



Responses of a common New Zealand coastal sponge to elevated suspended sediments: Indications of resilience

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ABSTRACT

Suspended sediments can affect the health of marine benthic suspension feeders, with concomitant effects on community diversity, abundance and ecosystem function. Suspended sediment loads can become elevated through trawling and dredging, and via resuspension of bottom sediments and/or direct input from land during storms. We assessed the functioning (survival, respiration, morphology) of a common New Zealand cushion sponge, *Crella incrustans* (Carter, 1885), during four weeks of exposure to a gradient of suspended sediment concentrations (SSC). Survival was high, and oxygen consumption was not affected. Sponges did, however, develop apical fistules, a phenomenon never-before observed in this species. Although sediments accumulated internally within the sponges, around a third had cleared these sediments two weeks after the elevated SSCs were removed. The environments these sponges inhabit may predispose them to coping with high SSCs. Such experiments are useful for defining SSC tolerances, which may influence how such impacts can be managed.

1. Introduction

Coastal marine environments are under increasing pressure from many natural and anthropogenic impacts operating at a range of temporal and spatial scales (Crain et al., 2009; Halpern et al., 2015). Of concern globally is the increasing amount of sediment entering coastal systems through waterways as a result of changes in land use, deforestation, and agricultural practices (Airoldi, 2003; Syvitski et al., 2005), and being disturbed and redistributed *in situ* from activities such as coastal and offshore dredging, trawling and seabed mining (Erftemeijer et al., 2012; Levin et al., 2016; Paradis et al., 2018). While many organisms are able to withstand natural levels of suspended and deposited sediment in coastal regions (Larcombe et al., 1995; Wolanski et al., 2005; Storlazzi et al., 2009), sustained high sediment loads can impact the health of marine organisms and, therefore, overall ecosystem function (Thrush and Dayton, 2002).

While larger sediment particles tend to settle quickly after suspension, fine particles can remain in suspension for extended periods and be transported over long distances by currents (Capuzzo et al., 1985; Rolinski et al., 2001). This means the impact of high suspended sediment concentrations (SSC) can occur some distance from the sediment

disturbance source (Oebius et al., 2001; Fisher et al., 2015; Jones et al., 2019). Excessive sedimentation and sediment resuspension can significantly affect the abundance, diversity and structure of benthic communities (Airoldi, 2003; Fabricius, 2005; Carballo, 2006; Knapp et al., 2013). These effects range from burial and smothering by settling sediment, which can be fatal, to more chronic effects on biological processes such as reduced larval survival and recruitment, settlement, feeding efficiency and growth (Airoldi, 2003; Fabricius, 2005; Cheung and Shin, 2005; Lohrer et al., 2006; Walker, 2007). High SSCs in the water column can be particularly detrimental to benthic suspension feeders and may lead to clogging of their filtering apparatus, thus affecting growth, reproduction and other physiological processes (Ellis et al., 2002; Hewitt and Norkko, 2007).

Sponges (Phylum Porifera) are an important and diverse suspension feeding group (Wilkinson and Evans, 1989; Bell and Barnes, 2000; Murillo et al., 2012) that have a number of important functional roles in benthic systems (Bell, 2008; Maldonado et al., 2017). In temperate regions, sponges can process large volumes of water and efficiently retain particulate and dissolved organic matter (Perea-Blázquez et al., 2012). While some sponge species can be found and even thrive in areas of high settled and suspended sediment (e.g. Bell and Barnes, 2000; Knapp et al.,

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2013), there is strong evidence, primarily from tropical species, that sediment is generally detrimental to sponges (Bell et al., 2015; but see Schönberg, 2016), and that their diversity and abundance is lower in high sediment environments (Leys et al., 2004; Bannister et al., 2012; Stubler et al., 2015).

Exposure to suspended sediments has been reported to clog the aquiferous system and to reduce or arrest water pumping in several sponge species (Gerrodette and Flechsig, 1979; Leys et al., 1999; Tompkins-MacDonald and Leys, 2008; Bannister et al., 2012; Strehlow et al., 2016; Grant et al., 2018). As pumping is required for feeding and respiration, clogging induced by fine sediments can alter particle retention (Lohrer et al., 2006) and oxygen consumption rates (Gerrodette & Flechsig, 1979). Despite these reported impacts on pumping however, respiration rates in sponges exposed to suspended sediments have shown contrasting results: increasing in some studies (Bannister et al., 2012; McGrath et al., 2017) and decreasing in others (Lohrer et al., 2006; Tjensvoll et al., 2013; Kutti et al., 2015; Pineda et al., 2017). Increased respiration rates may result from the sponges employing mechanisms to remove sediment from their aquiferous system, such as mucus production (see Biggerstaff et al., 2017; McGrath et al., 2017), while reduced respiration rates may result from a reduction in water pumping rates. A protracted reduction in sponge pumping has been correlated with reduced growth and reproduction, and lower survival (Roberts et al., 2006; Whalan et al., 2007; Maldonado et al., 2008). These contrasting results highlight the difficulty in making generalisations about impacts of sediment on sponges, and the need for location-specific and taxon-specific studies to understand suspended sediment impacts and determine SSC tolerance thresholds (e.g. Scanes et al., 2018).

In New Zealand, elevated sediment loads in coastal areas are recognized as a major threat to coastal biodiversity (Schwarz et al., 2006; Ministry for the Environment, 2015; Cussiolli et al., 2019; Siciliano et al., 2019). Land-based activities such as agriculture, forestry, and urban development may have detrimental impacts on New Zealand's coastal marine environment through increased export of terrestrial sediments and their subsequent resuspension by coastal waves and currents (Thrush et al., 2004; Schwarz et al., 2006). Changes in rainfall patterns as a result of climate change, including increases in the magnitude and frequency of storm events (Reisinger et al., 2014; Law et al., 2018), are likely to result in more frequent input of sediments to coastal regions. Additionally, larger and more frequent storms will also result in greater and more frequent resuspension of coastal seafloor sediments (e.g. Orpin and Ridd, 2012). Activities such as dredging and trawling are common around New Zealand, and known to resuspend sediments, which can persist in the water column for considerable time, and can thus influence widespread areas (Ellis et al., 2017).

Sponges are one of largest contributors to total biomass in many shallow water regions of New Zealand (Shears et al., 2007), particularly on rocky subtidal reefs (Kelly et al., 2009; Berman and Bell, 2010). To date, few studies have addressed the impacts of resuspended benthic sediments on New Zealand sponges (Murray, 2009), although comprehensive studies of impacts of terrestrial sediments (with predominantly silt/clay particles and very low acidity) have been conducted (Lohrer et al., 2006; Schwarz et al., 2006). There is need for more information to define environmentally relevant suspended sediment tolerance thresholds for sponges and to assess how they might respond to any future changes in SSCs, which in turn can influence how such impacts can be managed. In this study, we assess how the common shallow water and widely distributed New Zealand cushion sponge *Crella incrustans* (Carter, 1885) (Class: Demospongiae, Family: Crellidae) might respond to exposure to a range of elevated SSCs that could be encountered in the wild, and investigate whether there are thresholds of SSC beyond which normal functioning might become compromised.

