.7 d within 1 m^2. Some of the jellyfishes were already present before (n = 15), or remained after the end of, the documentation (n = 7), or both (n = 2). A vector diagram showing *Cassiopea* sp.'s movements is given in Fig. S4 in Supplement 1.

DISCUSSION

The present study, along with a recent paper on the related rhizostome *Mastigias* sp. (Katija & Dabiri 2009), is the first demonstration so far of jellyfish-mediated active vertical transport of nutrients across the interface separating oligotrophic surface waters from nutrient-replete interstitial and subthermocline deep water,

respectively. Our behavioural observations and nutrient and fluorescein-tracer measurements clearly show that the jellyfish release sediment-locked nutrient-rich pore waters into the overlying waters and are capable of utilising free ammonium. Ammonium uptake is enhanced by light, suggesting that photosynthesis is involved in the process. But how distinct are these sediment-water fluxes?

Pumping performance and pore-water flows

Permeable sandy sediments with their associated microbiota act as large-scale filters that trap organic matter and recycle and store this material in inorganic form as interstitial nutrients (Hansen et al. 1992, Holguin et al. 2001, Rasheed et al. 2002, Wild et al. 2006). The diffusive fluxes of these sedimentary nutrients into the overlying reef water are only poor (Al-Rousan et al. 2004). Currents and waves interacting with the sediment topography (i.e. sand ripples) may enhance nutrient fluxes by several orders of magnitude (Huettel & Rusch 2000, Huettel & Webster 2001, Rasheed et al. 2003). However, away from the surface, where waves and currents are weak (Precht & Huettel 2003), particularly in the Gulf of Aqaba where horizontal currents average only a few cm s^{-1} (Genin & Paldor 1998, Manasrah et al. 2006), bioturbation becomes more important. Goat fish have been shown to plough the upper centimetres of reef sediments in search of invertebrate food (Yahel et al. 2002), and mud shrimp may ventilate the sediments up to >1 m (Ziebis et al. 1996). Small disturbances as they commonly occur in the present study area, such as interactions between bottom water currents and sediment topography (Ziebis et al. 1996), wave influence (Precht & Huettel 2003) or bioturbation (Huettel et al. 2003), can cause considerable advective pore-water exchange and subsequent release of nutrients from the permeable sediments into the water column. The present study revealed that advective transport of pore-water nutrients may also be induced by the pumping movements of *Cassiopea* sp.

Our report is the first of a gelatinous organism releasing interstitial nutrients in considerable quantities from a depth of 2 cm within 1 h. While the biomechanical details are beyond the scope of the present paper, it is clear from our preliminary observations that the nutrient release is associated with the motion of the exumbrella against the substrate (Movie 1 in Supplement 2, available at www.int-res.com/articles/suppl/m411p117_supp/). The muscular contraction of the bell, antagonised by the flat or slightly cup-shaped mesogloea (Gladfelter 1972) sealed off against its margin with mucus (Gohar & Eisawy 1960; Movie 2 in Supplement 2), creates a pressure gradient drawing nutrient pore water up and into the jet of water forced through the oral appendages (Fig. 5). In contrast to corals and other sessile functional phototrophs, which are entirely at the mercy of the currents supplying essential nutrients to the passive animals, the mobile jellyfish *Cassiopea* sp. may actively enrich its nutrient environment by pumping nutrients from the sediments.

Small jellyfish (*Polyorchis penicillatus*, <3 cm diameter) expend between 8.9×10^{-5} and 14.0×10^{-5} J in the contraction phase, and between 1.7×10^{-5} and 2.1×10^{-5} J in the refilling phase of their swimming bells (DeMont & Gosline 1988a,b). For the ~1 order of magnitude larger *Cassiopea* sp. in the present study (×3 by bell diameter, equivalent to a conservative ×10 by bell volume and mass, considering the flat shape of the bell), we may conservatively assume an order of magnitude higher force (mass × acceleration) and energy (force × displacement), i.e. $\sim 2 \times 10^{-4}$ J in the refilling phase of their beat cycle. If we assume that this energy is used to refill both exumbrellar and subumbrellar

