

Sponges as important sources of nitrate on an oligotrophic continental shelf

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Abstract

In situ field measurements of dissolved inorganic nitrogen (DIN) release by sponges in southwestern Australia revealed nitrate release rates of 0.022 to 0.743 $\mu\text{mol g dry weight}^{-1} \text{ h}^{-1}$ and ammonium release rates of between 0.002 and 1.366 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$. The highest and most consistent rates of nitrate release were among the Thorectidae (0.324 to 0.725 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$), while mycalid and verongid sponges were highly variable (0.024 to 0.743 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$). The ratio of nitrate to ammonium in released nitrogen ranged from 0.1 to 197.0, indicating a wide range of nitrogen release modes by sponges, from predominantly ammonium to very efficient nitrate producers. The study more than doubles the number of temperate sponge species recorded to release nitrate. Nutrient concentrations near the seabed sponge assemblages were higher at low wind speed (a proxy for turbulent mixing). These observations and our measurements of nitrogen release rates from sponges are consistent with the hypothesis that primary production in the region depends on wave-induced mixing at the seabed for resupply of remineralized nitrogen to a nutrient-impoverished water column and that sponges make an important contribution to these fluxes. Based on known biomass of sponges in southwestern Australia, we calculate that sponges may contribute DIN of 1.8 to 3.2 $\text{g N m}^2 \text{ yr}^{-1}$. Taking into account the distribution of sponge habitat across the continental shelf to 100 m depth, this constitutes a contribution of 10% to 18% of the total recycled nitrogen flux required from the benthos to balance a regional nitrogen budget.

Sponges have a worldwide distribution and play a wide range of functional roles in marine ecosystems, yet they remain understudied and underappreciated for their importance (Bell 2008; Webster and Taylor 2011; Maldonado et al. 2012). Sponges are common and conspicuous members of shallow benthic community assemblages, where they compete for space with algae, sea grass, and corals. However, often sponges will dominate the diversity and biomass at the lower levels of the photic zone and deeper on many of the world's continental margins, including southwestern Australia (Fromont et al. 2011), the location of our study. Sponges have developed a range of adaptations that have made them highly successful; they filter huge volumes of seawater (Reiswig 1971; Weisz et al. 2008), consuming bacteria and picoplankton and retaining these very small particles not selected by other filter feeders (Reiswig 1975; Coma et al. 2001; Hanson et al. 2009). They have developed a range of bacterial and algal mutualisms, which provide benefits to the host and contribute to biogeochemical and ecological processes. Of particular interest are symbioses with photosynthetic cyanobacteria (Usher 2008; Lemloh et al. 2009), which provide the sponge with photosynthetically derived energy and carbon (Wilkinson 1983), and symbiotic nitrifying bacteria, which convert ammonium to nitrite and nitrate (Corredor et al. 1988; Diaz and Ward 1997; Bayer et al. 2008). In this way, sponges take particulate organic matter from the water column and return part of it as both ammonium and nitrate, providing a recycled source of nutrients for primary production. The recent finding that sponges are also capable of denitrification (Hoffmann et al. 2009; Schläppy

et al. 2010) adds to the complexity of the benthopelagic dynamics with which sponges are associated.

The marine environment of the eastern Indian Ocean off Western Australia has very low levels of nutrients and pelagic production (Lourey et al. 2006; Irvine et al. 2008) as a result of low rainfall and runoff and the dominant influence of the Leeuwin Current, a tropical low-nutrient boundary current that flows poleward along the continental shelf (Cresswell and Golding 1980), suppressing upwelling. Despite this, there are productive benthic ecosystems, in particular, those dominated by kelp and sea grasses (Kirkman 1984; Cambridge and Hocking 1997). A nitrogen budget developed for the southwestern Australian continental shelf (Feng and Wild-Allen 2010) found that more than 80% of primary production on the shelf relied on recycled nitrogen, with less than 10% injected from offshore sources. As a result, processes that aid recycling of nitrogen on the shelf are crucial in maintaining the shelf ecosystem. Feng and Wild-Allen (2010) concluded that a recycled flux of 6.2 $\text{g N m}^{-2} \text{ yr}^{-1}$ from the benthos on the continental shelf off Western Australia was required to balance the nitrogen budget. The source of this flux of nitrate from the benthos has not been specifically identified, but remineralization within sediments and benthic fauna, such as sponges, have been suggested by Lourey and Kirkman (2009), and Greenwood (2010) showed that wave-generated resuspension of nutrients from sediments is likely to be important in the benthic nutrient resupply process on this shelf. Nitrogen remineralization by nitrifying bacterial symbionts in a range of other invertebrates may also be important sources of recycled nitrogen (Welsh and Castadelli 2004).

Wide ranges of dissolved inorganic nitrogen (DIN) release rates, including the release of nitrate, have been

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measured in sponges. In the Caribbean, Corredor *et al.* (1988) and Diaz and Ward (1997) measured rates of 600 nmol N g dry weight⁻¹ (dry wt) h⁻¹ in *Chondrilla nucula* and 30–2666 nmol N g dry wt⁻¹ h⁻¹ in four species of sponges. For temperate sponges, there are fewer data; however, Jiménez and Ribes (2007) and Bayer *et al.* (2008) found similar rates (89–780 nmol N g dry wt⁻¹ h⁻¹) in several species in the Mediterranean, and Hoffmann *et al.* (2009) measured release rates of 196 nmol N g dry wt⁻¹ h⁻¹. In southwestern Australia near our study sites, Hatcher (1994) measured ammonium release rates of between 520 and 690 nmol N g dry wt⁻¹ h⁻¹ in the shallow-water sponges *Aplysina* sp. and *Iotrochota baculifera*. Sponges have also been recorded to release significant levels of DIN at community scales. In the Caribbean, Corredor *et al.* (1988) and Southwell *et al.* (2008b) measured rates of between 11.5 and 15.4 mmol N m⁻² of reef d⁻¹ (59 and 78 g N m⁻² of reef yr⁻¹) attributable to sponges on the coral reefs they studied. In the Mediterranean, Jiménez and Ribes (2007) made comparable measurements, which showed lower rates of between 2.5 and 7.9 mmol N m⁻² of reef day⁻¹ (13 and 40 g N m⁻² of reef yr⁻¹).

The objective of our study was to measure DIN release rates by sponges off southwestern Australia and to determine whether any sponges released significant amounts of nitrogen as nitrate. On the basis of these measurements, we also sought to determine whether sponges represent an ecologically significant source of nitrogen resupply in the region. Until our study, there had been no measurements of nitrate release rates from sponges anywhere in the Indian Ocean, and ours is the first to try to attempt to estimate the contribution of sponges to DIN fluxes at the scale of a continental shelf ecosystem rather than just at a community level.