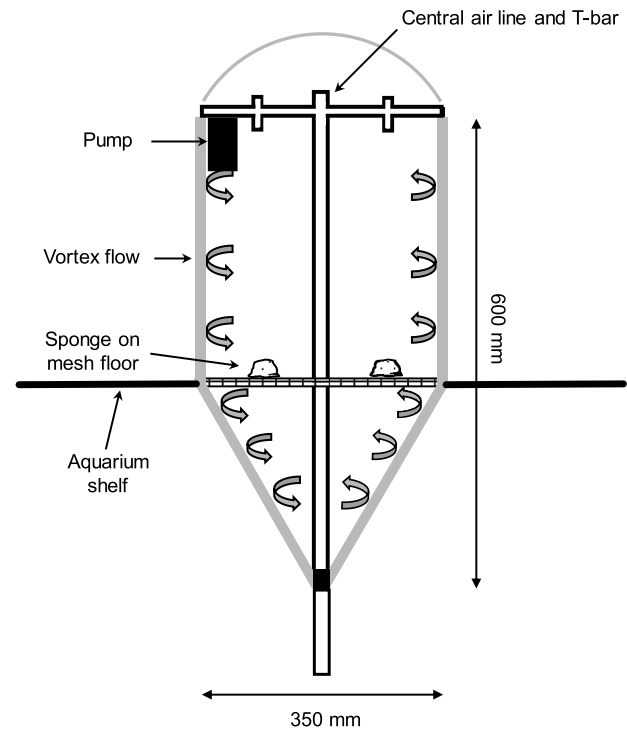


Fig. 1. Schematic of an experimental chamber (28 L), showing details of the mechanisms used to keep sediments in suspension.

2. Material and methods

2.1. Sponge collection and preparation

The cushion sponge *C. incrustans* was used for this experiment. Multiple sponges, ranging in size from 5 to 15 cm in diameter, were collected from 4 to 9 m depth in Breaker Bay, Wellington, New Zealand, by SCUBA divers. The sponges were immediately transferred to flow through holding tanks in NIWA Wellington's Marine Environmental Manipulation Facility (MEMF), with seawater from the adjacent bay (filtered to 0.1 μm) at temperatures similar to those at the collection site (16 °C). Any epibionts were removed from the sponge surfaces before they were carefully sectioned into $\sim 3 \times 3$ cm portions, and each portion was attached to a stainless steel mesh disc (4.5 cm diameter) using polyester thread (after Bates and Bell, 2018). They were subsequently left undisturbed for two weeks to allow membranes to reform and sponges to recover before being photographed (Nikon D850) and distributed randomly amongst 16 experimental chambers ($N = 4$ per chamber). The sponges were fed daily with *Nannochloropsis* microalgae (1–2 μm cell diameter; Nanno 3600™ Reed Mariculture, U.S.). Sponges were handled entirely underwater, from their collection and during all stages of the experiment, to prevent stress from exposure to air.

2.2. Chambers

Sixteen experimental chambers, each 28 L in volume and based on the Vortex resuspension tank design of Davies et al. (2009), were used to expose the experimental sponges to a range of SSCs. A vortex flow within the tanks was created by water being pumped into two vertical pipes using an aquarium pump (Eheim) positioned at the top of the tanks. A flow rate of 15 ml s^{-1} was used to force the water through small jets to create a directional flow (Fig. 1) and keep the sediment in suspension. Water jets in the lower half of the tank helped to re-suspend any settling sediment. Additionally, any sediment falling out of suspension that accumulated on the base of the chamber was pulled upwards by suction

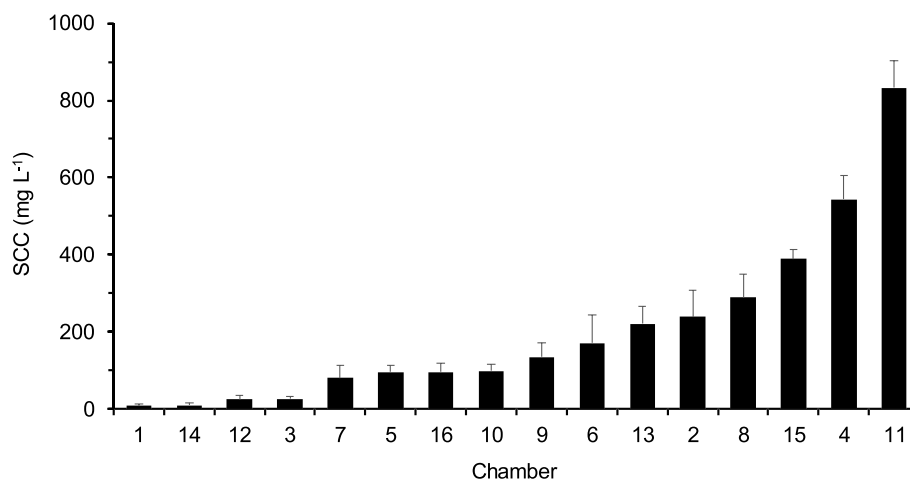


Fig. 2. The range of suspended sediment concentrations (SSC) used in the study. Data presented are means (+SE) of samples taken from a chamber on four separate occasions.

generated with an airlift system and subsequently reintroduced to the chamber via two outlets on a T bar pipe at the top of the chamber (Fig. 1). Chambers were supplied with seawater at a rate of approximately 1 L h^{-1} , providing complete replacement of seawater in each tank daily. A 58 cm long outflow pipe increased the opportunity for any sediments within the outflow water to fall out of suspension (due to no vortex and low flow) within this outflow pipe. A $5 \times 5 \text{ cm}$ square of polyester fibre placed in the outflow pipe also prevented sediments from leaving the system. This filter was cleared twice daily and any captured sediments reintroduced to the chamber.

2.3. Sediment treatments

The sponges were exposed to a gradient of suspended sediment concentrations (SSCs), ranging from a control (no added sediment) to a maximum of $\sim 832 \text{ mg L}^{-1}$ (Fig. 2). Fig. 2 shows average SSC in each chamber (+SE), determined from water samples collected weekly over 30 days. Water samples were filtered on a pre-dried and -weighed GF/F filter, before being dried at 60°C for 16 h.