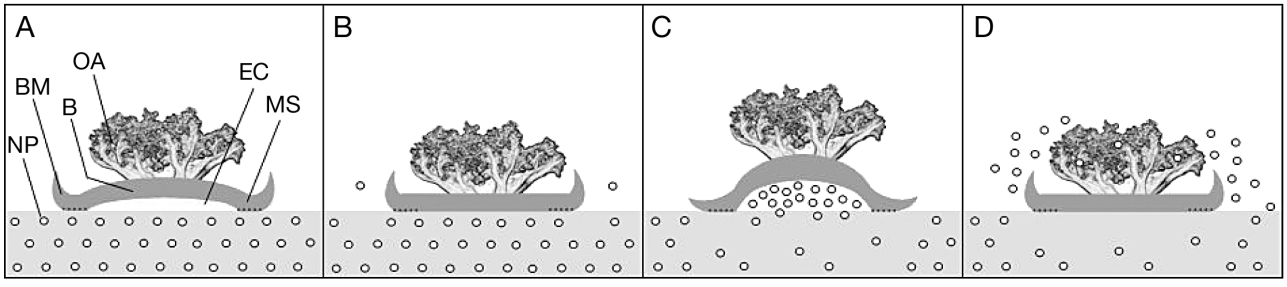

Fig. 5. *Cassiopea* sp. Scheme of pumping activity on sediment. (A) Freshly settled specimen on the sediment, revealing the concave exumbrella. (B) Contraction of the muscles causes the bell to flatten, forcing the enclosed water sideways into the overlying water. (C) The subsequent relaxation of the muscles allows the flexed bell to re-gain its former cup-like shape; the growing exumbrellar cavity sealed off at the bell margins draws pore waters into the exumbrellar space. (D) Contraction of the bell (beat) flushes nutrient-rich water out sideward, enriching the zooxanthellae-bearing oral appendages with nutrients. B: bell; BM: bell margins; EC: exumbrellar cavity; MS: mucus sealed bell seating; NP: nutrient-rich pore water; OA: oral appendages. Note that the vertical-scale exumbrellar cavity is exaggerated

spaces in the concave-shaped exumbrella of *Cassiopea* sp. (as opposed to *Polyorchis* spp. and other free-swimming medusae with convex exumbrellae, where only the subumbrella can be filled), this leaves us with an energy E of ~1×10^{-4} J to refill the exumbrellar space (assuming that the energy is partitioned to both sides of the bell in equal proportions). If we now consider *Cassiopea* sp.'s exumbrella to function as a d = 10 cm diameter suction piston with h = 5 mm vertical displacement, this energy may be used to draw pore-water flows upwards, as long as the mucus-lined bell margin acts as a seal isolating the exumbrellar space from the boundary layer waters. The corresponding upward force can be calculated as F = E/h = 0.0001 J / 0.005 m = 0.02 N. This force F exerted on a d = 0.1 m diameter circular area ($A = \pi \times (d/2)^2$) may thus generate a horizontal pressure gradient of p = F/A = 2.5 Pa between the exumbrella-covered and adjacent sediment areas. Such a pressure gradient may potentially drive pore-water flows between 0.4 and >3.7 l m^{-2} h^{-1} with washout depths between 2.5 and >10 cm, depending on the permeability of the sediment (Huettel & Gust 1992). However, no hydro-dynamical investigations were conducted, as they were beyond the scope of the present study, and therefore no concrete conclusions could be drawn.

Precht & Huettel (2003) investigated wave-induced pressure gradients around 1.1 Pa across the sediment-water interface driving flows of 116 l m^{-2} d^{-1}. Rasheed et al. (2004) found that a similar pressure gradient (1.2 Pa between the centre and rim of a stirred chamber) induced flow velocities around 0.6 cm s^{-1}, equivalent to a 4-fold pore-water release compared to diffusive fluxes.

The overall amount of released nutrients depends on the jellyfishes' densities. *Cassiopea* sp. covers an average of 3% of the sediment areas at the Marine Reserve of the MSS and may attain abundances of up to 30 ind. m^{-2} (Niggl & Wild 2009); they are also common in Caribbean lagoons (Arai 2001) and mangrove ecosystems along Florida (Fleck & Fitt 1999). Where they occur in high densities or 'countless numbers' (e.g. in Jamaica; Bigelow 1900), this jellyfish may furnish a substantial supply of otherwise unavailable sediment-locked nutrients in oligotrophic coral-reef waters.

The lack of correlation between fluorescence tracer release and *Cassiopea* sp. area pulse rate suggests that other factors unaccounted for in our experiments play a role in generating the pressure gradient driving the vertical flux of pore waters, such as the tightness of the mucus seal around the bell margin or varying pumping forces of the individual jellyfish. Data on the biomechanics of *Cassiopea* sp. pumping and induced pore-water flows are lacking and need to be characterised in future studies.

Although jellyfish have only recently been shown to enhance the vertical flux of nutrients in the pelagic realm (Katija & Dabiri 2009), *Cassiopea* sp. is the only example to the best of our knowledge of a gelatinous ecosystem engineer enhancing the supply of nutrients in coral reefs.

Nutrient uptake

Cassiopea sp. assimilated ammonium, known to be the preferred nitrogen source for symbiont-bearing cnidarians (Muscatine 1978, Burris 1983, Wilkerson & Trench 1986). Ammonium absorption by *Cassiopea* sp. was considerably enhanced under sunlight, indicating a stimulation of ammonium uptake by photosynthesis. This effect has also been found for other zooxanthellae-bearing organisms, such as the coral *Stylophora pistillata* (Grover et al. 2002) and other hosts (Summons et al. 1986). The jellyfish revealed a high photosynthetic efficiency under high light levels (as demonstrated by the RLCs), comparable to corals under similar light intensities (Ralph et al. 1999, 2002). Furthermore, *Cassiopea* sp. exhibited a high net photosynthesis to respiration quotient (Q), hinting towards functional autotrophy, as supported by the studies of Cates (1975) and Verde & McCloskey (1998). Therefore *Cassiopea* sp. is in need of organic nutrients to support the production of photosynthates by its symbionts. Despite intensive recycling of nutrients within the cnidarian-zooxanthellae symbiosis that retains essential nutrients inside the holobiont (Muscatine & Porter 1977, Falkowski et al. 1984, Rees 1986), and evidence indicating an uptake of host-derived ammonium by the zooxanthellae (Cates & McLaughlin 1976), *Cassiopea* sp. can profit from the release of fresh pore-water nutrients induced by its own body movement.

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