Bottom trawling reduces benthic denitrification and has the potential to influence the global nitrogen cycle

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Scientific Significance Statement
Benthic denitrification is a critical ecosystem function that removes bioavailable nitrogen from N-limited coastal marine waters, thereby helping to buffer against eutrophication driven by nitrogen over-enrichment. Here we show that trawling disturbance destroys the complex 3-dimensional redox structures in surface sediments that maximize denitrification potential, resulting in up to a 50% reduction in net denitrification.

Abstract
Bottom trawling and eutrophication are large stressors that are critically coupled. Here we show, using a before-after control-effect design, the significant reduction in denitrification as a result of experimental bottom trawling in a shallow coastal system. Trawl disturbance destroys the complex three-dimensional redox structures in surface sediments that maximize denitrification potential, resulting in up to a 50% reduction in net denitrification. The decrease in net denitrification also increased after each trawling event suggesting a declining resilience to trawling and eutrophication. Bottom trawling occurs at such a large scale that it could result in significant amounts of nitrogen being retained on the continental shelf. As such, impacts on the global ocean nitrogen cycle and associated eutrophication should be counted among the many negative consequences of extensive seafloor trawling.

The marine coastal zone contains some of the most biodiverse and biomass-rich ecosystems on earth (Heip et al. 2003). Marine ecosystems provide a wide range of ecosystem services that benefit humankind (Costanza et al. 1997; De Groot et al. 2012), but they are also subject to multiple anthropogenic stressors. Two synergistic stressors are bottom trawling, the greatest source of global seafloor disturbance (Thrush and Dayton 2002; Hinz et al. 2009), and nutrient enrichment and associated eutrophication, also one of the largest threats to coastal ecosystems (Nixon 1998; Valiela 2006). Soft-sediment seafloor habitats maintain a microbially mediated biogeochemical process known as denitrification, a critical ecosystem

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function that removes bioavailable nitrogen from N-limited coastal marine waters, thereby helping to buffer against eutrophication (Seitzinger et al. 2006; Eyre et al. 2016). Denitrification is enhanced by complex interactions between microbial and invertebrate communities (Webb and Eyre 2004; Eyre and Ferguson 2009), and may be impacted by changes in sediment redox structure and the loss of key invertebrate taxa, both of which are disturbed by heavy trawling gear. Bottom trawling and eutrophication are large stressors that are critically coupled; trawling-induced sediment structural changes (Peterson et al. 1987; Collie et al. 1997) and infauna species loss (Collie et al. 2000; Kaiser et al. 2006) may alter ecosystem functions such as denitrification, which in turn affect the system’s resilience to increased nutrient-enrichment and associated eutrophication.

The effect of bottom trawling on sediment infauna is well studied (Hinz et al. 2009; Hiddink et al. 2017). Much less is known about the effect of bottom trawling on benthic biogeochemical processes (ecosystem function) (e.g., Olsgard et al. 2008; Pusceddu et al. 2015; Sciberras et al. 2016); there has only been one study on the critical ecosystem process of denitrification, and it showed no effect of trawling (Trimmer et al. 2005). However, these few biogeochemical studies have mostly been comparative studies where the process of interest has been compared in areas of high and low trawl disturbance and/or in untrawled control areas. Comparative studies suffer from the patchy distribution of bottom trawling which leads to a mosaic of undisturbed, recently impacted and recovering benthic communities (Hiddink et al. 2017). As such, the trawl effect at the exact location where measurements were taken is not fully known, reducing the ability to detect change.

The hypothesis of this study is that benthic denitrification will be reduced due to bottom trawling. This was tested in a shallow coastal system using experimental bottom trawling in a before-after control-effect (BACI) design. Trawling was repeated three times to try and detect chronic effects. We expected a single trawl would destroy the complex three-dimensional redox structures in surface sediments resulting in a reduction in denitrification, and that repeated trawling would result in a chronic decline in denitrification.