This gradient design experiment was used in preference to a factorial design as we anticipated being able to generate response curves or to identify thresholds in the responses to SSC, and because similarly designed studies have demonstrated non-linear responses (e.g. Ellis et al., 2002; Hewitt and Norkko, 2007). SSC levels were chosen to encompass measured and modelled concentrations for coastal areas where these sponges are found (ranging from $\sim 10 \text{ mg L}^{-1}$ to 200 mg L^{-1} ; M. Hadfield NIWA, pers. comm.), storm generated resuspension of bottom sediments, high SSCs generated via runoff from forestry roads during storms (e.g. 1000 mg L^{-1} in the Marlborough Sounds; Fahey and Coker, 1992), and to incorporate levels used in other studies (Kutti et al., 2015; Tjensvoll et al., 2013). Target SSCs were maintained for four weeks, after which time the chambers were cleaned of sediments and supplied with ambient seawater only for another two weeks to allow a 'recovery period'.

2.3.1. SSC manipulation

The SSCs were obtained by adding a slurry of sediment (particle size range from 3 to $125 \mu\text{m}$; mean diam. $54 \mu\text{m}$) to each chamber. The sediment had been sourced from a nearby inlet and defaunated by freezing, then thawed and dried at 110°C for 24 h. To ensure that target concentrations were maintained, chamber SSCs were monitored twice daily using a hand-held optical turbidity meter (Seapoint Turbidity meter) connected to a multimeter which displayed mV. The relationship between mV and SSC had previously been determined for a broad range

of concentrations of the specific sediment used in this study (Supplementary Fig. 1). If required, more sediment was added to the chambers after each monitoring check, with the quantity of sediment required determined by the difference between target mV and actual mV within the chamber, using the calibration curve (Supplementary Fig. 2). The weekly water samples referred to above were collected immediately prior to mV readings being taken for SSC monitoring. These provided additional confirmation of the relationship between SSC and mV determined during the pre-experimental calibration curve generation, and that it was maintained during the experiment.

The particle size distribution of the sediment suspended in the water column (and thus, to which the sponges were actually exposed) was determined from water samples (each 30 ml) in five of the highest SSC chambers ($\text{SSC} = 135, 221, 288, 389, 544 \text{ and } 832 \text{ mg L}^{-1}$). Water samples were collected adjacent to the sponges in the chambers, on Days 5 and 29, (near the beginning and end, respectively, of the elevated SSC portion of the experiment). Samples were analysed for particle size using a Beckman Coulter LS 13-320 Dual Wavelength Laser Particle Sizer, covering a size range from 0.4 to $2000 \mu\text{m}$ and displayed as volume percent across 92 discrete size classes. Granulometric analyses were carried out in Excel using GRADISTAT version 8.0 (Blott, 2010), which calculates the standard granulometric statistics, textural descriptions and size fraction percentages. This showed that the particles in suspension were $\sim 47\%$ silt and $\sim 43\%$ very fine sand, and that this distribution did not change over time (Supplementary Fig. 2).

2.4. Evaluating sponge responses

Sponge responses to the SSC treatments were assessed at different time points during the experiment: after 8, 23 and 30 days of suspended sediment (SS) exposure ($\sim 1, 3$ and 4 weeks, respectively; hereafter Day 8, Day 23, and Day 30), and after two weeks without SS (~ 6 weeks after addition to the chambers; hereafter Day 44). At each time point, a single sponge from each chamber was sacrificed to measure respiration rates, assess morphological changes, and to evaluate the degree to which the sediments had infiltrated the animal. The exception was Day 44, when only 14 chambers contained live sponges.

2.4.1. Respiration rates

Oxygen consumption rates were assessed at each sampling time point in sealed 75 ml cylindrical Perspex respiration chambers with pre-calibrated PreSens oxygen sensor spots attached to their inner surface. The sealed respiration chambers were placed in a flow-through water bath to maintain constant water temperature, and the water was gently

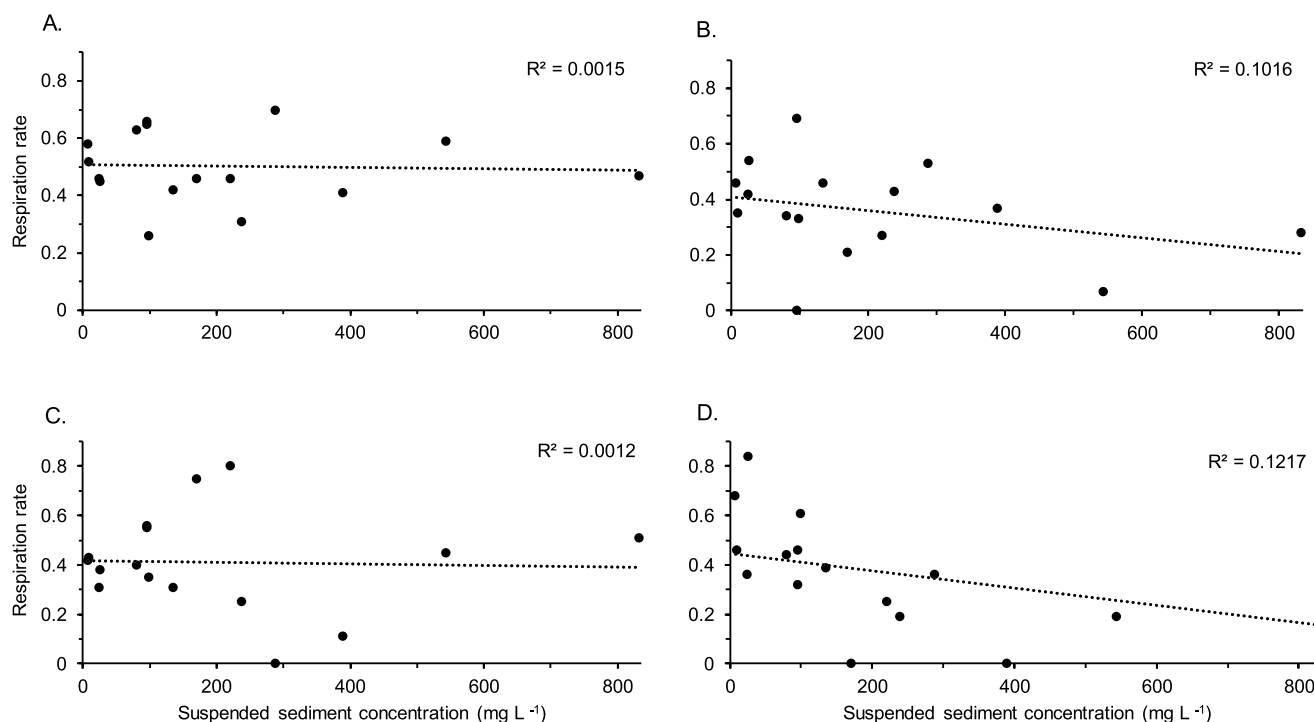


Fig. 3. Respiration rates of *Crella incrustans* (mg O₂ L⁻¹ g⁻¹ AFDW h⁻¹) recovered from each chamber after (A) 8 days, (B) 23 days, and (C) 30 days exposure to elevated SSCs. (D) shows rates on Day 44, following a two week recovery period in ambient seawater. Lines of best fit and R² values for the relationship with SSC at each time point are shown.

stirred using a magnetic stir bar located in a separate compartment at the bottom of each chamber. Sponges were added to the respiration chambers and “dark-adapted” for 30 min to minimize the potential oxygen production by photosynthetic symbionts and to allow the sponge to recover from being moved into the chambers, before the chambers were sealed. The microbial community composition of *C. incrustans* has been previously described using 16S sequencing (Astudillo Garcia, 2017), with a small proportion (approx. 5%) of cyanobacterial sequences being reported. However, earlier Pulse Amplitude Modulation (PAM) fluorometry work on *C. incrustans* (Bell unpublished data) found no evidence for photosynthetic activity (very low measurements of quantum yield (Y) of photosystem II). Dark respiration measurements were used a precaution, although it is unlikely these symbionts contribute significantly to the nutrition of *C. incrustans*.

