



# Rapid respiratory responses of the deep-water sponge *Geodia barretti* exposed to suspended sediments

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**ABSTRACT:** Sponges often dominate deep-water benthic faunal communities and can comprise up to 90 % of the benthic biomass. Due to the large amount of water that they filter daily, sponges are an important link between benthic and pelagic ecosystems. Across the Tromsø-flaket, Barents Sea, Norway, there are high biomasses of deep-water sponges. This area is also an important fishing ground, with fishing activity in some areas >27 000 trawl hours yr<sup>-1</sup>. Bottom trawling suspends large quantities of sediment into the water column, with measured concentrations up to 500 mg l<sup>-1</sup>. This is the first study on the effects of suspended sediment exposure on deep-water sponges. In a laboratory experiment, *Geodia barretti* (Bowerbank 1858) (Class: Demospongiae) was exposed to 5 different sediment concentrations (0, 10, 50, 100 and 500 mg l<sup>-1</sup>). Respiration rates were measured before, during and after the exposure period. The results demonstrate that *G. barretti* physiologically shuts down when exposed to concentrations of 100 mg l<sup>-1</sup> (86 % reduction in respiration), with thresholds of responses occurring between 10 to 50 mg l<sup>-1</sup>. However, rapid recovery to initial respiration levels directly after the exposure indicates that *G. barretti* can cope with a single short exposure to elevated sediment concentrations. Given the high bottom-trawling frequency in Tromsø-flaket, sponges may be frequently exposed to suspended sediments. Therefore, it is important that further investigations on the effects of suspended sediments on filter feeding organisms focus on the effects of repeated and long-term suspended sediment exposures to evaluate the overall ecological impacts.

**KEY WORDS:** Continental shelf · Porifera · Turbidity · Bottom trawling · Fisheries

## INTRODUCTION

On the continental shelf of Norway, deep-water benthic faunal communities are often dominated by sponges. In some areas they comprise as much as 90 % of the biomass of benthic fauna (Klitgaard & Tendal 2004, T. Kutti & R. J. Bannister unpubl. data), and represent an important functional component in benthic habitats (Bell 2008). Sponges play a crucial role in benthic-pelagic coupling due to their high water processing capacities (up to 14 l h<sup>-1</sup> g<sup>-1</sup> dry weight [dry wt], Reiswig 1974, Pile & Young 2006)

and efficient filtration of both dissolved and particulate matter from the water column (Yahel et al. 2003). *Geodia barretti* (Bowerbank 1858) (Class: Demospongiae) dominates the benthic fauna in Norwegian fjords (Hoffmann et al. 2005), as well as on the continental shelf along the Norwegian coastline (Klitgaard & Tendal 2004, T. Kutti & R. J. Bannister unpubl. data). It can be found from 30 to 1200 m depth on both hard and soft substrate (Klitgaard & Tendal 2004). In high-energy environments, *G. barretti* is found attached to stable substrates, while in areas with lower energy it is not attached, but incorporates

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small stones in order to maintain negative buoyancy. In low-energy environments it is covered in sediments, but is free from sediment in high energy environments. On the Norwegian continental shelf there are areas with aggregations of large sponges, commonly referred to as 'ostur', where *G. barretti* is one of the dominant species (Klitgaard & Tendal 2004). Across the Træna Deep marine protected area (MPA) the biomass of *G. barretti* is between 1 and 4 kg m<sup>-2</sup> (T. Kutti & R. J. Bannister unpubl. data), and in some areas of the Barents Sea biomasses of up to 6 kg m<sup>-2</sup> have been observed (Zenkevitch 1963).

Studies show that at least some sponges are sensitive to turbid water (Reiswig 1971, Genin et al. 1992, Tompkins-MacDonald & Leys 2008, Bannister et al. 2012). This is demonstrated by the reduced distribution, abundance and species richness of sponges in shallow reef environments (Carballo 2006, Maldonado et al. 2008, Bannister et al. 2010). The effects of suspended and deposited sediment include increased metabolic stress (Bannister et al. 2012), reduced pumping and filtration rate (Gerrodette & Flechsig 1979, Lohrer et al. 2006, Tompkins-MacDonald & Leys 2008), reduced growth (Wilkinson & Vacelet 1979), decreased reproduction (Roberts et al. 2006, Whalan et al. 2007), reduced larval settlement (Moran 1991, Whalan et al. 2007) and reduced survival (Maldonado et al. 2008). However, a number of other studies in shallow water systems demonstrate that some sponge species favour areas with high sedimentation rates (Carballo et al. 1996, Bell & Smith 2004), presumably a function of the morphological/physiological adaptation to such conditions. The effects can also depend on the composition of the sediment such as organic content and mineralogical composition (Maldonado et al. 2008, Bannister et al. 2012). It is noteworthy that human activities in deep water ecosystems are currently increasing (Glover & Smith 2003, Puig et al. 2012). Overall, a reduction in sponge abundance, biomass and species richness in benthic habitats can be followed by cascading impacts on the marine ecosystem (Peterson et al. 2006, Bell 2008). For example, a reduction of sponge abundance has been hypothesized to be the reason for the higher frequency of toxic algal blooms in Florida Bay (Peterson et al. 2006), thus showing the importance of their filtering capacity.