**Methods**

**Study site**

The study was conducted within a trawl-exclusion zone of the subtropical Moreton Bay, Australia, which allowed the experimental testing of trawling effects on previously untrawled sediments (Fig. S2). Benthic metabolism and nitrogen cycling at the study site were primarily controlled by seasonal and interannual variation in organic matter (OM) supply, temperature and light, with secondary controls imparted by bioturbation/bioirrigation (Ferguson and Eyre 2010, 2013). Briefly, the annual cycle was characterized by peak inputs of OM to the sediments from phytodetritus deposition during the summer wet season (January), followed by an opportunistic recruitment of benthic macrofauna which processed and depleted sediment OM throughout the autumn (April), and finally the development of more autotrophic benthic communities as OM supply waned and light climate improved during the winter–spring dry season (July to November). Experimental trawling was carried out during each of these stages and significant impacts on benthic microbial processes can be best explained with reference to this conceptual model (Ferguson and Eyre 2010, 2013). Our results thereby provide a comprehensive model of trawling impacts during different trophic states occurring within the annual cycle. However, our experimental trawl intensity is most likely less than adjacent areas along the trawl exclusion boundary for periods of the year.

**Experimental design**

The study had a beyond BACI design (Underwood 1993), with multiple control and impact sites, and multiple sampling times before and after trawling impact. Three replicate sites, each consisting of two subsites (paired treatment-control subsites), were selected along a northeast gradient away from the Caboolture River mouth in 4 m deep water (Fig. S2). The three sites were each separated by around 500 m. Each subsite was about 20 m × 20 m, and paired treatment-control subsites were separated by about 20 m. At each sample time, from each subsite, divers collected six replicate 95-mm ID × 500-mm long clear Plexiglas tubes, retaining approximately 200-mm sediment and 300 mm (2.5 L) of overlying water (36 in total for process measurements, sediment properties, and macrofauna). The sites were monitored every 3 months (April, July, November, January) prior to experimental trawling (pretrawling) to ensure that benthic processes changed similarly with time at the three main sites and that there was no significant difference between paired subsites within the main sites. During the experimental phase, one subsite (treatment) within each main site was intensively trawled during January, April, and May (the time of year with the highest trawling intensity), with the remaining subsites left undisturbed as controls. Before each trawling effort, all subsites (control and treatment) were sampled (36 cores in total). Trawling took place the following day with each treatment site subjected to six trawl passes. Towed subsites were then resampled within 3 h posttrawling (18 cores in total). Cores were collected carefully from sediments within the visible scars left by the trawl chains. Trawling was undertaken by a timber trawler (10.6 m × 4.2 m), powered by a Gardner 6LX, 195kw engine, with an Otter trawl setup.

The surface (top 5 mm) sediment properties (total organic carbon, and phytopigments), benthic macrofauna (>1 mm sieve), and dark and light (net die) benthic processes (O₂, NH₄⁺, NO₃⁻, and dinitrogen gas [N₂] fluxes) were measured at all sites using previously described techniques (Ferguson et al. 2003, 2004; Ferguson and Eyre 2010, 2013). Briefly, the cores were placed...
uncapped, with self-stirrers, in a 150-L tank of site water at collection temperature, left for a 24-h equilibration period, then capped and incubated over a light–dark diel cycle. Dissolved oxygen concentrations (±0.01 mg l−1) was measured electrochemically, and samples were taken for the analysis of N₂, NH₄⁺, and NOₓ every 3 h. Samples for N₂ : Ar were allowed to flow into gas-tight glass vials were preserved with HgCl and stored submerged at 2°C below ambient temperature until analysis. Samples for nutrient analysis were filtered immediately through 0.45-μm cellulose acetate filters and stored at −20°C until analysis. Because N₂ fluxes were measured, they include both denitrification and anammox. N₂ fluxes reflect the balance between N fixation and denitrification and, as such, are a measure of net denitrification. The terms net N₂ flux and net denitrification are used interchangeably (Eyre et al. 2013). Replicate oxygen microprofiles per core (n = 6) were measured using a Unisense Clark type microelectrode on control (n = 3) and treatment (n = 3) cores during the January sample effort. Zones of oxygen consumption/production were modeled for averaged oxygen microprofiles (control and treatment) using PROFILE (Version 1.0) software (Berg 1998).