Dissolved Oxygen (DO) readings were taken immediately after sealing and 30 min later using an optical fiber system (FIBOX 4, Pre-Sense GmbH, Germany). This time period was based on preliminary trials, to ensure oxygen levels did not drop below 75%. Blank incubations (N = 4) containing only seawater were used to correct for any microbial community respiration in the seawater. Respiration rates (mg O₂ L⁻¹ g⁻¹ AFDW h⁻¹) were determined after adjusting for the volume of water in the chamber and the sponge ash free dry weight (AFDW; after drying for 48 h at 60 °C to determine dry weight, followed by ashing at 500 °C for 5 h).

2.4.2. Morphology

Photographs were taken of all sponges immediately prior to the experiment start (Day 0), and of each sponge on the day it was removed from the chamber (Day 8, Day 23 or Day 44), using a Nikon D850 camera. Comparisons between Day 0 and later images enabled us to assess changes in the appearance of each sponge during the experiment. Each sponge was then sectioned (transversely) and photographs were taken of the internal surfaces. A scale and colour bar were included in each image, and analyses were conducted using ImageJ.

During the experiment some sponges grew projections on their dorsal surfaces, which we have termed “fistules”. These irregular shaped growths were often observed growing through layers of sediment that had accumulated on the sponge surface. The number of fistules on each sponge was quantified using the images, and is presented as a portion of the sponge surface area (fistules cm⁻²).

2.5. Statistical analysis

Plots were generated of respiration rate and number of fistules vs SSC, along with lines of best fit and R² values. The effect of SSC on each response variable was assessed using two-way ANOVA with interactions (SSC, Day, SSC x Day), after first confirming that assumptions of normality and homogeneity of variance were met (by examining the residual distribution plots and residuals vs predicted values and quantiles and using the Shapiro-Wilk test for normality). Any sponges that had died were excluded from the analyses. Analyses were conducted using SAS Version 9.4 (SAS Institute).

3. Results

3.1. Survival

There were four deaths across all of the SSC treatments during the six week experiment, three on Day 23 (from chambers with SSC levels of 96, 170 and 389 mg L⁻¹), and one on Day 30 (in the 288 mg L⁻¹ SSC chamber). The two dead sponges from the 96 and 389 mg L⁻¹ SSCs on Day 23 had originated from the same clone, so it is possible they were compromised during the pre-experiment sectioning, or that this sponge was unhealthy at the onset of the experiment.

3.2. Respiration rates

Respiration rates were variable between sponges (0.1–0.8 mg O₂ L⁻¹

Table 1

Results of statistical tests investigating the influence of elevated SSC on *Crella incrustans* (A) respiration rates and (B) number of fistules. DF = degrees of freedom, SS = sum of squares, MS = mean square.

	DF	SS	MS	F-value	Pr > F
A. Respiration rates (mg O₂ L⁻¹ g⁻¹ AFDW h⁻¹)					
Model	7	0.236	0.034	1.34	0.2516
Error	52	1.311	0.025		
Corrected total	59	1.548			
SSC	1	0.064	0.064	2.53	0.1178
Day	3	0.027	0.009	0.35	0.7881
SSC x Day	3	0.063	0.021	0.83	0.4808
B. Number of fistules (cm⁻²)					
Model	7	22.328	3.190	2.87	0.0130
Error	52	57.734	1.110		
Corrected total	59	80.063			
SSC	1	8.622	8.622	7.77	0.0074
Day	3	2.651	0.883	0.80	0.5017
SSC x Day	3	3.260	1.087	0.98	0.4099

g⁻¹ AFDW h⁻¹; Fig. 3). There was a slight negative relationship between respiration rate and SSC, which was strongest on Day 23 ($R^2 = 0.1016$; Fig. 3B) and at the end of the two week recovery period in ambient seawater (Day 44 $R^2 = 0.1217$; Fig. 3D). This relationship was not detected as statistically significant using two way ANOVA (SSC $F_{1,52} = 2.53$, $p = 0.1178$; Table 1A).

3.3. Morphology

The appearance of fistules was noted over the course of the experiment (Figs. 4 and 5). The control sponges had <1 fistule cm⁻² on all sampling dates (Fig. 4). In all other treatments fistule numbers increased after Day 8. There was a positive relationship between fistule abundance and SSC which was strongest on Days 23 and 44 (Fig. 4). This relationship was statistically significant across all sampling Days (SSC $F_{1,52} = 7.77$, $p = 0.0074$; Table 1B).



Fig. 5. An image of the surface of a sponge after 30 days exposure to SSC of 170 mg L⁻¹, showing fistules protruding from sediment that had settled on the sponge surface.

Dissections revealed internal sediment accumulation in many sponges (Fig. 6; Supplementary data). Qualitative visual assessments showed internal sediment build up even after only eight days exposure (Fig. 6). On this sampling date about half of the sponges in the elevated SSC chambers contained sediments, including those from the four highest levels. On Days 23 and 30, sediments were apparent in all sponges exposed to elevated SSCs, with one exception (99 mg L⁻¹ SSC on Day 30). No sediment was observed in control sponges. The magnitude of this sediment incursion was variable, regardless of SSC treatment (Fig. 6). At the Day 44 time point, after two weeks in ambient seawater, two thirds of sponges still contained sediments; those that were 'sediment free' included sponges from the two lowest SSCs, and one each from the 96 and 221 mg L⁻¹ SSC chambers.