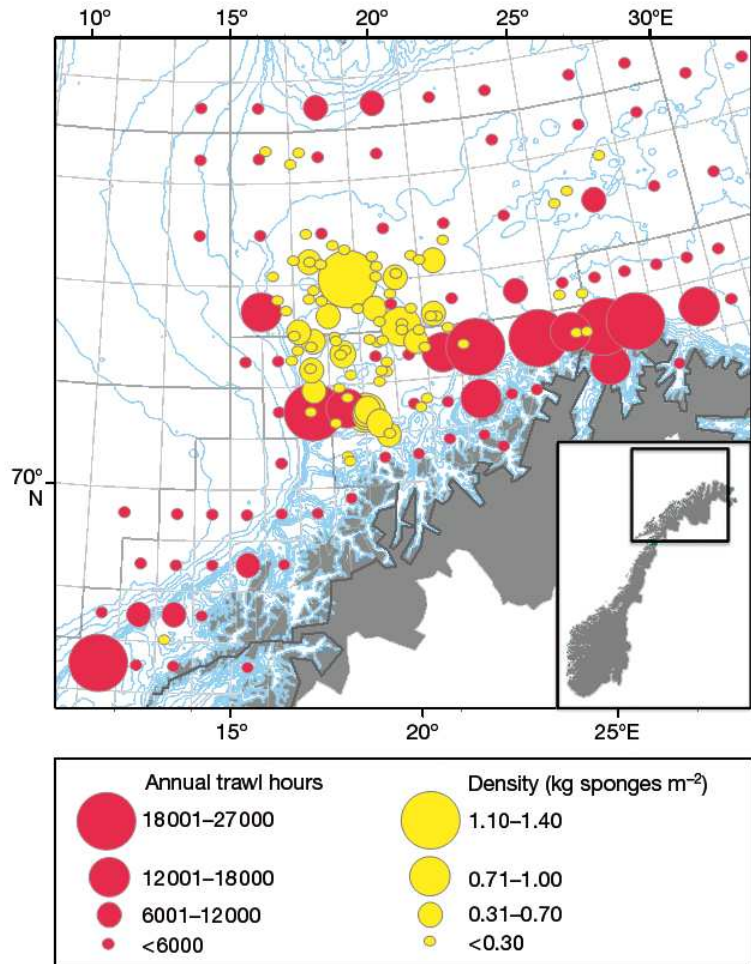


Fig. 1. Distribution of bottom trawling effort (1996–2000) on northern Norwegian continental shelf estimated for the smallest statistical subarea units reported for catch and effort in Norway, i.e. a 'location' of  $\sim 0.5^\circ \times 1^\circ$  as shown on map (light grey rectangles). Records of sponge by-catch from the Institute of Marine Research's ground fish trawl surveys in the same area. Map modified from Steingrimssson et al. (2006)

Along the Norwegian continental shelf, areas with high sponge abundance co-occur with important fishing grounds (Fig. 1). Bottom trawlers are designed to penetrate several centimetres into the seafloor and re-suspend large quantities of bottom sediment into the water column (Schoellhamer 1996, Durrieu de Madron et al. 2005, Bradshaw et al. 2012). Suspended sediment concentrations after a single trawl pass have been measured to vary between 5 and 500 mg l<sup>-1</sup> (Schubel et al. 1978, Schoellhamer 1996, Durrieu de Madron et al. 2005, Bradshaw et al. 2012). The largest particles settle within minutes or hours due to gravity, but 10 to 20% of the suspended load remains in suspension for several days (Durrieu de Madron et al. 2005, Bradshaw et al. 2012). Bradshaw et al. (2012) measured that 95% of suspended

sediment particles had a diameter  $<10\ \mu\text{m}$ , with  $>50\%$   $<4\ \mu\text{m}$ , and could take several days to settle again. Bottom trawling can therefore contribute substantially to sediment re-suspension and sediment transport in areas where natural sediment suspension has little or no impact, especially in deep water systems (Ferré et al. 2008).

Fishing effort is quite patchily distributed within the North Sea (Jennings & Kaiser 1998), the Norwegian Sea (Olsen & Auran 2007) and the Barents Sea (Kolle et al. 2002). In the Barents Sea alone, trawling intensity can range from  $<6000$  trawl hours  $\text{yr}^{-1}$  in some regions to  $27000$  trawl hours  $\text{yr}^{-1}$  in others (Fig. 1). In these high intensity areas, it is likely that trawling activity has an impact on sessile suspension-feeding benthic communities both directly (i.e. by-catch and direct physical damage) and indirectly (i.e. burial and clogging of filtration apparatus) (Hall-Spencer et al. 2002). Despite the overlapping spatial distribution of demosponge aggregations with bottom trawling (Fig. 1), no studies have investigated the effects of bottom trawling activity on deep water sponges along the Norwegian continental shelf.

The aim of this study was to elucidate the physiological response of the common deep water sponge *Geodia barretti* to short-term exposure of suspended sediment and to identify threshold levels of suspended sediment concentration. In addition, the study was designed to look at the potential for *G. barretti* to recover from short-term suspended sediment exposure.

## MATERIALS AND METHODS

### Collection and maintenance

Fifteen specimens of *Geodia barretti* were collected using a remotely operated underwater vehicle (ROV) from onboard the RV 'Håkon Mosby'. Sponges (size range: 1 to 2  $\text{dm}^3$ ) were collected from a soft sediment habitat located at a depth of 200 m within the Lungenuen passage, a small branch of the Hardanger Fjord, Bergen, Norway. Whole, undamaged *G. barretti* individuals attached to small stones or dead coral rubble were carefully selected and placed within a large collection box fitted to the ROV. This ensured that the individuals were not exposed to air during collection or subsequent transfer to a larger tank onboard the research vessel. Whilst onboard the research vessel, sponges were maintained under low light conditions and supplied with a constant flow of deep-water (from  $\sim 100$  m) using a pump

to ensure stable water quality (i.e. oxygen, temperature, salinity and food). After collection, sponges were transferred to the deep-sea ecology lab at the Institute of Marine Research (IMR), Bergen.