**Data analysis**

Each parameter was tested for both chronic and acute impacts of trawling as follows:

1. Chronic effects were investigated by comparing control and pretrawl data from all six sampling times using sequential ANOVAs, as described by Underwood (1993), except that the asymmetry of the design was in the number of sampling times before and after, rather than in the number of control and impacted sites. The factors used were treatment (two levels: control or pretrawl), site (three levels), impact (two levels: before or after), and date nested within impact (four levels “before”: April 2003, July 2003, November 2003, and January 2004; two levels “after”: April and May 2004).

2. Acute effects were investigated by comparing pretrawl and postrawl data in January to May 2004 (once trawling had commenced). These were analyzed using a three-way ANOVA with factors of treatment (two levels: pretrawl or postrawl), site (three levels), and date (January 2004, April 2004, and May 2004). Where there was an interaction between factors, two-way or one-way ANOVAs were used to further investigate the component parts. For example, where there was an interaction between treatment and time, separate one-way ANOVAs were run to investigate the effect of treatment at each time.

For all analyses, normality of data was confirmed using Shapiro–Wilk tests. Levene’s test was used to check for homogeneity of variances. Where Levene’s test returned a significant result (p > 0.05), log-transformed data were used where this improved homogeneity of variances. In interpreting the statistical output, a precautionary approach was adopted (Underwood 1997), aiming to reduce the chance of a Type II error (i.e., incorrectly concluding that there is no impact of trawling). For all tests of chronic or acute trawling effect, results were therefore deemed to be statistically insignificant when p > 0.10. Significant results were either moderately significant (0.05 ≤ p < 0.10), significant (0.001 ≤ p < 0.05), or highly significant (p < 0.001) (Tables S1 and S2).

The data suggested that both denitrification and respiration may be impacted by trawling. To investigate if trawling changed the relationship between these two parameters, net N₂ flux vs. dark DO flux data were fit with separate generalized additive models (GAMs) for nonimpacted samples (control and pretrawl) and impacted samples (posttrawl). These GAMs
were determined using the mgcv package in R and the default REML smoothing (Wood 2011; R Core Team 2019).

**Results**

**Acute effects of trawling**

Trawling caused resuspension of surface sediments to approximately 40 mm depth and homogenization of the sediment surface texture due to removal of burrow structures and resorting of sediment particles (visual observations by divers; Fig. 1). Corresponding with this, there was a reduction in O₂ penetration depth and a simplified depth profile of O₂ (Fig. 2). In addition, the lack of a modeled increase in O₂ at 15–20 mm depth in the trawled sediments, compared to the untrawled sediments, probably reflects the lack of bio-irrigation (Fig. 2). Changes in sediment structure did not affect sediment total organic carbon content, and although mean phaeophytin concentrations were higher posttrawl than pretrawl at all times, this difference was only statistically significant for Site 1 ($p = 0.035$; Table S1). Sediment disturbance through trawling had a moderately significant effect on macrofauna species richness ($p = 0.064$, Table S1), with faunal species richness higher posttrawl across all sites and times. Macrofauna biomass was significantly affected by trawling on two occasions (treatment × time interaction, $p = 0.047$; Table S1), with a significant increase in biomass in January and a decrease in April ($p = 0.013$ and 0.037, respectively; Table S1).

Trawling produced detectable acute effects on all measured sediment-water fluxes except NO$_3$-, but in most cases there was variation in the direction of effect (increase or decrease).
and/or the sites and/or times where an impact was detected (Table S1). Productivity was enhanced following trawling at two of the three sites in January \( (p \leq 0.001; \text{Table S1}) \) and a single site in April \( (p = 0.098; \text{Table S1}) \), but was unaffected in May. Trawling in January also increased \( \text{NH}_4^+ \) fluxes (all sites, \( p = 0.019; \text{Table S1} \)), but \( \text{NH}_4^+ \) fluxes were mainly unaffected thereafter, except for decreases at a single site in April and May \( (p = 0.003 \text{ and } p < 0.001, \text{respectively}) \). Dissolved organic nitrogen (DON) fluxes decreased after trawling in January and May (although the effect was only moderately significant, \( p < 0.1 \)), and were unaffected in April (Table S1).