4. Discussion

This study has provided new information on the effect of elevated SSC on a common and widely distributed coastal New Zealand sponge, *C. incrustans*. Survival was high during the four week-long exposure to elevated SSCs, even at the highest concentration (832 mg L⁻¹). There

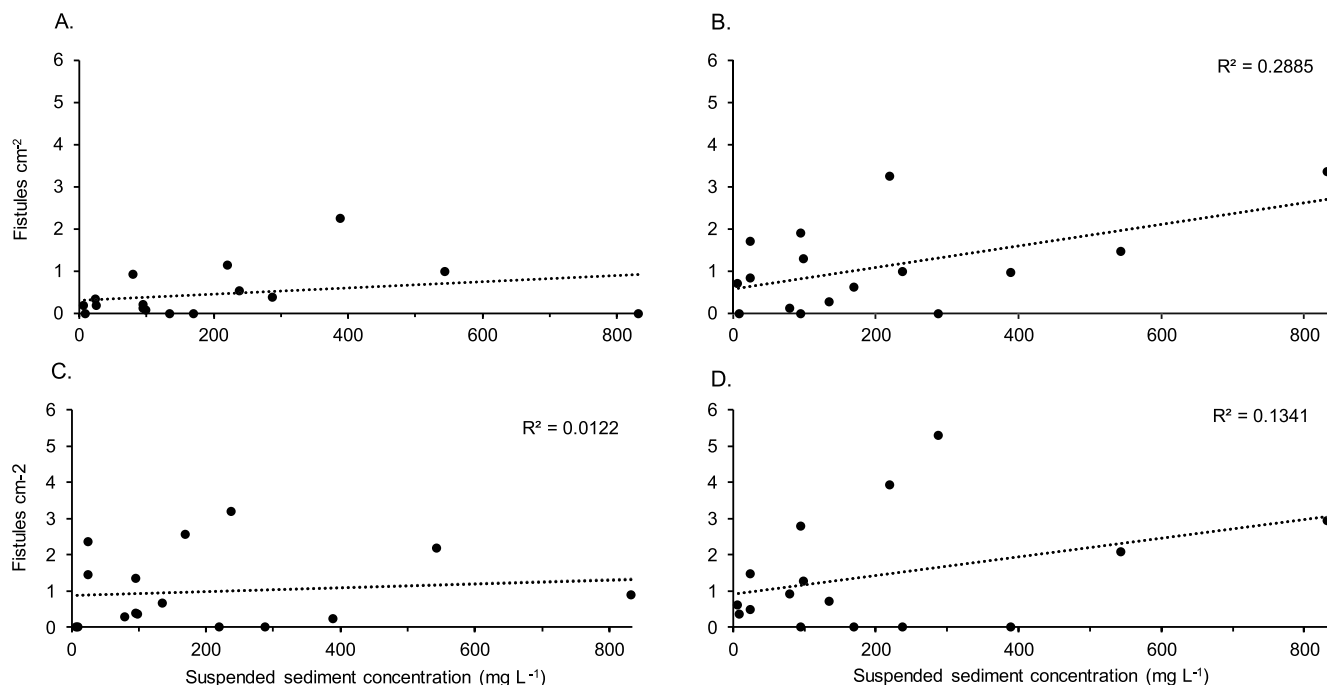


Fig. 4. Number of fistules cm⁻² on the surface of sponges recovered from each chamber after (A) 8 days, (B) 23 days, and (C) 30 days exposure to elevated SSCs. (D) shows rates on Day 44, following a two week recovery period in ambient seawater. Lines of best fit and R^2 values for the relationship with SSC at each time point are shown.

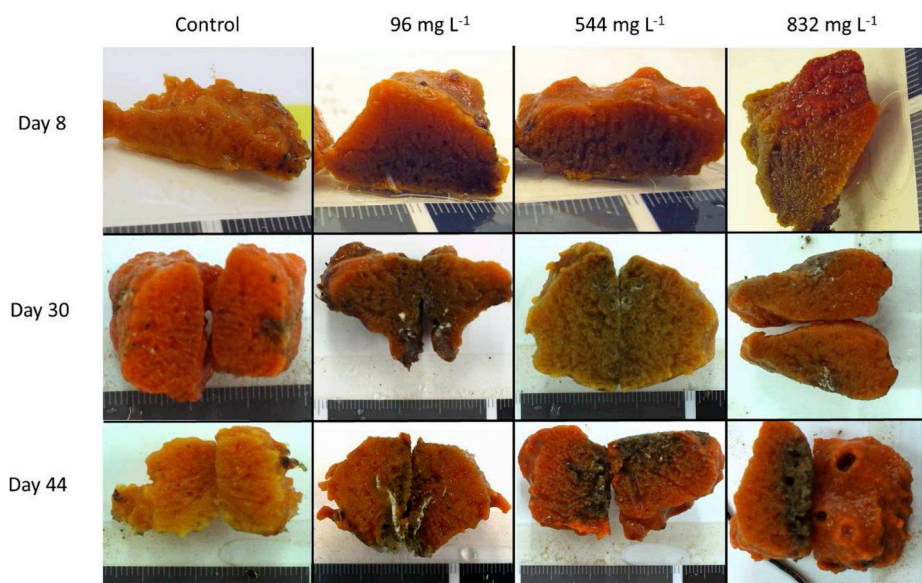


Fig. 6. Images of cross-sectioned sponges showing the accumulation of sediments. Examples are shown of control and sediment-exposed sponges after 8 days and 30 days, and at 44 days.

was considerable variation in responses amongst sponges, and no strong negative effects were detected, even at the highest SSCs.

4.1. Respiration

There was no significant effect of increased SSC on sponge respiration rates. It is possible that the duration of our experiment was not long enough to detect strong effects. However, many previous studies have reported significant effects of elevated SSCs on sponge respiration from much shorter exposure periods (Tjensvoll et al., 2013; Kutti et al., 2015). There are contrasting and variable reports of the effects of SSCs on sponge respiration and also pumping rates. Some experimental studies have reported increases in respiration and pumping rates in response to increased SSCs (Bannister et al., 2012; McGrath et al., 2017; Pineda et al., 2017), while others have shown decreases (Kutti et al., 2015; Pineda et al., 2017). In addition, *in situ* reductions in pumping rates have been reported in response to storm generated turbidity for some tropical sponge species (Reiswig, 1971). Several authors have linked increased respiration rates to energetically costly mucus production as a sediment tolerance mechanism/response (see Biggerstaff et al., 2017; McGrath et al., 2017), while decreased respiration rates have been linked to reduction or arrest in pumping in order to prevent sediment entering the sponge (Grant et al., 2018). Mucus production by *C. incrustans* was not measured (or observed) during our experiment. In contrast, we found no strong effect of elevated SSC on *C. incrustans* respiration rates, a result that is consistent with a recent study by Grant et al. (2019) who noted no change in pumping rates in one glass sponge species.

The lack of effects on respiration in our study is surprising, since the sponges were clearly accumulating sediment internally, which might be expected to compromise sponge pumping efficiency. *C. incrustans* appears to have limited loss of metabolic function in response to the SSCs we tested. Unfortunately, it is not possible to directly compare the actual respiration rates from our study with those of the other studies on sponge sediment impacts because of differences in the way respiration rates are standardized between studies. However, Bates et al. (2018) examined the effects of different pH treatments on *C. incrustans* and found similar respiration rates for their control sponges as we report in the present study (assuming an AFDW to DW ratio of 50–65%), which provides further support for the limited effect of elevated SSCs on the respiration rate of our study species.