At the deep-sea ecology lab, sponges were maintained in 600 l flow-through tanks supplied with unfiltered water pumped from  $\sim 120$  m depth from Byfjord, Bergen. No additional food was added. The temperature in the system was very stable, with constant temperature (8 to  $9^\circ\text{C}$ ) and salinity (34.5) during the experimental period. The sponges were acclimated to laboratory conditions for 2 mo prior to the start of the experiment. Earlier work by Hoffmann et al. (2006) had demonstrated that cultivated *Geodia barretti* individuals maintained under laboratory conditions in Bergen for  $>8$  mo maintained a similar bacterial symbiotic community to those of freshly collected *G. barretti* individuals. Therefore, we assumed that a shift in the symbiotic community of our acclimated sponges was unlikely given the time frame in the aquaria.

### Respiration chamber design

To perform the respiration measurements, closed transparent perspex respiration chambers (80 l) were used. Each chamber was placed in a larger flow-through tank (600 l) used as a water jacket to maintain constant temperature. Both chambers were equipped with 2 pumps. The first pump maintained a continuous water re-circulation within the chamber, and the second was used to flush the chamber at specific time intervals to renew the water and prevent oxygen depletion below 80%. A pressure-controlled valve was built into the chamber to let the water out during flushing. Oxygen concentration and temperature were recorded every 30 s using a Fibox oxygen optode (PreSens). The chamber had an extra hole in the lid that could easily be opened and closed to add sediment and fluorescent dye.

### Experimental design

To determine short-term physiological responses of *Geodia barretti* to elevated suspended sediment concentrations, replicate individuals ( $n = 3$  per treatment) were exposed to 5 different treatments (initial concentrations of 0, 10, 50, 100 and  $500\ \text{mg dry wt l}^{-1}$ ). The sponges were randomly selected for each of the 5 different treatments. The natural sediment (sieved to  $<1\ \text{mm}$ ) used in the experiment was collected using a

box core at the site of sponge collection, and the top 5 cm of sediment was collected. The selected sediment concentrations are ecologically relevant according to measurements taken after bottom trawling (Schubel et al. 1978, Schoellhamer 1996, Durrieu de Madron et al. 2005, Bradshaw et al. 2012).

*Geodia barretti* individuals were transferred to respiration chambers for an acclimation period of 8 h prior to the beginning of each experiment. After acclimatisation, the respiration rate of sponge individuals was measured over 5 consecutive 4 h periods. During the 1st period the baseline respiration rate was measured. During the 2nd period, sponges were exposed to the different sediment concentrations, added in suspension directly to the water through the hole in the lid. The 3rd, 4th and 5th periods were recovery periods to assess the recovery rates. Between each period, chambers were flushed for 30 min with new water to replenish the water and oxygen. Additionally, after the second period (sediment exposure) the chambers were flushed for 60 min to ensure that all the sediment in suspension was flushed out from the chambers. To account for potential respiration of microorganisms, chambers ( $n = 3$ ) were kept empty during measurements for each of the 5 concentrations. The changes in respiration in the blank chambers were added or subtracted from treatment chambers. Sponge respiration rate ( $R$  in  $\mu\text{mol O}_2 \text{ g}^{-1} \text{ min}^{-1}$ ) was calculated as follows:

$$R = [\mu\text{mol O}_2 (t_0) - \mu\text{mol O}_2 (t_1) - \text{correction}] \times V_{\text{cham}} / W_{\text{dry/wet}} \quad (1)$$

where  $t_0$  is the beginning and  $t_1$  is the end of the 4 h period of oxygen concentrations in  $\mu\text{mol O}_2$ ; 'correction' is the average change in oxygen in the blank chambers,  $V_{\text{cham}}$  is the volume of the chamber (l) and  $W_{\text{dry/wet}}$  is dry or wet wt (g).

For each sponge, a percentage change in respiration rate was calculated based on the difference from the baseline measurements, both for the exposure and for each of the recovery intervals:

$$\% \text{ change in } R = 100 \pm [\mu\text{mol O}_2 \text{ min}^{-1} / \mu\text{mol O}_2 \text{ min}^{-1} (\text{baseline})] \times 100 \quad (2)$$

Volume ( $\text{cm}^3$ ), wet and dry wt were recorded for every sponge after all the measurements were done. Water displacement was performed on whole sponge individuals to determine the volume. To obtain the dry wt, several subsamples were taken from each sponge and dried to constant weight at  $60^\circ\text{C}$ . Respiration rates were standardised to either  $\text{cm}^3$ , wet wt

or dry wt of sponge tissue, in order to enable comparisons with literature values.

Pumping activity was visually assessed before exposure, after exposure and during recovery intervals using fluorescent dye, which was gently released into the oscula of each sponge. Due to poor visibility in the high sediment concentration treatments (50, 100 and  $500 \text{ mg l}^{-1}$ ), pumping activity was not assessed directly after the exposure interval.

The grain size of the sediment was analysed with a mastersizer 2000 (v 5.40, Malvern Instruments), following the methodology outlined in Maldonado et al. (2008).