Methods

Site and habitat descriptions—The experiment was carried out at South Lumps (latitude 31°47.612 S, longitude 115°42.990 E), which is typical of rocky limestone reefs in southwestern Australia (Fig. 1), on 15 March 2011. The experiment was conducted after an earlier (2008) pilot study of small-scale variability in nutrient concentrations close to and away from beds of filter feeders (predominantly sponges and ascidians) at South Lumps and four other similar reefs (North Lumps, Whitfords Rock, Wreck Rock, and Cow Rock; *see* Fig. 1) suggested concentrations of ammonium and nitrate were higher near the seabed containing patches of filter feeders than away from them. South Lumps is a shallow limestone patch reef 1.5 km offshore and within Marmion Lagoon, which is somewhat sheltered by the offshore limestone reef 2 km to the southwest. However, waves break across South Lumps in heavy swell conditions. The water depth at the base of the reef is 5.5 m (range 4.4–7.2 m), and caves and fissures dissect and intersect the reef basally. The prevailing wind is from the southwest year-round, and in the summer, strong morning easterlies also create substantial surge at the seabed, which features a diverse habitat of broken reef, sand patches, and sea grass beds. The reef is dominated by

a cover of macroalgae, in particular, the kelp *Ecklonia radiata*. Sponges are very common on the seabed and close to the reef.

In situ measurements on individual sponges—Sponges were selected to provide a good representation of species present, although our method precluded including many types of encrusting sponges and very large specimens. Divers carefully enclosed individual sponges in plastic bags, ranging from 3 to 30 liter capacity depending on the size of the sponge. The plastic bags were filled with seawater prior to fitting them around the sponge and then closed tightly around the base of the sponge and secured with a plastic cable tie (Fig. 2). Immediately after this, two water samples were taken using a 60 mL syringe and needle, one from inside and one from outside the bag. Three further water samples were taken in the same way 15, 30, and 60 min after bagging. Each sponge was kept in the bag for 1 h, and in total, 37 sponges comprising 15 species in 11 families (*see* Table 1) were sampled in this way over a period of 5 h between 09:20 h and 14:20 h. Five controls consisting of bags without sponges secured to weights were used to account for any influence of the bags on water chemistry and to quantify any flux of nutrients from sources other than sponges. The water samples were regularly ferried by divers to the surface vessel, where they were transferred from the syringes into two replicate 10 mL polypropylene nutrient tubes and then frozen and later analyzed for ammonium, nitrate + nitrite, silicate and phosphate as per the following methods.

At the end of the 1 h observation period, each sponge was collected with their plastic bags intact and transferred back to the vessel, where the sponges were photographed, and then frozen, and the volume of water in the bags was measured to the nearest 50 mL. Sponges were later identified by examining classical taxonomic characters, including morphological, skeletal, and spicule features. Samples of sponge tissue have been lodged in the collections of the Western Australian Museum (*see* Table 1 for museum registration number). Sponges were measured to the nearest centimeter to calculate an approximate volume and weighed to nearest 0.1 gram. Sponges were then oven dried at 60°C for 72 h when constant dry weight was achieved.

Water chemistry analyses—Nutrients were analyzed using a flow injection analysis, with ammonium concentration determined using a gas diffusion, derivatization–fluorescence detection method. For silicate (silicic acid), Si species were reacted with molybdate at 45°C and pH 1.2 and then reduced with stannous chloride to form a heteropoly blue complex that was measured at 820 nm. Phosphate was reacted with molybdate and antimony potassium tartrate in acid medium, which was then reduced with ascorbic acid to form a blue complex that was measured at 880 nm. Nitrate was first reduced to nitrite by passing it through a copperized cadmium column. Nitrite was then reacted with sulfanilamide under acidic conditions to form a diazonium salt, which was then coupled with N-(1-naphthyl) ethylenediamine dihydrogenchloride to form a

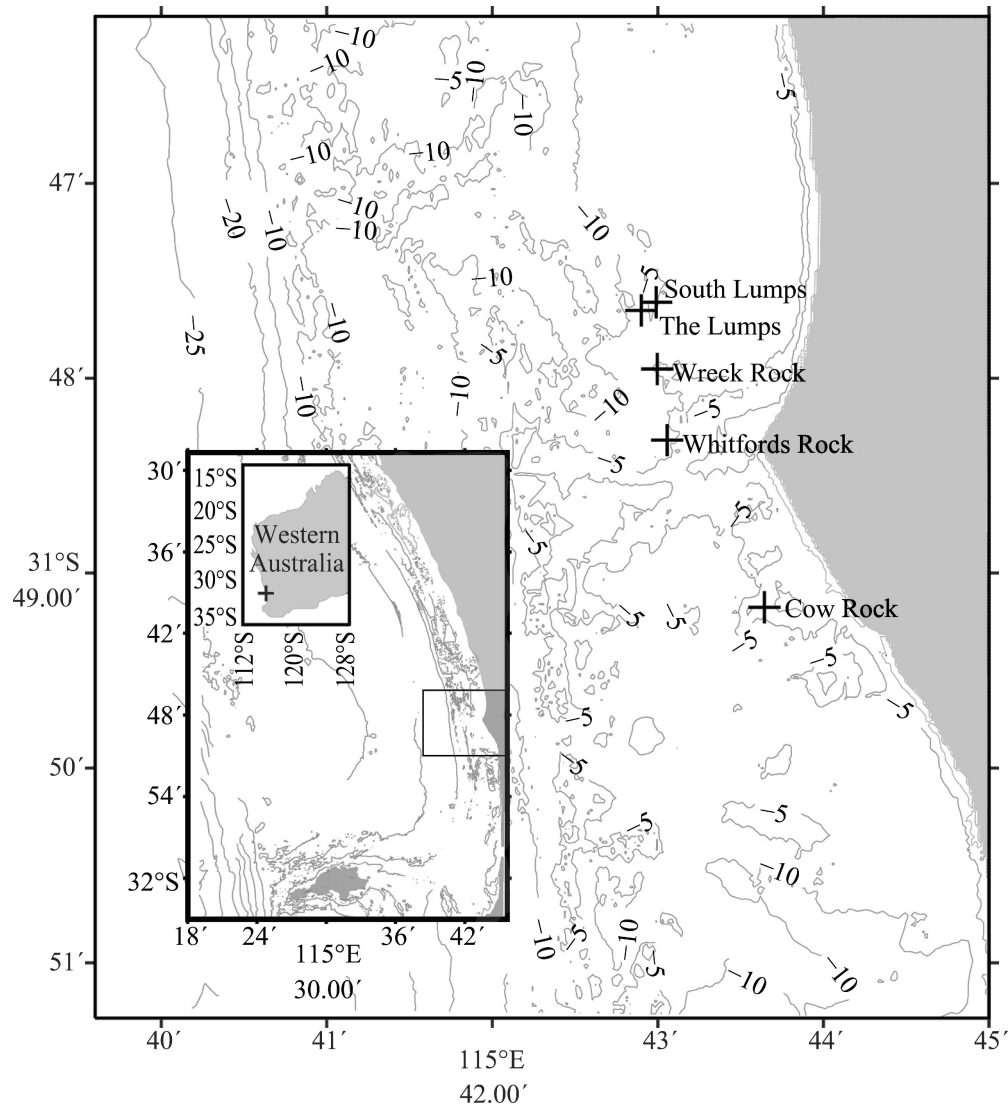


Fig. 1. Map showing location of study sites within Marmion Lagoon, nearby reefs, and bathymetry.

pink complex that was measured at 520 nm. For ammonium, a sodium hydroxide solution was added to liberate ammonium, which was then diffused across a polytetrafluoroethylene (PTFE) membrane to react with ortho-phthaldialdehyde (OPA)-sulfite solution. This solution was then excited at 310 nm, and the fluorescence was measured at 390 nm.