There was a significant interacting effect of time and treatment on rates of benthic respiration \( (p < 0.001; \text{Table S1}) \). Benthic respiration increased significantly in posttrawl subsites in January and May \( (p < 0.001 \text{ and } p = 0.010, \text{respectively}; \text{Table S1}) \), but decreased in April (moderately significant, \( p = 0.064; \text{Table S1}; \text{Fig. S1} \)). Trawling decreased net \( \text{N}_2 \) fluxes (denitrification) across all times (Fig. 3A), and this effect appeared to increase over successive trawling occasions. Mean net \( \text{N}_2 \) fluxes were \( 11.3\% \pm 2.7\% \) lower in posttrawl compared to pretrawl subsites in January, \( 30.7\% \pm 6.2\% \) lower in April, and \( 49.5\% \pm 4.2\% \) lower in May (Fig. 3B). In support of this, there was a significant time \( \times \) treatment interaction \( (p = 0.033; \text{Table S1}) \), reflecting a nonsignificant decrease in net \( \text{N}_2 \) fluxes on the first trawling occasion and an increasingly significant decrease in net \( \text{N}_2 \) fluxes over the last two trawling occasions \( (p = 0.004 \text{ and } p < 0.001, \text{respectively}) \).

GAM fits through net diel \( \text{N}_2 \) flux vs. dark \( \text{O}_2 \) fluxes (respiration) for control/pretrawl and posttrawl sediments showed two distinct curves. The estimated degree of freedom for control/pretrawl sediments was 3.274 and for the posttrawl sediments was around 1. As such, GAM fits are best approximated by a cubic polynomial function through the control/pretrawl sediments \( (y = -3E-08x^3 + 7E-05x^2 - 0.035x + 22.984) \), and a linear function through the posttrawl sediments \( (y = 0.008x + 9.076) \). The control/pretrawl sediments showed a distinct peak in net \( \text{N}_2 \) fluxes at about 1200 \( \mu \text{mol} \text{O}_2 \text{ m}^{-2} \text{ h}^{-1} \). For a given dark \( \text{O}_2 \) flux rate net \( \text{N}_2 \) fluxes were lower in the posttrawl sediments.

**Chronic effects of trawling**

No statistically significant chronic effect of trawling was detected for any measured parameter at any site or time. Although a significant treatment effect (control vs. pretrawl) was detected for respiration and macrofauna biomass, this interacted with an effect of sampling time nested in before/after trawling (i.e., there was a treatment \( \times \) time [BA] interaction; Table S2). Further investigation revealed that there was only a difference in control and pretrawl samples collected at times before trawling began, that is, there was no trawling effect.

**Discussion**

Denitrification is a critical ecosystem process that removes bioavailable nitrogen from N-limited marine waters, but may be effected by bottom trawling due to sediment structural changes (Peterson et al. 1987; Collie et al. 1997) and infauna species loss (Collie et al. 2000; Kaiser et al. 2006). However, little is known about the effect of bottom trawling on benthic denitrification. Using a BACI design, we showed a significant reduction in denitrification as the result of experimental bottom trawling in a shallow coastal system. Trawl disturbance destroys the complex three-dimensional redox structures in surface sediments that maximize denitrification potential, resulting in up to a 50% reduction in net denitrification. The decrease in net denitrification also increased after each trawling event, suggesting a declining resilience to trawling.