### Statistical analysis

A 2-way ANOVA for repeated measures was used to examine differences in respiration rates between levels of sediment concentration (i.e. 0, 10, 50, 100,  $500 \text{ mg l}^{-1}$ ) over time. The assumption of sphericity for this analysis was not met, so a Greenhouse-Geisser adjusted significance level was used (Quinn & Keough 2002). A Tukey's post hoc test was performed to test for significant differences between each of the 4 h intervals (baseline, exposure, recovery 1, recovery 2, recovery 3). In addition, a 1-way ANOVA was used to test the percentage change of respiration during the 4 h exposure interval as a function of sediment concentration (i.e. 0, 10, 50, 100,  $500 \text{ mg l}^{-1}$ ). Planned post hoc tests were used to identify the particular sediment concentrations responsible for significant changes in the respiratory percentage compared with the control treatment ( $0 \text{ mg l}^{-1}$ ). All the statistics were performed in Statistica 10 (StatSoft) and SigmaPlot 11.0. All results are presented with mean  $\pm$  standard error, unless stated otherwise.

### RESULTS

The sediment had a median grain size of  $71 \mu\text{m}$  (mean  $139 \mu\text{m}$ ), with 7% clay  $< 3.9 \mu\text{m}$ , 42% clay of 3.9 to  $62.5 \mu\text{m}$ , and 23% of the volume being fine sand (62 to  $125 \mu\text{m}$ ) (Fig. 2).

The pre-exposure respiration rate for all 5 treatments (sediment concentrations) was  $1.599 \pm 0.158 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g dry wt}^{-1}$  ( $0.33 \pm 0.036 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g wet wt}^{-1}$ ). These values are within the range presented in other studies for other species (Witte & Graf 1996, Osinga et al. 1999).

Exposure to suspended sediments had a clear effect on the respiration over time ( $p = 0.00083$ ,

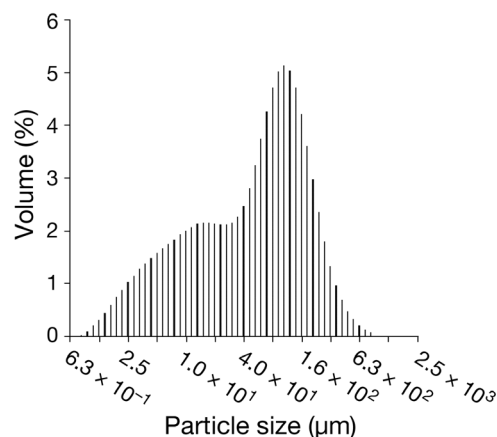


Fig. 2. Grain size distribution of sediment added in suspension and in different concentrations during the exposure intervals

Table 1. Repeated measures ANOVA comparing the respiration rate of *Geodia barretti* measured across the 5 consecutive 4 h periods (baseline, exposure and recovery periods) during the sediment exposure experiment. Adj p: Greenhouse-Geisser adjusted p-value; Sed. conc.: sediment concentration

	df	MS	F	p	Adj p
Between subject					
Sed. conc.	4	2.618	3.042	0.076	
Error	9	0.861			
Within subject					
Time	4	1.172	11.292	0.000	0.001
Time × Sed.conc.	16	0.125	1.204	0.311	0.352
Error	36	0.104			

Table 1), where the exposure period clearly showed a reduced respiration compared with baseline ( $p = 0.000126$ ) as well as the 3 recovery periods (recovery 1:  $p = 0.000494$ , recovery 2:  $p = 0.00167$ , recovery 3:  $p = 0.000503$ ). There was no large difference observed in respiration rates between baseline and recovery periods. The baseline respiration rate changed in response to the different exposure treatments, with low concentrations of natural sediment ( $10 \text{ mg l}^{-1}$ ) having little or no effect on respiration activity ( $1.77 \pm 0.41 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g dry wt}^{-1}$ ) of *G. barretti* (Fig. 3, Table 2). The 20% reduction in respiration activity during the exposure period for the  $10 \text{ mg l}^{-1}$  treatment group was also detected for the control treatment ( $0 \text{ mg l}^{-1}$ ) (Fig. 4). Furthermore, the constant respiration rate observed during the recovery period suggests that the 4 h exposure period did not affect the sponges for an additional 12 h post exposure (Fig. 3). A significant effect of elevated suspended sediment exposure on *Geodia barretti* was detected at higher concentrations (i.e. 50, 100 and