Data analyses—Nutrient concentrations are presented in $\mu\text{mol L}^{-1}$, and fluxes are in $\mu\text{mol L}^{-1} \text{h}^{-1}$ or $\mu\text{mol g dry weight}^{-1}$ (dry wt) h^{-1} . Note that these rates are for dry weight, not ash-free dry weight. The rate of nitrite and nitrate, ammonium, phosphate, and silicate release by each bagged sponge was determined from the slope values of linear regressions calculated for the change in concentration during hourly measurements. Two rates were calculated: average, where each of the four measurements (0, 15, 30, and 60 min) was included, and maximum, where only

the three measurements that resulted in the maximum slope were included. The maximum rates therefore remove any possible artifacts that may have occurred in the first 15 min, when the sponge may have been disturbed by the bagging process, or the last 30 min, when the sponge may have been physiologically stressed from excessive refiltration. There was little evidence of such disturbance in the data, with most sponges showing a uniform change in nutrient concentrations over time. The exception to this was one sponge, *Diplastrella* sp. ML1, which produced minimal ammonium and consumed a small amount of nitrate. Data from this sponge are presented here (Fig. 3) for completeness but were excluded from calculation of nutrient fluxes. To further examine for evidence of artifacts caused by enclosing the sponges in bags, we looked for any size-dependent change in nitrogen release rates within species. For the two species with sufficient sample size to make a correlation analysis, there was no relationship between dry

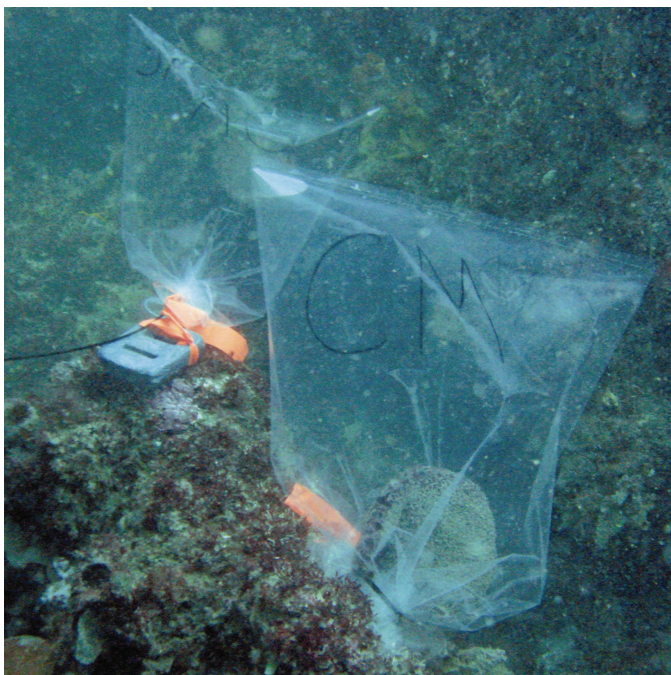


Fig. 2. Example of sponge, *Mycale* (*Arenochalina*) cf. *mirabilis*, within bag and control bag.

weight of sponge, volume of sponge, ratio of volume of bag: volume of sponge and any of the rates of nitrogen release (average or maximum) for ammonium, nitrate, or total DIN (*Mycale* [*Arenochalina*] cf. *mirabilis*, $n = 6$, $p = 0.229$ – 0.583 ; *Aplysinella* sp. ML1, $n = 13$, $p = 0.168$ – 0.429). Over a much larger size range of sponges, there was a significant relationship between dry weight of sponge and total DIN release (average and maximum) when all species and all specimens sampled were included ($n = 36$, excluding one outlier, as explained previously, $p = 0.031$ and $p = 0.020$ for average and maximum release rates, respectively). However, it is not unexpected that DIN release rates per

unit of mass may be lower in larger sponges, given it is well known that other mass-specific rate measurements such as respiration and filtration rates decrease with an increase in sponge weight (Thomassen and Riisgård 1997; Ribes *et al.* 1999).

In controls (bags without sponges), average fluxes (mean ± 1 standard deviation [SD]) were: nitrite and nitrate ($-0.015 \pm 0.097 \mu\text{mol L}^{-1} \text{h}^{-1}$), ammonium ($-0.035 \pm 0.017 \mu\text{mol L}^{-1} \text{h}^{-1}$), silicate ($0.020 \pm 0.023 \mu\text{mol L}^{-1} \text{h}^{-1}$), and phosphate ($0.001 \pm 0.007 \mu\text{mol L}^{-1} \text{h}^{-1}$). As these values were very small relative to treatments (*see* Fig. 3), they were not deducted from treatments but are presented alongside the treatment data for the reader to compare. Data for multiple sponges of the same species were pooled to calculate means and variance for each of these parameters for each species.

Wind data—Wind data used in this study were from the closest recording station (Ocean Reef 31.76°S, 115.73°E, 10 m above sea level, 3.7 km from South Lumps) collected at 1 min intervals (source: Australian Bureau of Meteorology, <http://www.bom.gov.au>). Wave data were not available from this station or anywhere else near this site.

Results

Nitrogen release rates of individual sponges—Maximum nitrate release rates ranged from 0.078 to 4.728 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (excluding one outlier, *Diplastrella* sp. ML1, which consumed nitrate; *see* Fig. 3), while ammonium release rates varied between 0.012 and 2.676 $\mu\text{mol L}^{-1} \text{h}^{-1}$. The highest rates of nitrate release were 4.728 $\mu\text{mol L}^{-1} \text{h}^{-1}$ by *Taonura* sp. J1, (Thorectidae) and 4.422 $\mu\text{mol L}^{-1} \text{h}^{-1}$ by one *Mycale* (*Arenochalina*) cf. *mirabilis* (Mycalidae). The highest rates of ammonia release were also among the *M.* (*A.*) cf. *mirabilis* (range 0.984 to 2.478 $\mu\text{mol L}^{-1} \text{h}^{-1}$) and *Haliclona* cf. sp. SS3 (Chalinidae) (2.676 $\mu\text{mol L}^{-1} \text{h}^{-1}$). The ratio of nitrate to ammonium in released nitrogen (ignoring instances of nitrate or ammonium consumption)

Table 1. Identification table for sponges sampled for nitrogen release rates. Western Australian Museum (WAM) registration numbers are shown. Species assignment to families and orders follows van Soest *et al.* (2011). Species with names ending in ML1, J1, SS2, and SS3 are unique species identifiers used by WAM to denote species that are possibly new species but that have not yet been exhaustively compared with material in other collections.