4.2. Morphology

Fistules were noted in many *C. incrustans* over the experiment, with their numbers positively correlated with SSC. Sponges living in soft sediment environments often have apical fistular structures that protrude upwards, ensuring some of the sponge is elevated above the sediment (Schönberg, 2016 and references therein). These elevated structures have been reported to be where the water is inhaled into the sponge (see Rützler, 1997). While fistules have been reported for many sponge species living in sediments and also for some hard substratum species (e.g. *Polymastia* spp. at Lough Hyne; Bell pers. obs.), to our knowledge this is the first report of such structures being produced during a sediment experiment. The production of fistules in *C. incrustans* was unexpected, as these have not been observed for this species at their field collection site (Bell pers. obs.). The generation of fistules in our experiment may be a natural adaptation strategy in response to sediment that had settled on the sponge surface rather than to increased SSC. This morphological change could potentially be the result of remodeling of the sponge body plan to move the inhalant pores to a higher position than the main sponge surface, enabling it to continue to pump water. Alternatively, the build up of sediment internally may have promoted fistule production. Further examination of these structures is required to determine whether these hypotheses are correct.

Our qualitative observations of accumulated internal sediment in *C. incrustans* suggest it may take longer than two weeks for sediment removal, with several sponges showing internal sediments after two weeks' recovery. A similar, variable response was noted for *Ianthella basta* after two weeks in control conditions, although internal sediment had decreased to a very low level (Strehlow et al., 2017). Some sponges are known to take up and incorporate sediments into their body and in some species, incorporation of sediment in their tissues is beneficial and can actually enhance growth and provide structural support (Schönberg, 2016, and references therein). However, previous experiments and taxonomic work with *C. incrustans* (Berman and Bell, 2010) have not noted any internal sediment in specimens from the field.

4.3. Tolerance of coastal temperate sponges to sediment

The SSC concentrations we used are high compared to those used in most previous experiments on sponges (see Bell et al., 2015; Schönberg, 2016) and likely represent conditions expected under major seafloor

disturbance (e.g. extreme storms, mining or trawling; De Madron et al., 2005; Bradshaw et al., 2012). Despite this, we found no strong evidence for negative impacts of elevated SSC on *C. incrustans*, nor did the thin film of sediment that settled on the surface of the sponge appear to have detrimental effects. These results, combined with those of Bell (2004) from Ireland, and reports of dense sponge assemblages in other temperate regions that experience high SSCs and settled sediment (see Bell and Barnes, 2000), support the view that shallow temperate sponges may be able to tolerate high levels of suspended sediment, and that sensitivity of sponge species to SSC is likely influenced by pre-adaptation to the turbidity of the natural habitat (e.g. Abdul Wahab et al., 2017; Grant et al., 2019). However, the properties of the disturbed sediment are also important, as shown by the detrimental effects of terrestrial sediments (with predominantly clay-silt particle size composition and very low pH) on *Aoptos* spp. (Lohrer et al., 2006) and *Tethya burtoni* (Schwarz et al., 2006).

5. Conclusions

Elevated SSCs do not appear to have strong effects on the physiology of the common New Zealand cushion sponge *C. incrustans*, at least over the time frame of this experiment. There were morphological changes, with the development of apical fistules that may be an adaptation to the sediment settling on their external surfaces, or accumulating internally, during the experiment. Sediment was taken up by *C. incrustans*, but the species has mechanisms to clear the sediment once the source of SSC is removed. We conclude that the coastal environments that these sponges live in may predispose them to coping with high SSCs, and that they may also be tolerant of sediment deposition events that temporarily cover their surfaces.

Declaration of competing interest

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

CRediT authorship contribution statement

Vonda J. Cummings: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Jennifer Beaumont:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Valeria Mobilia:** Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing. **James J. Bell:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Dianne Tracey:** Conceptualization, Methodology, Writing - review & editing. **Malcolm R. Clark:** Conceptualization, Writing - original draft, Writing - review & editing. **Neill Barr:** Methodology, Investigation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2020.104886>.