**Trawling removes sediment structure that supports benthic denitrification**

Trawling homogenized the texture of surface sediments due to the removal of burrow structures and resorting of sediment particles (Fig. 1). Similar observations have been made for other trawled coastal sediments (Warnken et al. 2003; Trimmer et al. 2005), suggesting that this mode of disturbance to the physical sediment structure is common. These changes...
to the three-dimensional structure of the surface sediments contributed to changes in sediment–water fluxes of NH$_4^+$, NO$_3^-$, DON and dissolved oxygen (respiration and productivity) that varied with site and sampling time. However, there was a clear, notable impact of trawling on net N$_2$ fluxes (denitrification). Trawling reduced in denitrification rates in the surface sediments. Clearly net denitrification is a very sensitive indicator of disturbance, reflecting its reliance on a complex three-dimensional structure in the sediments.

Net denitrification was broadly driven by the seasonal OM supply, as reflected in the sediment oxygen demand (Fig. 4). In untrawled sediments maximum net denitrification occurs around sediment oxygen demand of approximately 1200 μmol O$_2$ m$^{-2}$ h$^{-1}$ and where there is maximum overlap of aerobic and anaerobic respiration zones (Eyre and Ferguson 2009). Denitrification is enhanced due to anaerobic microniches within the oxic zone, and oxidized burrow structures penetrating into the anaerobic zone, which improves both the organic carbon and nitrate supply to denitrifiers (Eyre and Ferguson 2009). Denitrification is reduced on either side of the optimum zone. At low organic carbon loadings (low sediment oxygen demand), a thick oxic zone with low macrofauna biomass exists, resulting in limited anoxic sites for denitrification, and at high carbon loadings, there is a thick anoxic zone and a resultant lack of oxygen for nitrification and associated NO$_3^-$ production (Eyre and Ferguson 2009; Ferguson and Eyre 2010, 2013). The destruction of the heterogeneous three-dimensional structure of the surface layer of sediments by trawling resulted in a reduction in net denitrification at all sediment oxygen demands (OM loadings) below about 1700 μmol O$_2$ m$^{-2}$ h$^{-1}$ (Fig. 4). In particular, the zone of denitrification enhancement around 1200 μmol O$_2$ m$^{-2}$ h$^{-1}$ was completed removed by trawling. Respiration increased post-trawling in January and May, suggesting that without the complex three-dimensional structure in the trawled sediments it may fuel processes other than denitrification.

Recovery of sediment structure following trawling

The return frequency of experimental trawling disturbance during this study (1–3 months) was insufficient to incur detectable chronic impacts on net denitrification. This suggests that the heterogeneous sediment structure recovered within weeks of disturbance and that processes affecting denitrification are relatively resilient to one-off trawling, which is consistent with reported short-term impacts on macrofauna due to one-off trawl disturbance (Pranovi et al. 2000). It is difficult to estimate realistic trawl intensities for our study site due to the unpredictable nature of fisheries and fishing effort in response to seasonal and interannual variation in prey dynamics. However, based on the inspection of 5 years of trawl effort data supplied by the trawler employed for this study, it is likely that effort is considerably higher in adjacent areas along the trawl exclusion boundary for periods of the year. As such, chronic impacts on benthic denitrification may still occur under higher trawl intensities or from trawling over a longer period (see Hinz et al. 2009). This will particularly be the case if, under higher trawl intensities, there is a long-term negative effect on benthic infauna abundance, biomass and/or diversity, as has previously been reported (Collie et al. 2000; Kaiser et al. 2006; Sköld et al. 2018). Loss of infauna and associated bioturbation and bioirrigation would add to the loss in denitrification efficiency (Pelegri et al. 1994; Webb and Eyre 2004; Ferguson and Eyre 2013).