Order	Family	Genus and species	Museum voucher
Poecilosclerida	Mycalidae	<i>Mycale</i> (<i>Arenochalina</i>) cf. <i>mirabilis</i> Lendenfeld, 1887	Z28906–28911
	Microcionidae	<i>Clathria</i> (<i>Wilsonella</i>) sp. ML1	Z28915, Z28916
	Crambeidae	<i>Monanchora</i> sp. ML1	Z28912
	Iotrochotidae	<i>Iotrochota</i> cf. <i>baculifera</i> Ridley 1884	Z28303–28305
Dictyoceratida	Thorectidae	<i>Thorectandra</i> cf. <i>choanoides</i> (Bowerbank, 1872)	Z28913
		<i>Thorectandra</i> sp. ML1	Z28922
		<i>Taonura</i> sp. J1	Z28924, Z28925
		<i>Hyrrios</i> sp. ML1	Z28918
Verongida	Aplysinellidae	<i>Aplysinella</i> sp. ML1	Z28939–28952
		<i>Diplastrella</i> sp. ML1	Z28923
Hadromerida	Spirastrellidae	<i>Craniella</i> sp. ML1	Z28917
Spirophorida	Tetillidae	<i>Isops</i> cf. sp. SS2	Z28920
Astrophorida	Geodiidae	<i>Isops</i> sp. ML1	Z28919
		<i>Acanthella</i> cf. <i>pulcherrima</i> Ridley and Dendy, 1886	Z28921
Halichondrida	Dictyonellidae	<i>Haliclona</i> (<i>Haliclona</i>) cf. sp. SS3	Z28914
Haplosclerida	Chalinidae		

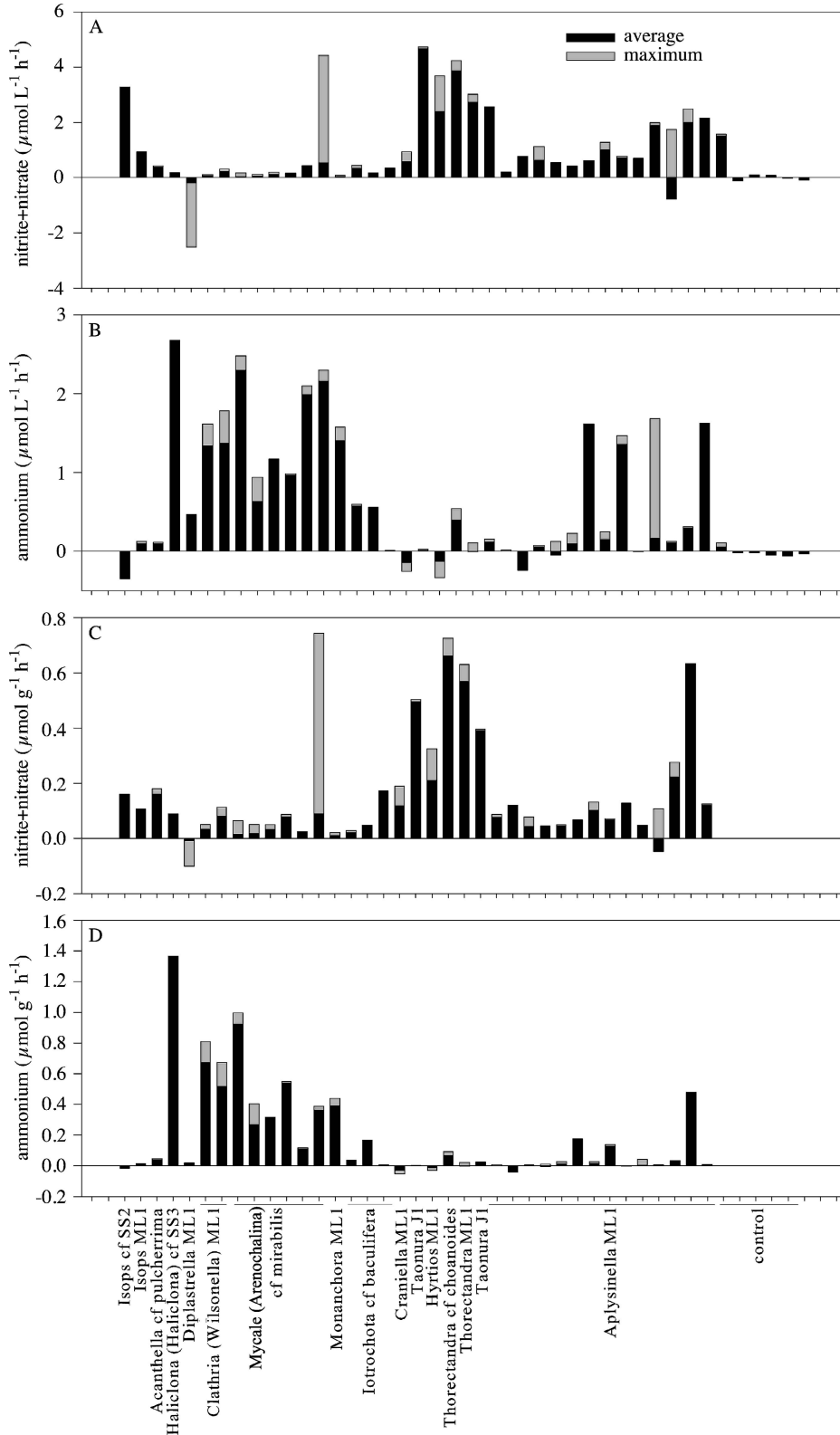


Fig. 3. Hourly changes in nitrogen concentrations ($\mu\text{mol L}^{-1} \text{h}^{-1}$) and weight-normalized flux of nitrogen ($\mu\text{mol g dry wt}^{-1} \text{h}^{-1}$) for each sponge sampled.

Table 2. Mean average and maximum flux of nitrogen ($\mu\text{mol g dry wt}^{-1} \text{ h}^{-1} \pm 1 \text{ SD}$) and coefficient of variation (CV) for five species with more than one individual and all taxa represented by a single species.

Species	Sample size	Average flux of $\text{NO}_2+\text{NO}_3 \pm \text{SD}$ (CV)	Maximum flux of $\text{NO}_2+\text{NO}_3 \pm \text{SD}$ (CV)	Average flux of $\text{NH}_4^+ \pm \text{SD}$ (CV)	Maximum flux of $\text{NH}_4^+ \pm \text{SD}$ (CV)
<i>Clathria</i> (<i>Wilsonella</i>) ML1	2	0.06 ± 0.03 (0.60)	0.08 ± 0.04 (0.53)	0.59 ± 0.11 (0.19)	0.74 ± 0.1 (0.13)
<i>Mycale</i> (<i>Arenochalina</i>) cf. <i>mirabilis</i>	6	0.04 ± 0.03 (0.77)	0.17 ± 0.28 (1.65)	0.42 ± 0.28 (0.67)	0.46 ± 0.3 (0.65)
<i>Iotrochota</i> cf. <i>baculifera</i>	3	0.08 ± 0.08 (0.99)	0.08 ± 0.08 (0.93)	0.07 ± 0.08 (1.22)	0.07 ± 0.08 (1.21)
<i>Taonura</i> sp. J1	2	0.44 ± 0.07 (0.17)	0.45 ± 0.08 (0.17)	0.01 ± 0.01 (1.23)	0.01 ± 0.02 (1.14)
<i>Aplysinella</i> sp. ML1	14	0.12 ± 0.16 (1.34)	0.14 ± 0.15 (1.13)	0.06 ± 0.13 (2.28)	0.07 ± 0.13 (2.00)
All species represented by a single specimen*	9	0.23 ± 0.23 (0.98)	0.27 ± 0.25 (0.92)	0.20 ± 0.46 (2.26)	0.21 ± 0.46 (2.19)
Overall mean of all taxa*	14	0.20 ± 0.20 (1.01)	0.24 ± 0.22 (0.90)	0.21 ± 0.38 (1.82)	0.23 ± 0.40 (1.74)

* Excludes *Diplastrella* sp. ML1, an outlier that produced a negligible amount of ammonium and consumed a small amount of nitrate (see Fig. 3).

ranged from 0.1 to 197.0. The highest nitrate to ammonium ratios were recorded in *Thorectandra* sp. ML1, *Thorectandra* cf. *choanoides*, and *Taonura* sp. J1 (Thorectidae) (range 7.8 to 197.0), while *M. (A.)* cf. *mirabilis* (range 0.1 to 1.9) had the lowest, and *Aplysinella* sp. ML1 (Verongida) were the most variable (range 0.4 to 14.6). In all, we recorded 14 species from 10 families (see Table 1) releasing nitrate.