References

- Abdul Wahab, M.A., Fromont, J., Gomez, O., Fisher, R., Jones, R., 2017. Comparisons of benthic filter feeder communities before and after a large-scale capital dredging program. *Mar. Pollut. Bull.* 122, 176–193.
- Airolidi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanogr. Mar. Biol. Annu. Rev.* 41, 161–236.
- Astudillo Garcia, M.D.C., 2017. Microbiology of Marine Sponges: from Community Structure to Symbiont Function. PhD thesis. The University of Auckland, New Zealand. <http://hdl.handle.net/2292/36039>.
- Bannister, R.J., Battershill, C.N., 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. *Contin. Shelf Res.* 32, 86–95.
- Bates, T.E., Bell, J.J., 2018. Responses of two temperate sponge species to ocean acidification. *N. Z. J. Mar. Freshw. Res.* 52 (2), 247–263.
- Bell, J.J., 2004. Evidence for morphology-induced sediment settlement prevention on the tubular sponge *Haliciona urceolus*. *Mar. Biol.* 146 (1), 29–38.
- Bell, J.J., 2008. The functional roles of marine sponges. *Estuar. Coast Shelf Sci.* 79 (3), 341–353.
- Bell, J.J., Barnes, D.K., 2000. The distribution and prevalence of sponges in relation to environmental gradients within a temperate sea lough: inclined cliff surfaces. *Divers. Distrib.* 6 (6), 305–323.
- Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., Shaffer, M., 2015. Sediment impacts on marine sponges. *Mar. Pollut. Bull.* 94 (1–2), 5–13.
- Berman, J., Bell, J.J., 2010. Spatial variability of sponge assemblages on the Wellington south coast, New Zealand. *Open Mar. Biol. J.* 4, 12–25.
- Biggerstaff, A., Smith, D.J., Jompa, J., Bell, J.J., 2017. Metabolic responses of a phototrophic sponge to sedimentation supports transitions to sponge-dominated reefs. *Sci. Rep.* 7 (1), 2725.
- Blott, S.J., 2010. GRADISTAT Ver. 8.0: A Grain Size Distribution and Statistics Package for the Analysis of Unconsolidated Sediments by Sieving or Laser Granulometer. Kenneth Pye Associates Ltd, UK. www.kpal.co.uk/gradistat.html.
- Bradshaw, C., Tjensvoll, I., Sköld, M., Allan, J.J., Molvaer, J., Magnusson, J., Naes, K., Nilsson, H.C., 2012. Bottom trawling resuspends sediment and releases bioavailable contaminants in a polluted fjord. *Environ. Pollut.* 170, 232–241.
- Capuzzo, J.M., Burt, W.V., Duedall, I.W., Park, P.K., Kester, D.R., 1985. The impact of waste disposal in nearshore environments. In: Ketchum, B.H., et al. (Eds.), *Wastes in the Ocean. Volume 6. Nearshore Waste Disposal*. John Wiley, New York, pp. 3–38.
- Carballo, J.L., 2006. Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience* 13 (1), 119–130.
- Cheung, S.G., Shin, P.K.S., 2005. Size effects of suspended particles on gill damage in green-lipped mussel *Perna viridis*. *Mar. Pollut. Bull.* 51, 801–810.
- Crain, C.M., Halpern, B.S., Beck, M.W., Kappel, C.V., 2009. Understanding and managing human threats to the coastal marine environment. *Ann. N. Y. Acad. Sci.* 1162 (1), 39–62.
- Cussioli, M.C., Bryan, K.R., Pilditch, C.A., de Lange, W.P., Bischof, K., 2019. Light penetration in a temperate meso-tidal lagoon: implications for seagrass growth and dredging in Tauranga Harbour, New Zealand. *Ocean Coast Manag.* 174, 25–37.
- Davies, A.J., Last, K.S., Attard, K., Hendrick, V.J., 2009. Maintaining turbidity and current flow in laboratory aquarium studies, a case study using *Sabellaria spinulosa*. *J. Exp. Mar. Biol. Ecol.* 370 (1–2), 35–40.
- De Madron, X.D., Ferré, B., Le Corre, G., Grenz, C., Conan, P., Pujo-Pay, M., Buscail, R., Bodiot, O., 2005. Trawling-induced resuspension and dispersal of muddy sediments and dissolved elements in the Gulf of Lion (NW Mediterranean). *Contin. Shelf Res.* 25 (19–20), 2387–2409.
- Ellis, J.I., Clark, M.R., Rouse, H.L., Lamarche, G., 2017. Environmental management frameworks for offshore mining: the New Zealand approach. *Mar. Pol.* 84, 178–192.
- Ellis, J., Cummings, V., Hewitt, S., Thrush, S., Norkko, A., 2002. Determining effects of suspended sediment on condition of a suspending feeding bivalve (*Atrina zelandica*): results of a survey, a laboratory experiment and a field transplant experiment. *J. Exp. Mar. Biol. Ecol.* 267, 147–174.
- Ertmeijer, P.L., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. *Mar. Pollut. Bull.* 64 (9), 1737–1765.
- Fabricsius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50 (2), 125–146.
- Fahey, B.D., Coker, R.J., 1992. Sediment production from forest roads in Queen Charlotte forest and potential impact on marine water quality, Marlborough Sounds, New Zealand. *N. Z. J. Mar. Freshw. Res.* 26, 187–195.
- Fisher, R., Stark, C., Ridd, P., Jones, R., 2015. Spatial patterns in water quality changes during dredging in tropical environments. *PloS One* 10 (12), e0143309.
- Gerrodette, T., Flechsig, A.O., 1979. Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Mar. Biol.* 55 (2), 103–110.
- Grant, N., Matveev, E., Kahn, A.S., Leys, S.P., 2018. Suspended sediment causes feeding current arrests in situ in the glass sponge *Aphrocallistes vastus*. *Mar. Environ. Res.* 137, 111–120.
- Grant, N., Matveev, E., Kahn, A.S., Archer, S.K., Dunham, A., Bannister, R.J., Eerkes-Medrano, D., Leys, S.P., 2019. Effect of suspended sediments on the pumping rates of three species of glass sponge in situ. *Mar. Ecol. Prog. Ser.* 615, 79–100.

- Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J. S., Rockwood, C.R., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat. Commun.* 6, 7615.
- Hewitt, J.E., Norkko, J.T., 2007. Incorporating temporal variability of stressors into studies: an example using suspension-feeding bivalves and elevated suspended sediment concentrations. *J. Exp. Mar. Biol. Ecol.* 341, 131–141.
- Jones, R., Fisher, R., Bessell-Browne, P., 2019. Sediment deposition and coral smothering. *PLoS One* 14 (6), e0216248.
- Kelly, M., Edwards, A.R., Wilkinson, M.R., Alvarez, B., Cook, S. de C., Bergquist, P.R., Buckeridge, J.S., Campbell, H.J., Reisinger, H.M., Valentine, C., Vacelet, J., 2009. *Phylum Porifera - Sponges*. New Zealand Inventory of Biodiversity, vol. 1. Canterbury University Press, pp. 23–46.
- Knapp, I.S.S., Williams, G.J., Carballo, J.L., Cruz-Barraza, J.A., Gardner, J.P.A., Bell, J.J., 2013. Restriction of sponges to an atoll lagoon as a result of reduced environmental quality. *Mar. Pollut. Bull.* 66, 209–220.
- Kutti, T., Bannister, R.J., Fosså, J.H., Krogness, C.M., Tjensvoll, I., Søvik, G., 2015. Metabolic responses of the deep-water sponge *Geodia barretti* to suspended bottom sediment, simulated mine tailings and drill cuttings. *J. Exp. Mar. Biol. Ecol.* 473, 64–72.
- Larcombe, P., Ridd, P.V., Prytz, A., Wilson, B., 1995. Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. *Coral Reefs* 14, 163–171.
- Law, C.S., Rickard, G.J., Mikaloff-Fletcher, S.E., Pinkerton, M.H., Behrens, E., Chiswell, S. M., Currie, K., 2018. Climate change projections for the surface ocean around New Zealand. *N. Z. J. Mar. Freshw. Res.* <https://doi.org/10.1080/00288330.2017.1390772>.
- Levin, L.A., Mengerink, K., Gjerde, K.M., Rowden, A.A., Van Dover, C.L., Clark, M.R., Ramirez-Llodra, E., Currie, B., Smith, C.R., Sato, K.N., Gallo, N., Sweetman, A.K., Lily, H., Armstrong, C.W., Bridger, J., 2016. Defining “serious harm” to the marine environment in the context of deep-seabed mining. *Mar. Pol.* 74, 245–259.
- Leys, S.P., Mackie, G.O., Meech, R.W., 1999. Impulse conduction in a sponge. *J. Exp. Biol.* 202 (9), 1139–1150.
- Leys, S.P., Wilson, K., Holeten, C., Reisinger, H.M., Austin, W.C., Tunnicliffe, V., 2004. Patterns of glass sponge (Porifera, Hexactinellida) distribution in coastal waters of British Columbia, Canada. *Mar. Ecol. Prog. Ser.* 283, 133–149.
- Lohrer, A.M., Hewitt, J.E., Thrush, S.F., 2006. Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Mar. Ecol. Prog. Ser.* 315, 13–18.
- Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., Leys, S.P., 2017. Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. In: Rossi, S., Bramanti, L., Gori, A., Orejas Saco del Valle, C. (Eds.), *Marine Animal Forests, Volume 1: the Ecology of Benthic Biodiversity Hotspots*, pp. 145–183.
- Maldonado, M., Giraud, K., Carmona, C., 2008. Effects of sediment on the survival of asexually produced sponge recruits. *Mar. Biol.* 154 (4), 631–641.
- McGrath, E.C., Smith, D.J., Jompa, J., Bell, J.J., 2017. Adaptive mechanisms and physiological effects of suspended and settled sediment on barrel sponges. *J. Exp. Mar. Biol. Ecol.* 496, 74–83.
- Ministry for the Environment and Statistics New Zealand, 2015. New Zealand's environmental reporting series: Environment Aotearoa 2015. Available from: www.mfe.govt.nz.
- Murillo, F.J., Muñoz, P.D., Cristobo, J., Ríos, P., González, C., Kenchington, E., Serrano, A., 2012. Deep-sea sponge grounds of the Flemish Cap, Flemish Pass and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): distribution and species composition. *Mar. Biol. Res.* 8 (9), 842–854.
- Murray, H.J.R., 2009. Oxygen consumption rates of sponges and the effect of UV-B radiation and sediment. MSc thesis, Victoria University of Wellington, New Zealand.
- Oebius, H.U., Becker, H.J., Rolinski, S., Jankowski, J.A., 2001. Parametrization and evaluation of marine environmental impacts produced by deep-sea manganese nodule mining. *Deep-Sea Res. Part II* 48, 3453–3467.
- Orpin, A., Ridd, P., 2012. Exposure of inshore corals to suspended sediments due to wave-resuspension and river plumes in the central Great Barrier Reef: a reappraisal. *Contin. Shelf Res.* 47, 55–67.
- Paradis, S., Masque, P., Puig, P., Juan-Diaz, X., Gorelli, G., Company, J.B., Palanques, A., 2018. Enhancement of sedimentation rates in the Foix Canyon after the renewal of trawling fleets in the early XXIst century. *Deep-Sea Res. Part I* 132, 51–59.
- Perea-Blázquez, A., Davy, S.K., Bell, J.J., 2012. Estimates of particulate organic carbon flowing from the pelagic environment to the benthos through sponge assemblages. *PLoS One* 7 (1), e29569. <https://doi.org/10.1371/journal.pone.0029569>.
- Pineda, M.C., Strehlow, B., Sternel, M., Duckworth, A., Jones, R., Webster, N.S., 2017. Effects of suspended sediments on the sponge holobiont with implications for dredging management. *Sci. Rep.* 7 (1), 4925.
- Reisinger, A., Kitching, R.L., Chiew, F., Hughes, L., et al., 2014. Australasia. In: Barros, V. R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A. N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1371–1438.
- Reiswig, H., 1971. In situ pumping activities of tropical Demospongiae. *Mar. Biol.* 9, 38–50.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312 (5773), 543–547.
- Rolinski, S., Segsneider, J., Sundermann, J., 2001. Long-term propagation of tailings from deep-sea mining under variable conditions by means of numerical simulations. *Deep-Sea Research II* 48, 3469–3485.
- Rützler, K., 1997. The role of psammobiontic sponges in the reef community. In: Lessios, H.A., Macintyre, I.G. (Eds.), *Proceedings of the Eighth International Coral Reef Symposium*, Panama City, 24 – 29 June 1996, vol. 2. Smithsonian Tropical Research Institute, Balboa, pp. 1393–1398.
- Scanes, E., Kutti, T., Fang, J.K.H., Johnston, E.L., Ross, P.M., Bannister, R.J., 2018. Mine waste and acute warming induce energetic stress in the deep-sea sponge *Geodia atlantica* and coral *Prinnoea resedaeformis*; results from a mesocosm study. *Front. Mar. Sci.* 5, 129. <https://doi.org/10.3389/fmars.2018.00129>.
- Schönberg, C.H.L., 2016. Happy relationships between marine sponges and sediments - a review and some observations from Australia. *J. Mar. Biol. Assoc. U. K.* 96 (2), 493–514.
- Schwarz, A.M., Taylor, R., Hewitt, J., Philips, N., Shima, J., Cole, R., Budd, R., 2006. Impacts of terrestrial runoff on the biodiversity of rocky reefs. *New Zealand Aquatic Environment and Biodiversity Report* 7 (109), 1176–9440.
- Shears, N.T., 2007. Biogeography, community structure and biological habitat types of subtidal reefs on the South Island West Coast, New Zealand. *Sci. Conserv.* 281, 53 p.
- Siciliano, A., Schiel, D.R., Thomsen, M.S., 2019. Effects of local anthropogenic stressors on a habitat cascade in an estuarine seagrass system. *Mar. Freshw. Res.* 70, 1129–1142.
- Storlazzi, C.D., Field, M.E., Bothner, M.H., Presto, M.K., Draut, A.E., 2009. Sedimentation processes in a coral reef embayment: Hanalei Bay, Kauai. *Mar. Geol.* 264, 140–151.
- Strehlow, B.W., Jorgensen, D., Webster, N.S., Pineda, M.C., Duckworth, A., 2016. Using a thermistor flowmeter with attached video camera for monitoring sponge excurrent speed and oscular behaviour. *PeerJ* 4, 2761.
- Strehlow, B.W., Pineda, M., Duckworth, A., Kendrick, G.A., Renton, M., Abdul Wahab, M. A., Webster, N.S., Clode, P.L., 2017. Sediment tolerance mechanisms identified in sponges using advanced imaging techniques. *PeerJ* 5, e3904. <https://doi.org/10.7717/peerj.3904>.
- Stubler, A.D., Duckworth, A.R., Peterson, B.J., 2015. The effects of coastal development on sponge abundance, diversity, and community composition on Jamaican coral reefs. *Mar. Pollut. Bull.* 96, 261–270.
- Syvitski, J.P.M., Vörösmarty, C.J., Kettner, A.J., Green, P., 2005. Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science* 308, 376–380.
- Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annu. Rev. Ecol. Systemat.* 33 (1), 449–473.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J., Ellis, J.I., Hatton, C., Lohrer, A., Norkko, A., 2004. Muddy waters: elevating sediment input to coastal and estuarine habitats. *Front. Ecol. Environ.* 2 (6), 299–306.
- Tjensvoll, I., Kutti, T., Fosså, J.H., Bannister, R.J., 2013. Rapid respiratory responses of the deep-water sponge *Geodia barretti* exposed to suspended sediments. *Aquat. Biol.* 19 (1), 65–73.
- Tompkins-MacDonald, G.J., Leys, S.P., 2008. Glass sponges arrest pumping in response to sediment: implications for physiology of the hexactinellid conduction system. *Mar. Biol.* 154, 973–984.
- Walker, J.W., 2007. Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. *Mar. Ecol. Prog. Ser.* 331, 109–118.
- Whalan, S., Battershill, C., De Nys, R., 2007. Variability in reproductive output across a water quality gradient for a tropical marine sponge. *Mar. Biol.* 153, 163–169.
- Wilkinson, C.R., Evans, E., 1989. Sponge distribution across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. *Coral Reefs* 8 (1), 1–7.
- Wolanski, E., Fabricius, K., Spagnol, S., Brinkman, R., 2005. Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. *Estuar. Coast Shelf Sci.* 65, 153–158.