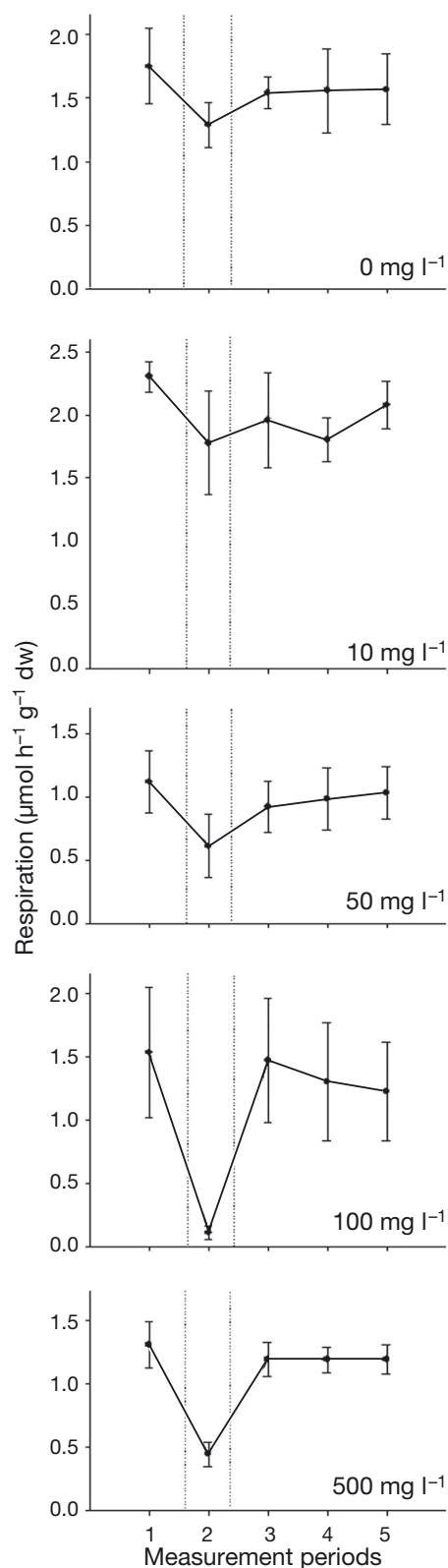


Fig. 3. Respiration rate of *Geodia barretti* measured over 5 consecutive 4 h periods: 1 = baseline, 2 = exposure, 3, 4, 5 = recovery. Dotted line: period of exposure to suspended sediment. dw: dry weight



Table 2. One-way ANOVA performed on the percentage reduction between the different treatments during the exposure period, followed by a planned comparison test comparing the exposure period measurements in the control treatment (0 mg l<sup>-1</sup>) with each of the 4 sediment concentrations (10, 50, 100 and 500 mg l<sup>-1</sup>). Data for 500 mg l<sup>-1</sup> is based on data from 2 sponges

Sediment exposure (mg l <sup>-1</sup> )	Estimate	SE	<i>t</i>	<i>p</i>
10	0.6187	20.26034	0.03054	0.976304
50	-28.8053	20.26034	-1.42176	0.188810
100	-63.2835	20.26034	-3.12352	0.012249
500	-43.9593	22.65175	-1.94066	0.084220

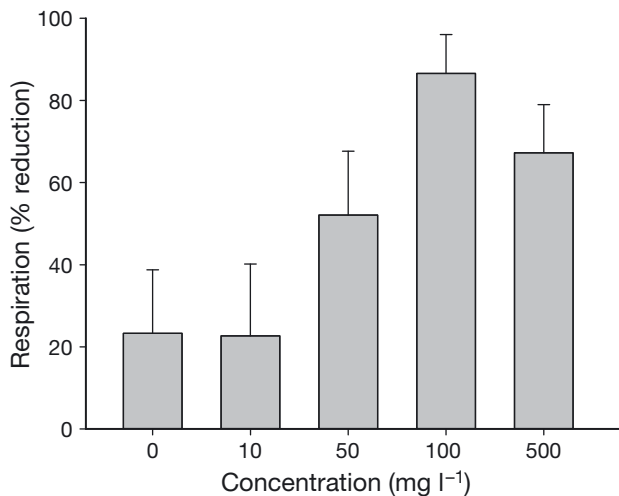


Fig. 4. *Geodia barretti*. Reduction in respiration given in % during the 4 h exposure period calculated relative to baseline measurements for each of the 5 sediment concentrations

500 mg l<sup>-1</sup>). During the exposure period, respiration rates decreased by 52% ( $0.607 \pm 0.43 \mu\text{mol O}_2 \text{ h}^{-1} \text{ g dry wt}^{-1}$ ,  $p = 0.189$ ), 86% ( $0.108 \pm 0.0.93$ ,  $p = 0.012$ ) and 67% ( $0.44 \pm 0.13$ ,  $p = 0.084$ ), when exposed to suspended sediment concentrations of 50, 100 and 500 mg l<sup>-1</sup>, respectively (Table 2, Fig. 4). During the exposure period for one of the sponges exposed to 500 mg l<sup>-1</sup>, the oxygen optode failed to log the oxygen measurements, so unfortunately no data were collected during this period.

Interestingly, despite significant reductions in metabolic activity during the exposure period to the higher sediment loading levels (50, 100 and 500 mg l<sup>-1</sup>), *Geodia barretti* metabolic activity showed little variation between the 3 recovery periods and the respective baseline measurements (Fig. 3).

During the 4 h sediment exposure, the sediment concentration was reduced by an average of 35%. Only the largest particles settled out of suspension

throughout the exposure period. Observations after the exposure period showed that the sponges were clearly covered with sediment in all of the treatments except for the control (0 mg l<sup>-1</sup>).

The addition of fluorescent dye showed that the sponges were pumping before exposure and at the end of each of the 3 recovery periods in all the treatments. This was also true for the sponges in the control (0 mg l<sup>-1</sup>) and the lowest concentration (10 mg l<sup>-1</sup>) directly after the exposure period. Sponges exposed to the higher sediment loads were actively pumping 1 h after the exposure period ended.

## DISCUSSION

Exposure to elevated concentration of suspended sediment resulted in rapid changes in the respiration rate of the deep-water sponge *Geodia barretti*. The rate of respiration was clearly impeded at higher concentrations of natural sediment, with reductions of 52, 86 and 67% occurring during short-term exposure periods to 50, 100 and 500 mg l<sup>-1</sup>, respectively. Earlier studies by Reiswig (1971) and Gerrodette & Flechsig (1979) demonstrated a reduction in pumping activity during exposure to suspended sediments and made the assumption that this would lead to a reduction in respiration. Both respiration and filtration rely on the water current through the canals and are thereby closely related to each other (Reiswig 1971, Gerrodette & Flechsig 1979). In the present study there were no observations of the pumping activity during exposure, but we can assume that the reduction in respiration rates observed here relates to a reduction in pumping activity, as suggested by the latter 2 studies.