Nutrient fluxes—Weight-specific nitrate release rates ranged from 0.022 to 0.743 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$ (excluding one outlier, which consumed nitrate; see Fig. 3), while ammonium release rates varied between 0.002 and 1.366 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$. The highest weight-specific rate of nitrate release was 0.743 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$ in one *M. (A.)* cf. *mirabilis* (Mycalidae), although the five other individuals of this species had low levels of nitrate release (range 0.024 to 0.087 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$). Among the four thorectid species (*Hyrtios* sp. ML1, *Thorectandra* sp. ML1, *Thorectandra* cf. *choanoides*, and *Taonura* sp. J1), weight-specific nitrate release rates were consistently high (range 0.324 to 0.725 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$), and *Aplysinella* sp. ML1 (Verongida) rates were quite variable (range 0.045 to 0.632 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$). Fluxes of silicate were low (range -0.044 to 0.060 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$); only seven sponges were net removers of silica, and of these, only three recorded fluxes of more than $-0.010 \mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$. Twelve recorded fluxes of more than 0.010 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$. Fluxes of phosphate were also low (range -0.019 to 0.312 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$). Only three sponges consumed phosphate, and of these, only two recorded fluxes of more than $-0.010 \mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$. One *Aplysinella* sp. ML1 released 0.312 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$ phosphate, but this was an exception, with only two of the 32 sponges recording a positive phosphate flux, releasing more than 0.050 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$.

Means and variability of weight-specific nitrogen release rates within species—Of the 15 species sampled, five had multiple individuals. Table 2 shows the mean $\pm 1 \text{ SD}$ for weight-specific release rates (average and maximum) of both nitrite and nitrate and of ammonium for these species. The species for which we had the most measurements, *Aplysinella* sp. ML1, had the most variable weight-specific average release rates, with coefficients of variation (CV) of

1.34 to 2.28, while *Clathria* (*Wilsonella*) ML1 showed the most consistent weight-specific average release rates, with CV of 0.19 to 0.60. The overall mean rates of nitrogen release for all taxa were 0.202 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$ (average nitrate) and 0.212 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$ (average ammonia) (Table 2), with the mean total average rate of DIN release for all taxa being 0.414 $\mu\text{mol g dry wt}^{-1} \text{ h}^{-1}$ (SD = 0.367, standard error = 0.098).

Temporal change in nutrient concentrations and wind patterns—Variation in ambient nutrient concentration during the experiment is shown in Fig. 4. Concentrations were low at the beginning of the measurement period, averaging $0.71 \pm 0.31 \text{ SD}$ (nitrate) and $0.28 \pm 0.16 \text{ SD}$ (ammonium) between 09:20 h and 10:50 h. There was a rapid increase at 11:00 h to at least double the initial concentrations, to average values of $1.88 \pm 0.52 \text{ SD}$ (nitrate) and $0.53 \pm 0.19 \text{ SD}$ (ammonium) between 11:00 h and 14:20 h. Over this latter period, nutrients continued to increase until the end of the measurement period, albeit at a slower rate. This rate of increase of nutrients over time was significant for all nutrients (linear regression, $p < 0.05$). Mean wind speed during sampling was $6 \pm 1 \text{ m s}^{-1}$

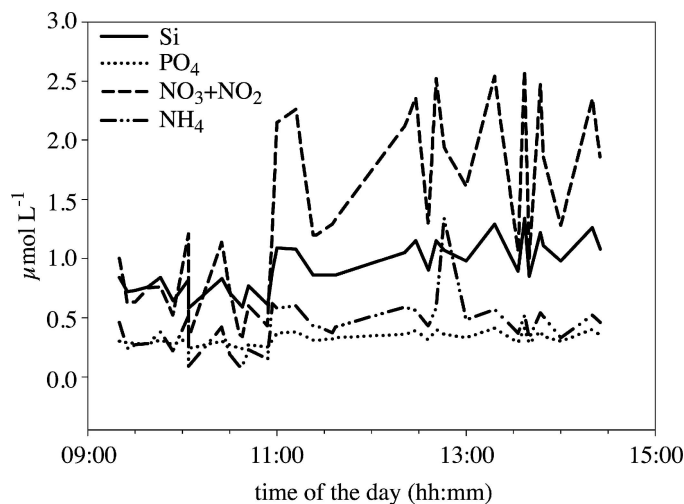


Fig. 4. Changes in concentrations of nutrients in seawater close to the seabed ($\sim 0.5 \text{ m}$) over the course of the sampling on 15 March 2011.

Table 3. Correlation among nutrients and wind speed (Pearson correlation [r]). Sample size $n = 40$ for all tests.

	PO ₄		NO ₂ +NO ₃		NH ₄₊		Wind	
	r	p	r	p	r	p	r	p
Si	0.958	<0.0001	0.966	<0.0001	0.696	<0.0001	-0.334	0.0351
PO ₄			0.978	<0.0001	0.727	<0.0001	-0.301	0.0588
NO ₂ +NO ₃					0.724	<0.0001	-0.384	0.0145
NH ₄₊							-0.292	0.0677

(21.6 km h⁻¹) from the east-northeast, turning north-northeast after 10:25 h and back to east-northeast after 11:10 h. In the afternoon, around 13:00 h, the wind swung to a southerly direction, staying south-southeast until the end of the sampling. Wind speed was highest at the beginning of sampling (8.7 m s⁻¹) and quickly abated to 6 m s⁻¹. At 11:30 h, wind increased to 7.7 m s⁻¹ for a short period and then decreased to 5 m s⁻¹; at 12:30 h, wind dropped further to 3.6 m s⁻¹. At 13:00 h, wind quickly increased and fluctuated between 5 and 7 m s⁻¹ until the end of sampling.

All nutrients were significantly and positively correlated with each other ($p < 0.0001$; see Table 3 for all r and n values), and nutrients were inversely correlated with wind speed, although only silicate ($r = -0.334$, $p < 0.0351$, $n = 40$) and nitrite + nitrate ($r = -0.384$, $p < 0.0145$, $n = 40$) were significant (Table 3). There was significant positive correlation between total DIN and phosphate ($r = 0.880$, $p < 0.0001$, $n = 41$) for water samples taken outside the bags containing sponges. All the samples showed nitrogen limitation when the Redfield ratio was used as a criterion (Fig. 5).