Although net denitrification returned to control rates following disturbance, the effect of trawling appeared to increase over subsequent trawling events. This may simply be due to seasonal variation, with a greater effect in April than in January, and a greater effect in May than in April or January. However, the apparent increase in effect may also indicate a decline in the resilience of net denitrification to repeated trawling, which may reflect changes in the structure and diversity of sediment communities at microbial or higher levels. It is generally understood that species diversity, including within microbial communities, is important for the resilience of ecological systems and their resistance to perturbation (Bisett et al. 2013); functional redundancy allows ecosystem function to be maintained and/or returned following disturbance, despite changes to community structure (Gunderson 2000). However, the new community may then have reduced functional redundancy and, therefore, reduced resistance to disturbance (Gunderson 2000). This may have occurred in the current study, with repeated trawling adversely impacting sediment fauna and/or microbial communities. This was not supported by changes in macrofauna species richness in the current study, which appeared to increase after trawling (Table S1). However, this increase is at odds with a number of studies that have found a reduction in faunal diversity due to trawling (e.g., Collie et al. 2000; Kaiser et al. 2006) and may reflect the patchiness of fauna communities in the current study that was not captured in the small cores. Regardless of the underlying mechanism, the increasing effect of repeated trawling on net denitrification rates further supports the potential for a chronic effect on net denitrification of trawling at higher intensities or over a longer period. Further work at high trawl intensities, over larger spatial and temporal scales, is required to see if there a chronic effect on benthic denitrification.

Similar impacts in other areas will depend on the sediment type, natural disturbance regime, sensitivity of key macrofauna species responsible for maintaining ecosystem complexity at microbial levels, and trawl intensity (Thrush et al. 1998; Lohrer et al. 2004). Impacts would be most significant in areas where natural physical disturbance due to wind and wave energy is sufficiently low to allow biological processes to influence sediment structure (Dupilsea et al. 2001). Our study site was situated in shallow water (~4 m; the effective upper depth limit to benthic trawling) subject to relatively high wind and wave energy. The impacts described here therefore apply to a relatively high energy environment; the impacts would probably be greater in...
low energy environments, such as deeper regions and the upper continental shelf into which trawling is expanding (Gordon et al. 2003). As such, our results would apply to most of the trawled soft sediments globally.

**Potential effect of trawling on regional and global nitrogen cycles**

The reduction in denitrification by 11–50% (Fig. 3B) due to the trawl-induced disturbance in the top 40 mm of coastal soft sediments highlights the need to maintain ecosystem complexity at microbial levels. For example, if we assume 50% of Moreton Bay is trawled, an 11–50% loss of denitrification would result in the retention of approximately 1205–5477 t of extra nitrogen within the bay. The upper range is of similar magnitude to the total atmospheric, catchment, and wastewater nitrogen load delivered to the bay (6848 t; Wulff et al. 2011). Our results validate the maintenance of trawl exclusion zones along the western fringe of the bay. These areas are the most exposed to river and groundwater nitrogen loads (Santos and Eyre 2011) from the catchment and maintain some of the highest denitrification rates within the system, which is the most important nitrogen removal pathway in Moreton Bay (Eyre and McKee 2002; Eyre et al. 2011; Wulff et al. 2011) and many other coastal ecosystems (Seitzinger et al. 2006; Eyre et al. 2016).

More importantly, benthic trawling affects a significant proportion of coastal sediments worldwide (Thrush and Dayton 2002). There is clearly a high uncertainty associated with scaling a single study, at a single site, to the whole earth, but it is still a useful exercise to highlight the potential for trawling to affect the global nitrogen cycle. Estimates of how much of the seafloor is trawled per year range from older estimates of 15 million km² (Malakoff 1998) to more recent estimates of 34 million km² (Kroodsma et al. 2018). If we assume much of this trawling occurs on the continental shelf, this equals 47% to over 100% of the total shelf area of 32 million km² (Harris et al. 2014). The shelf removes around 250 Tg of nitrogen via denitrification annually, which is 44% of the global total (Seitzinger et al. 2006). If we use a conservative estimate that 50% of the shelf is trawled annually, an 11–50% loss of denitrification results in an extra 14–63 Tg of nitrogen being retained on the shelf per year. The upper range is greater than the total annual global river load of dissolved inorganic nitrogen (23 Tg; Sharples et al. 2017), and similar to the total nitrogen load (66 Tg; Vilmin et al. 2018), delivered to the shelf. The retention of more bioavailable N in coastal ecosystems due to reduced denitrification associated with bottom trawling has implications for the global ocean nitrogen cycle and associated eutrophication.

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