Variation in baseline respiration was observed between individuals from the different sediment treatments. This was not unsurprising given that previous observations/measurements of the pumping activity of *Geodia barretti* individuals did not show any pattern between pumping speed (ranging between 1 to 15 cm s<sup>-1</sup>) and sponge size (R. J. Bannister unpubl. data); therefore, differences in respiration rate of sponges both within and between sponge size could be plausible. Thus, direct comparisons of respiration activities between similar sized *G. barretti* individuals between treatments should be made with care, with comparisons with percent change in respiration being a more appropriate comparison between individuals.

Interestingly, exposure to low concentrations of natural sediment (i.e. 10 mg l<sup>-1</sup>), which have induced

physiological responses in other sponge species (Gerrodette & Flechsig 1979, Tompkins-MacDonald & Leys 2008), did not significantly change the metabolic activity in the present study. However, variation in the respiration rate was observed during the 3 recovery periods for the low sediment concentration ( $10 \text{ mg l}^{-1}$ ) compared with exposure to the higher sediment concentrations. One possible explanation for this variation in respiration is that the lower sediment concentrations were not high enough to induce a complete shutdown in pumping activity. As such, these sponge individuals may have filtered sediment into their canal system, leading to irritation of the sponge, and consequently modified pumping behaviour in order to cope with sediment particles clogged inside the canal system and trapped on the choanocytes (feeding cells).

The threshold concentration of suspended sediment that initiates a change in respiration for *Geodia barretti* was between  $10$  and  $50 \text{ mg l}^{-1}$ . Differences in sediment threshold levels observed between different sponge species may be a function of their different ambient environments and the different abilities of sponges to cope with suspended sediments (Carballo et al. 1996, Bell & Smith 2004). The rapid response of *G. barretti* was also seen during recovery, when respiration rates returned quickly to baseline levels. Both Tompkins-MacDonald & Leys (2008) and Bannister et al. (2012) measured recovery after exposure to suspended sediment, and these studies demonstrated that sponges returned to their initial respiration and pumping rates respectively, between 3 and 25 h after exposure ended.

The reduction in metabolic activity of *Geodia barretti* contradicts the results of Bannister et al. (2012), who clearly demonstrated that the respiration activity of the tropical demosponge *Rhopaloeides odorabile* increased slightly during a 7 h exposure period to elevated suspended sediment concentrations ( $64 \text{ mg l}^{-1}$ ), and significantly (+43%) during a longer exposure period (24 h) to the same concentration. A study by Murray (2009) demonstrated that exposing the temperate sponge *Tethya bergquistae* to a very high sediment concentration of  $2.5 \text{ g l}^{-1}$  does not initiate any respiratory response, while exposure to 8.5 and  $16.5 \text{ g l}^{-1}$  resulted in an 80% reduction in respiration. In that study a very high sediment concentration ( $16.5 \text{ g l}^{-1}$ ) together with a short exposure time (15 min) resulted in a rapid respiratory response. During the present study the respiratory response of *G. barretti* showed a rapid 86% reduction in respiration, but for a significantly lower suspended sediment concentration compared to that used by Murray

(2009). It has been argued that the sensitivity and response of sponges to elevated suspended sediment concentrations is both species specific and a function of their ambient environment (Carballo et al. 1996, Bell & Smith 2004). The contrasting responses of different sponge species exposed to suspended sediment in the current literature further support this statement.

The mechanisms driving the observed changes in demosponges exposed to sediment stress are still unresolved. It has been a long-held theory that sponges are non-selective filter feeders, with inhaled particles discriminated solely on the size of the sponge's inhalant canals and ostia (Bergquist 1978). Thus, fine sediment particles that do enter the ostia will clog the canal and filtration system of the sponge. However, there is evidence that demonstrates that sponges can selectively ingest preferred food items (Maldonado et al. 2010), suggesting that the physiological functioning of sponges is complex and requires further examination. There are many different strategies described for coping with suspended sediment and clogged canals in sponges. Bannister et al. (2012) showed that increased mucus production can protect sponges from smothering inhalant pores, but that this may be at a high energetic cost (Riegl & Branch 1995) and therefore may only be used for short-term protection. Other studies have also demonstrated that pumping stops in response to short exposure of suspended sediment followed by a continuous on-off pumping activity, also known as pacemaker movements, in order to clean the canals (Tompkins-MacDonald & Leys 2008). For other sponges, a contraction activity has been described that can reduce the body volume by up to 70% (Nickel 2004). Other sponge species are able to reorganize their cells to create new inflow and outflow canals (ostia and oscula respectively) (Bond 1992, Ilan & Abelson 1995), or modify their morphology to suit their ambient environment (McDonald et al. 2003, Bell 2004). The different strategies mentioned here most likely have very different energetic demands, which can be related to differences in the observed physiological responses observed in sponges (Reiswig 1971, Gerrodette & Flechsig 1979, Murray 2009, Bannister et al. 2012, present study).

Deep sea sponges in or near bottom-trawled areas are probably exposed to sediment plumes that can impact both their abundance and distribution, as has been observed for other sponge species (Bell & Barnes 2000, Carballo 2006, Bannister et al. 2010). Sponges have an important role when it comes to benthic-pelagic coupling and recycling of nutrients

(Pile & Young 2006, Yahel et al. 2007, Maldonado et al. 2012), and if that is disturbed a cascading ecological effect can be expected (Peterson et al. 2006, Bell 2008). Nevertheless, sponges are not included in many monitoring programs (Bell 2008).