Discussion

Nitrogen release by sponges—We measured maximum nitrogen release rates, which ranged from 0.078 to 4.728 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (nitrate) and between 0.012 and

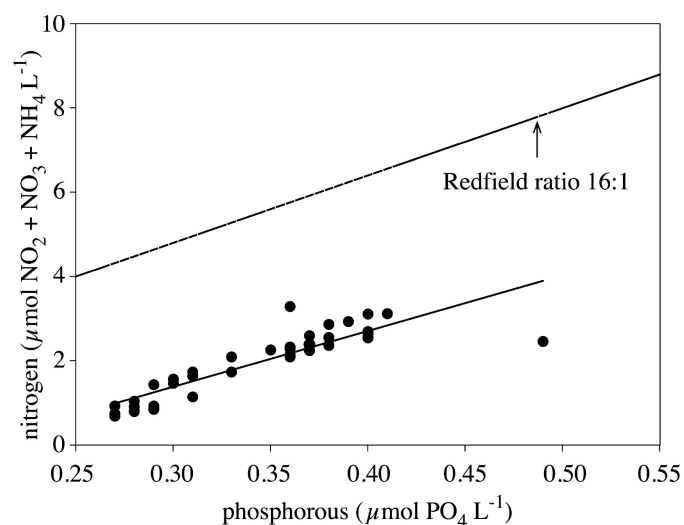


Fig. 5. Relationship between nitrogen and phosphorous concentrations in seawater close to the seabed (c.a. 0.5 m) over the course of the sampling on 15 March 2011.

2.676 $\mu\text{mol L}^{-1} \text{h}^{-1}$ (ammonium). Low release rates might mean sponges stopped filtration in response to disturbance from the experimental procedure; however, only one of the 37 sponges had average release rates of less than 0.02 $\mu\text{mol L}^{-1} \text{h}^{-1}$ for both nitrate and ammonium, indicating any disturbance was minimal. We have also presented both average and maximum rates of release because any disturbance to filtration rates from the bags that did occur is likely to have been in the initial stage of the experiment. Nitrogen release rates varied substantially between species and between individuals, and the ratios of nitrate to ammonium release rates varied from 0.1 to 197.0. The ratio of nitrate to ammonium release rates provides an indication of the relative importance of nitrification potential among different species, and the results indicate some species release significant amounts of nitrogen as nitrate in place of ammonium, but that others produce little or no nitrate. This result is consistent with that of Jiménez and Ribes (2007), who found five of six species, including *Aplysina aerophoba*, released predominantly nitrate, not ammonium, and Perea-Blázquez et al. (2012), who found *Haliclona* sp. released significant amounts of ammonia and minimal amounts of nitrate. In our study, *Haliclona* cf. sp. SS3 also released high amounts of ammonia and low amounts of nitrate (see Fig. 3). Maximum dry weight (dry wt) specific nitrate release rates in our study ranged from 0.022 to 0.743 $\mu\text{mol g dry wt}^{-1} \text{h}^{-1}$ (22–743 nmol g dry wt⁻¹ h⁻¹), while ammonium release rates varied between 0.002 and 1.366 $\mu\text{mol g dry wt}^{-1} \text{h}^{-1}$ (2–1366 nmol g dry wt⁻¹ h⁻¹). Schläppy et al. (2010) measured nitrification rates equivalent to 73–122 nmol g dry wt⁻¹ h⁻¹ in two sponge species (*Dysidea avara* and *Chondrosia reniformis*) from the Adriatic Sea, and Hoffmann et al. (2009) measured a nitrification rate of 196 nmol g dry wt⁻¹ h⁻¹ in *Geodia barretti* in Norway. These are within the range found in our study. Most published rates are given as combined rates of nitrogen release expressed as total dissolved inorganic nitrogen (DIN) in nmol g dry wt⁻¹ h⁻¹. Our total rates of DIN release ranged from 67 to 1455 nmol DIN g dry wt⁻¹ h⁻¹ (maximum rates) and from 10 to 1455 nmol DIN g dry wt⁻¹ h⁻¹ (average rates). Published rates of nitrogen (as DIN) release in both tropical and temperate sponges are similar to our measurements and are also variable. Diaz and Ward (1997) measured rates of 30–2666 nmol N g dry wt⁻¹ h⁻¹ in four species of sponges in the Caribbean. Also in the Caribbean, Corredor et al. (1988) found rates of nitrogen release of 600 nmol N g dry wt⁻¹ h⁻¹ in *Chondrilla nucula*. For temperate sponges, there are fewer data; however, in addition to the Hoffmann (2009) and Schläppy et al. (2010)

studies cited already, Jiménez and Ribes (2007) found similar rates (180–780 nmol N g dry wt⁻¹ h⁻¹) in several species in the Mediterranean. Also in the Mediterranean, Bayer *et al.* (2008) measured nitrate release by *A. aerophoba* (Order Verongida, Family Aplysinidae) in aquaria between 89 and 344 nmol g dry wt⁻¹ h⁻¹, which is within the range of our measurements for verongids. Bayer *et al.* (2008) measured highly variable ratios of nitrate to ammonium, 0.06 to 3.27, which are also consistent with our field measurements. Nitrogen release rates (of ammonium) measured in two shallow-water species of sponges (*Aplysina* sp., and *I. baculifera*) in our study region of southwestern Australia by Hatcher (1994) were between 520 and 690 nmol g dry wt⁻¹ h⁻¹, which is also within the range found in our study (*I. baculifera* in our study [$n = 3$] ranged from 360 to 1038 nmol g dry wt⁻¹ h⁻¹). In New Zealand, Perea-Blázquez *et al.* (2012) recorded significant elevation in nitrate in exhalant water as opposed to inhalant water in three species of sponges: *Haliciona venustina*, *Strongylacidon* sp., and *Crella incrustans*. These authors also recorded seasonal variability in the difference in nitrate and ammonia concentration in exhalant water as opposed to inhalant water in these species, but there was no consistent seasonal pattern among species. In total, we recorded 14 species from 10 families (all Demospongiae) releasing nitrate, which, when added to the previous published records (listed in Table 4), brings the total recorded nitrate-releasing species to 45 from 26 families of sponges. Of these, 26 species from 20 families are from temperate regions, and 19 species from 12 families are from tropical coral reefs (Table 4).

Water-column nutrient concentrations—Average nitrate concentrations were low (0.1 to 2.6 $\mu\text{mol L}^{-1}$) but comparable to measurements reported in other studies for this area (Lourey *et al.* 2006; Lourey and Kirkman, 2009). Lourey and Kirkman (2009) recorded monthly long-term (5 yr) modal DIN levels of about 1.5 $\mu\text{mol L}^{-1}$, pulsing to about 4 $\mu\text{mol L}^{-1}$ during storm events. They attributed the pulses of nutrients, which were rapidly taken up by primary producers, to wave-generated disturbance at the seabed, resulting in a supply of remineralized nitrogen from the sediment and other benthos to the water column. Their measurements, made in 1983 daily for 30 d (0.4 to 3.6 $\mu\text{mol L}^{-1}$) and hourly for 36 h (0.5 to 2.7 $\mu\text{mol L}^{-1}$), are similar to concentrations measured in our study. Their samples were taken at the surface and away from the rocky limestone reef. Our findings over the course of a day, that DIN levels close to the reef seabed are higher at lower wind speeds, are consistent with those of Lourey and Kirkman (2009) when we consider that if the benthos is an important source of nutrient resupply, then you would expect greater mixing at higher wind speeds, and thus at lower winds speeds, nutrient levels at the seabed are likely to be more concentrated. Thus, our results are not inconsistent with the hypothesis that wave-induced turbulence at the seabed facilitates resupply of remineralized nitrogen from the benthos to the water column (Lourey and Kirkman 2009; Greenwood 2010). Our results also show wind speed-associated variation in silicate as well as nitrate, but not

ammonium or phosphate. Diatoms, which require silicate, form an important component of the coastal phytoplankton biomass in this region (Kendrick *et al.* 1998; Thompson and Waite 2003; Hanson *et al.* 2005). Lourey *et al.* (2006) suggested that low levels of silicate (< 2 $\mu\text{mol L}^{-1}$) may be limiting, so wave-induced silicate resupply may also be an important mechanism acting in this region. However, while our results show that sponges may be important in contributing to high nitrate fluxes from the seabed, this is not the case for silicate fluxes, as we measured only minute fluxes of silicate in sponges. Elsewhere, sponges are known to be significant sinks of silicate (Maldonado *et al.* 2005). Our data also confirm results from other studies in the region (Lourey *et al.* 2006) showing that nitrogen is the limiting nutrient in primary production, with N:P ratios (~ 4) consistently below that of the Redfield ratio.

Importance of nitrogen release by sponges to nitrogen resupply and budget—This region of the southeastern Indian Ocean off Western Australia has very low levels of nutrients and pelagic production (Lourey *et al.* 2006; Irvine *et al.* 2008). It is subject to the dominant influence of the Leeuwin Current, which brings warm, low-nutrient, low-salinity tropical water along the continental shelf (Cresswell and Golding 1980). The Leeuwin Current flows all year-round, suppressing upwelling and vertical mixing (Feng *et al.* 2007), and advection associated with the current is thought to provide less than 10% of nitrogen used for primary production on the shelf (Feng and Wild-Allen 2010). Despite this, highly biodiverse (Keesing and Irvine 2005) and productive benthic ecosystems thrive in the region and are dominated by sea grass (Cambridge and Hocking 1997) and kelp (Kirkman 1984). A nutrient budget developed for the southwestern Australian continental shelf (Feng and Wild-Allen 2010) found that 84% of primary production relied on recycled nitrogen and calculated that a recycled flux of 6.2 g N m⁻² yr⁻¹ was required to balance the budget. The main source of recycled nitrogen on the shelf in this region has been thought to be the resupply of nutrients from sediments as a result of wave-driven disturbance (Lourey and Kirkman 2009; Greenwood 2010). However, nitrogen release by sponges, including remineralization by bacterial sponge symbionts, may be another important source of recycled nitrogen.

Sponge biomass surveys conducted at, or offshore of, our study sites (Keesing *et al.* 2012) found between 53 and 850 g wet weight of sponges m⁻² of rocky reef-covered seabed, (average biomass 218 g wet weight [wet wt] m⁻² at 30–50 m depth and 325 g wet wt m⁻² at 50–100 m depth). Surveys in the vicinity of our South Lumps study site at Marmion Lagoon in < 20 m water (Keesing 2011) found sponge biomass to average 36 g dry weight of sponges m⁻² of reef-covered seabed. Application of the wet weight to dry weight conversion measured in our study (0.198) to these average biomass measurements yields a range of average sponge biomasses of 36–64 g dry weight m⁻² out to 100 m water depth. Using the mean total DIN (0.414 $\mu\text{mol g dry wt}^{-1}$ h⁻¹) and nitrate (0.202 $\mu\text{mol g dry wt}^{-1}$ h⁻¹) release rates measured in this study, it is possible to estimate average possible nitrogen fluxes for sponges of 1.8 to 3.2 g

Table 4. List of species of sponges recorded to release nitrate from studies in tropical (trop) and temperate (temp) seas. Species assignment to order and family follows van Soest et al. (2011).

Order	Family	Genus or species	Trop or temp	Reference
Agelasida	Agelasidae	<i>Agelas conifera</i>	Trop	Southwell (2007)
Agelasida	Agelasidae	<i>Agelas oroides</i>	Temp	Jiménez and Ribes (2007)
Astrophorida	Geodiidae	<i>Geodia barretti</i>	Temp	Hoffmann et al. (2009)
Astrophorida	Geodiidae	<i>Isops</i> cf. sp. SS2	Temp	This study
Astrophorida	Geodiidae	<i>Isops</i> sp. ML1	Temp	This study
Chondrosida	Chondrillidae	<i>Chondrilla nucula</i>	Trop	Diaz and Ward (1997); Corredor et al. (1988)
Chondrosida	Chondrillidae	<i>Chondrosia reniformis</i>	Temp	Jiménez and Ribes (2007); Schläppy et al. (2010)
Dictyoceratida	Dysideidae	<i>Dysidea avara</i>	Temp	Schläppy et al. (2010)
Dictyoceratida	Irciniidae	<i>Ircinia campana</i>	Trop	Southwell (2007)
Dictyoceratida	Irciniidae	<i>Ircinia felix</i>	Trop	Southwell et al. (2008a)
Dictyoceratida	Irciniidae	<i>Ircinia oros</i>	Temp	Jiménez and Ribes (2007)
Dictyoceratida	Irciniidae	<i>Ircinia strobilina</i>	Trop	Southwell et al. (2008a)
Dictyoceratida	Thorectidae	<i>Hyrtios</i> sp. ML1	Temp	This study
Dictyoceratida	Thorectidae	<i>Taonura</i> sp. J1	Temp	This study
Dictyoceratida	Thorectidae	<i>Thorectandra</i> cf. <i>choanoides</i>	Temp	This study
Dictyoceratida	Thorectidae	<i>Thorectandra</i> sp. ML1	Temp	This study
Dictyoceratida	Thorectidae (Thorectinea)	<i>Hyrtios</i> (syn. <i>Oligoceras</i>) <i>violacea</i>	Trop	Diaz and Ward (1997)
Dictyoceratida	Thorectidae (Thorectinea)	<i>Smenospongia aurea</i>	Trop	Southwell et al. (2008a)
Hadromerida	Clionaidae	<i>Cliona</i> 'Anthosigmella' <i>varians</i>	Trop	Corredor et al. (1988); Southwell et al. (2008a)
Halichondrida	Axinellidae	<i>Axinella polypoides</i>	Temp	Jiménez and Ribes (2007)
Halichondrida	Axinellidae	<i>Svenzea</i> (syn. <i>Pseudaxinella</i>) <i>zeai</i>	Trop	Diaz and Ward (1997)
Halichondrida	Dictyonellidae	<i>Acanthella</i> cf. <i>pulcherrima</i> sp.	Temp	This study
Halichondrida	Heteroxyidae	<i>Higginsia thielei</i>	Temp	van Duyl et al. (2008)
Haplosclerida	Callyspongiidae	<i>Callyspongia</i> (<i>Cladochalina</i>) <i>vaginalis</i>	Trop	Southwell et al. (2008a)
Haplosclerida	Chalinidae	<i>Haliclona</i> (<i>Haliclona</i>) cf. sp. SS3	Temp	This study
Haplosclerida	Chalinidae	<i>Haliclona venustina</i>	Temp	Perea-Blázquez et al. (2012)
Haplosclerida	Nyphatidae	<i>Nyphates erecta</i>	Trop	Southwell et al. (2008a)
Haplosclerida	Petrosiidea	<i>Xestospongia muta</i>	Trop	Southwell et al. (2008a)
Homosclerophorida*	Plakinidae	<i>Plakortis halichondrioides</i>	Trop	Diaz and Ward (1997)
Lyssacosida*	Rossellidae	<i>Nodastrella</i> (syn. <i>Rossella</i>) <i>nodastrella</i>	Temp	van Duyl et al. (2008)
Poecilosclerida	Chondropsidae	<i>Strongylacidon</i> sp.	Temp	Perea-Blázquez et al. (2012)
Poecilosclerida	Crambeidae	<i>Monanchora</i> sp. ML1	Temp	This study
Poecilosclerida	Crellidae	<i>Crella incurstans</i>	Temp	Perea-Blázquez et al. (2012)
Poecilosclerida	Iotrochotidae	<i>Iotrochota</i> cf. <i>baculifera</i> ?	Temp	This study
Poecilosclerida	Microcionidae	<i>Clathria</i> (<i>Wilsonella</i>) sp. ML1	Temp	This study
Poecilosclerida	Mycalidae	<i>Mycala</i> (<i>Arenochalina</i>) cf. <i>mirabilis</i>	Temp	This study
Spirophorida	Tetillidae	<i>Craniella</i> sp. ML1	Temp	This study
Verongida	Aplysinellidae	<i>Aplysinella</i> sp. ML1	Temp	This study
Verongida	Aplysinidae	<i>Aplysina</i> (<i>Verongia</i>) 'rigidia'†	Trop	Southwell et al. (2008a)
Verongida	Aplysinidae	<i>Aplysina aerophoba</i>	Temp	Jiménez and Ribes (2007); Bayer et al. (2008)
Verongida	Aplysinidae	<i>Aplysina archeri</i>	Trop	Southwell et al. (2008a)
Verongida	Aplysinidae	<i>Aplysina cauliformis</i>	Trop	Southwell et al. (2008a)
Verongida	Aplysinidae	<i>Aplysina fistularis</i>	Trop	Southwell (2007)
Verongida	Aplysinidae	<i>Aplysina lacunosa</i>	Trop	Southwell et al. (2008a)
Verongida	Pseudoceratinidae	<i>Pseudoceratina</i> 'crassa'†	Trop	Southwell et al. (2008a)