The exposure time in the present study was only 4 h, which is relevant for areas with bottom currents where the sediment plume will be transported away from the trawl track and expose the surroundings to shorter pulses of sediment loadings. Additionally, exposure to repeated short pulses could have an impact on the respiration rate, e.g. Reiswig (1974) documented an 80% decrease in pumping rate related to an unstable environment. Furthermore, Bannister et al. (2012) demonstrated that a longer exposure time (24 to 96 h) had detrimental results on the metabolism of tropical coral reef sponges. Given that fine particles from trawl-induced sediment plumes may take several days to settle out of suspension (Bradshaw et al. 2012), it can be hypothesized that sponge aggregations in the vicinity of trawling grounds may be subjected to increased turbidity from bottom trawling activity.

This study demonstrates that the deep-water sponge *Geodia barretti* has a quick response to elevated suspended sediment, as documented by the reduced respiration rate of up to 86%. Furthermore, *G. barretti* can quickly return to baseline respiration levels directly after a short pulse-exposure to natural suspended sediments. It is clear that *G. barretti* has established mechanisms to protect itself from short periods with elevated suspended sediment concentrations. However, it is unclear how this mechanism is initiated and how long *G. barretti* can tolerate such conditions. Repeated and longer exposure periods to high concentrations of suspended sediment may have consequences for the physiology, energetic and reproductive output, as has been demonstrated for other sponges (Gerrodette & Flechsig 1979, Roberts et al. 2006, Bannister et al. 2012). The results of this study and future studies assessing long-term exposure of suspended sediments on deep-water sponge communities will be vital in improving management advice to the bottom trawling industry in areas characterized as vulnerable habitats by the Oslo and Paris Convention (OSPAR) and United Nations Environment Programme (UNEP) (Hogg et al. 2010).

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#### LITERATURE CITED

- Bakus GJ (1968) Sedimentation and benthic invertebrates of Fanning Island, central Pacific. *Mar Geol* 6:45–51
- ▶ Bannister RJ, Battershill CN, de Nys R (2010) Demographic variability and long-term change in a coral reef sponge along a cross-shelf gradient of the Great Barrier Reef. *Mar Freshw Res* 61:389–396
- ▶ Bannister RJ, Battershill CN, de Nys R (2012) Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: impacts on the physiology of a coral reef sponge. *Cont Shelf Res* 32:86–95
- ▶ Bell JJ (2004) Evidence for morphology-induced sediment settlement prevention on the tubular sponge *Haliciona urceolus*. *Mar Biol* 146:29–38
- ▶ Bell JJ (2008) The functional roles of marine sponges. *Estuar Coast Shelf Sci* 79:341–353
- ▶ Bell JJ, Barnes DKA (2000) The distribution and prevalence of sponges in relation to environmental gradients within a temperate sea lough: vertical cliff surfaces. *Divers Distrib* 6:283–303
- ▶ Bell JJ, Smith D (2004) Ecology of sponge assemblages (Porifera) in the Wakatobi region, south-east Sulawesi, Indonesia: richness and abundance. *J Mar Biol Assoc UK* 84:581–591
- Bergquist PR (1978) *Sponges*. University of California Press, Berkeley, CA
- ▶ Bond C (1992) Continuous cell movements rearrange anatomical structures in intact sponges. *J Exp Zool* 263: 284–302
- ▶ Bradshaw C, Tjensvoll I, Sköld M, Allan IJ and others (2012) Bottom trawling resuspends sediment and releases bio-available contaminants in a polluted fjord. *Environ Pollut* 170:232–241
- ▶ Carballo JL (2006) Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience* 13:119–130
- ▶ Carballo JL, Naranjo SA, Garcia-Gomez JC (1996) Use of marine sponges as stress indicators in marine ecosystems at Algeciras Bay (southern Iberian Peninsula). *Mar Ecol Prog Ser* 135:109–122
- ▶ Durrieu de Madron X, Ferré B, Le Corre G, Grenz C and others (2005) Trawling-induced resuspension and dispersal of muddy sediments and dissolved elements in the Gulf of Lion (NW Mediterranean). *Cont Shelf Res* 25: 2387–2409
- ▶ Ferré B, Durrieu de Madron X, Estournel C, Ulses C, Le Corre G (2008) Impact of natural (waves and currents) and anthropogenic (trawl) resuspension on the export of particulate matter to the open ocean: application to the Gulf of Lion (NW Mediterranean). *Cont Shelf Res* 28: 2071–2091
- ▶ Genin A, Paull CK, Dillon WP (1992) Anomalous abundances of deep-sea fauna on a rocky bottom exposed to strong currents. *Deep-Sea Res A, Oceanogr Res Pap* 39: 293–302



- Gerrodette T, Flechsig AO (1979) Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Mar Biol* 55:103–110
- Glover AG, Smith CR (2003) The deep-sea floor ecosystem: current status and prospects of the anthropogenic change by the year 2025. *Environ Conserv* 30:219–241
- Hall-Spencer J, Allain V, Fossa JH (2002) Trawling damage to Northeast Atlantic ancient coral reefs. *Proc Biol Sci* 269:507–511
- Hoffmann F, Larsen O, Tore Rapp H, Osinga R (2005) Oxygen dynamics in choanosomal sponge explants. *Mar Biol Res* 1:160–163
- Hoffmann F, Rapp HT, Reitner J (2006) Monitoring microbial community composition by fluorescence *in situ* hybridization during cultivation of the marine cold-water sponge *Geodia barretti*. *Mar Biotechnol* (NY) 8:373–379
- Hogg MM, Tendal OS, Conway KW, Pomponi SA, Soest RWMV (2010) Deep-sea sponge grounds: reservoirs of biodiversity. UNEP-WCMC Biodiversity Ser 32, Cambridge
- Ilan M, Abelson A (1995) The life of a sponge in a sandy lagoon. *Biol Bull* 189:363–369
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. In: Blaxter JHS, Southward AJ, Tyler PA (eds) *Advances in marine biology*. Academic Press, London, p 201–352
- Klitgaard AB, Tendal OS (2004) Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic. *Prog Oceanogr* 61:57–98
- Kolle J, Havelin T, Rudi TO, Lorentsen E, Jensen P, Rasmussen D, Berg Ø (2002) Fiskeriaktiviteten i området Lofoten-Barentshavet—delrapport til kensekvensutredning av fiskeri, havbruk og skipstrafikk. Norwegian Fisheries Directorate, Bergen
- Lohrer AM, Hewitt JE, Thrush SF (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Mar Ecol Prog Ser* 315:13–18
- Maldonado M, Giraud K, Carmona C (2008) Effects of sediment on the survival of asexually produced sponge recruits. *Mar Biol* 154:631–641
- Maldonado M, Zhang X, Cao X, Xue L, Cao H, Zhang W (2010) Selective feeding by sponges on pathogenic microbes: a reassessment of potential for abatement of microbial pollution. *Mar Ecol Prog Ser* 403:75–89
- Maldonado M, Ribes M, Duyl FC (2012) Nutrient fluxes through sponges: biology, budgets, and ecological implications. *Adv Mar Biol* 62:113–182
- McDonald JL, McGuinness KA, Hooper JN (2003) Influence of re-orientation on alignment to flow and tissue production in a *Spongia* sp. (Porifera: Demospongiae: Dictyoceratida). *J Exp Mar Biol Ecol* 296:13–22
- Moran PJ (1991) The effects of dredging on the larval settlement and community development of fouling organisms in Port Kembla Harbour, Australia. *Water Res* 25:1151–1155
- Murray HJR (2009) Oxygen consumption rates of sponges and the effect of UV-B radiation and sediment. MSc thesis, Victoria University of Wellington
- Nickel M (2004) Kinetics and rhythm of body contractions in the sponge *Tethya wilhelma* (Porifera: Demospongiae). *J Exp Biol* 207:4515–4524
- Olsen E, Auran JA (2007) Helhetlig forvaltningsplan for Norskehavet: Sårbarhet for særlig verdifulle områder i forhold til petroleumsvirksomhet, fiskeri, skipstrafikk og annen påvirkning. Ministry of the Environment, Oslo
- Osinga R, Tramper J, Wijffels RH (1999) Cultivation of marine sponges. *Mar Biotechnol* (NY) 1:509–532
- Peterson BJ, Chester CM, Jochem FJ, Fourqurean JW (2006) Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. *Mar Ecol Prog Ser* 328:93–103
- Pile AJ, Young CM (2006) The natural diet of a hexactinellid sponge: benthic–pelagic coupling in a deep-sea microbial food web. *Deep-Sea Res I* 53:1148–1156
- Puig P, Canals M, Company JB, Martín J and others (2012) Ploughing the deep sea floor. *Nature* 489:286–289
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*, 1st edn. Cambridge University Press, Cambridge
- Reiswig HM (1971) *In situ* pumping activities of tropical Demospongiae. *Mar Biol* 9:38–50
- Reiswig HM (1974) Water transport, respiration and energetics of three tropical marine sponges. *J Exp Mar Biol Ecol* 14:231–249
- Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *J Exp Mar Biol Ecol* 186:259–275
- Roberts DE, Davis AR, Cummins SP (2006) Experimental manipulation of shade, silt, nutrients and salinity on the temperate reef sponge *Cymbastela concentrica*. *Mar Ecol Prog Ser* 307:143–154
- Schoellhamer DH (1996) Anthropogenic sediment resuspension mechanisms in a shallow microtidal estuary. *Estuar Coast Shelf Sci* 43:533–548
- Schubel JR, Carter HH, Wilson RE, Wise WM, Heaton MG (1978) Field investigations of the nature, degree, and extent of turbidity generated by open-water pipeline disposal operations. Tech Rep D78-30, US Army Engineer Waterways Experiment Stn, Vicksburg, MS
- Steingrímsson SA, Fosså JH, Tendal OS, Ragnarsson SA (2006) Vulnerable habitats in Arctic waters: In: Garcia EG (ed) *Bottom trawling and scallop dredging in the Arctic*. TemaNord 2006:529, Nordic Council of Ministers, Copenhagen, p 247–285
- Tompkins-MacDonald GJ, Leys SP (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Mar Biol* 154:973–984
- Whalan S, Battershill C, Nys R (2007) Variability in reproductive output across a water quality gradient for a tropical marine sponge. *Mar Biol* 153:163–169
- Wilkinson CR, Vacelet J (1979) Transplantation of marine sponges to different conditions of light and current. *J Exp Mar Biol Ecol* 37:91–104
- Witte U, Graf G (1996) Metabolism of deep-sea sponges in the Greenland-Norwegian Sea. *J Exp Mar Biol Ecol* 198: 223–235
- Yahel G, Sharp JH, Marie D, Hase C, Genin A (2003) *In situ* feeding and element removal in the symbiont-bearing sponge *Theonella swinhoei*: bulk DOC is the major source for carbon. *Limnol Oceanogr* 48:141–149
- Yahel G, Whitney F, Reiswig HM, Eerkes-Medrano DI, Leys SP (2007) *In situ* feeding and metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep temperate fjord with a remotely operated submersible. *Limnol Oceanogr* 52:428–440
- Zenkevitch L (1963) *Biology of the seas of the USSR*. George Allen & Unwin, London