* All species are from the Class Demospongiae except *Plakortis halichondrioides* (Homoscleromorpha) and *Nodastrella nodastrella* (Hexactinellida).

† van Soest et al. (2011) does not record *Aplysina* (*Verongia*) 'rigidia' or *Pseudoceratina* 'crassa'.

N m² yr⁻¹ (DIN) and 0.9 to 1.6 g N m² yr⁻¹ (nitrate only) for these types of habitats. These rates are lower than those calculated for sponges in the Caribbean and Mediterranean. Jiménez and Ribes (2007) estimated that sponges,

which covered 7% to 22% of the bottom, were responsible for nitrogen fluxes of 2.5 to 7.9 mmol N m⁻² d⁻¹ or 12.7 to 40.4 g N m⁻² yr⁻¹. Studies by Corredor et al. (1988) and Southwell et al. (2008b) provide measurements of rates

equivalent to between 59 and 78 g N m⁻² yr⁻¹ in the coral reef habitats they studied. However, these studies were conducted on coral reefs with much higher biomasses of sponges than those in our study.

In the context of nitrogen demand at the ecosystem level, the rates measured in our study indicate that sponges are significant contributors of recycled nitrogen within rocky reef habitats to 100 m depth in southwestern Australia. However, on average, reef habitats only occupy about 35% of the seabed to this depth (Keesing 2011), meaning that the average contribution of sponges to DIN resupply on the shelf out to 100 m is likely to be in the range of 0.64 to 1.14 g N m⁻² yr⁻¹, or 10% to 18% of the recycled nitrogen flux required to balance the nutrient budget calculated for the shelf in this region (Feng and Wild-Allen 2010). This nutrient budget applies to all shelf waters to 200 m, while our calculations are limited to the first 100 m. Even though sponges deeper than 570 m have been shown to release nitrate (van Duyl *et al.* 2008), extrapolating our shallow-water nitrogen release results to beyond 100 m would carry risk, so we have not done this. However, the shelf from 100 to 200 m occupies only 23% of the total area in the region and supports an average sponge biomass of 18 g wet wt (3.6 g dry wt) m⁻² (Keesing 2011), and so extending our results for the entire shelf to 200 m, even assuming no net release of DIN by sponges between 100 and 200 m, would not diminish the contribution of sponges below the lower extent of the range (10%) calculated above.

These calculations do make the assumptions that the sponge species sampled and release rates measured in our study were representative of all sponges out to 100 m water depth and are representative of year-round average release rates. Four of the genera sampled in our study were the same as those among the 17 genera sampled by Keesing *et al.* (2012) from depths of 40–100 m immediately offshore from South Lumps. That study aimed to sample as wide a range of sponge taxa and morphotypes between 40 and 150 m depth as possible, so we would not expect a high degree of overlap given the different objectives and methodologies, but it does indicate that there is significant representation of similar sponges to those used in our study out to 100 m. Keesing *et al.* (2012) also sampled *Geodia* at 75 m, which is the same genus shown by Hoffmann *et al.* (2009) to release high levels of nitrate in Norway, and Table 4 shows that diverse ranges of species (45), families (26), orders (12), and classes (3) of sponges release nitrate. Most sponges that release nitrate have high levels of microbial abundance (HMA) (Maldonado *et al.* 2012), and the extent to which most sponges on the shelf in this region are HMA sponges needs more investigation. The few studies that have attempted to measure seasonal variability in nitrogen release rates in sponges have not yielded any consistent seasonal patterns. In New Zealand, Perea-Blázquez *et al.* (2012) showed an inconsistent range of release rates of three species, *H. venustina*, *Strongylacidon* sp., and *C. incrustans*, between seasons and years. Bayer *et al.* (2008) found that overall DIN release rates in *A. aerophoba* in the Mediterranean were lower in April at 12–14°C than in September at 22–25°C by a factor of 3–4 times, but that the proportions of nitrate and ammonium varied over time unrelated to temperature. The

temperature at our site on the day of sampling was 21.3°C, which is slightly above midrange for this area (annual range 17.5–23.5°C; Pearce *et al.* 2006). It is possible that temperature-dependent seasonal variation in release rates would affect our calculations.

Given the range of sources of possible variation in our data (variation between species and between individuals and possible differential responses to experimental methods) and the cautions outlined previously in scaling up our data (possible spatial and seasonal differences; limited range of taxa and depth range sampled), these results need to be viewed as preliminary. Despite these caveats, given the difficulties of attaining data on sponge biomass distribution to a high level of taxonomic discrimination in highly speciose ecosystems such as southwestern Australia (Fromont *et al.* 2011) and the difficulty in obtaining seasonally representative nitrogen flux measurement coverage of such a taxonomically diverse group, we would argue that the extrapolations made in our study are a necessary and valid approach and that our results support the conclusion that sponges contribute significantly to benthic resupply of nitrogen at the scale of the continental shelf off southwestern Australia.

Acknowledgments

We thank Ryan Crossing, Peter Hughes, Stelios Kondylas, and Leah Segui for helping undertake the fieldwork. Peter Hughes also carried out all the nutrient analyses on the water samples. We also thank Oliver Gomez for assistance in preparing sponges for identification and Louise Bell and Stephanie Contardo for preparing some of the figures. Comments from Martin Lourey and two anonymous reviewers improved the manuscript. The research was supported in part by funding from the Western Australian Marine Science Institution.

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Associate editor: Markus H. Huettel

Received: 01 December 2012

Accepted: 13 May 2013

Amended: 19 June 2013