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Seafloor ecological functioning over two decades of organic enrichment

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ABSTRACT

Climate change and anthropogenic nutrient enrichment are driving rapid increases in ocean deoxygenation. These changes cause biodiversity loss and have severe consequences for marine ecosystem functioning and in turn the delivery of ecosystem services upon which humanity depends (e.g. fisheries). We seek to understand how such changes will impact seafloor functioning using biological traits analysis. Results from a sewage-sludge disposal site in the Firth of Clyde, UK spanning 26 years of monitoring showed that substantial changes in macrobenthic nutrient cycling and the provision of food for predators occurred, with elevated functioning on the margins 1–2 km from the centre of the disposal grounds. Thus, changes in food-web dynamics are expected, that weaken benthic pelagic coupling and lower secondary production (such as fisheries). Generally, functioning was conserved, but declined below a ~6% total organic carbon threshold. Similar to other severely deoxygenated systems, the recovery was slow and hysteresis was apparent.

1. Introduction

One of the consequences of climatic warming is a decrease in the amount of dissolved oxygen in seawater due to reduced gas solubility, temperature stratification inhibiting vertical mixing, and changes in the delivery of nutrients to the sea. To date most studies of the ecological impacts of climate change have focussed on changes in temperature and the impacts of other significant drivers of ecological change, e.g. ocean deoxygenation and acidification, are less well-known. Ocean deoxygenation, e.g. hypoxia (dissolved oxygen content 1–30% of saturation) or anoxia (no oxygen), is one of the greatest threats to marine ecosystem health and functioning (United Nations, 1992). Over the last 50 years ocean oxygen content has decreased by a mean rate of 0.06–0.43% per year (Stramma et al., 2010) and models predict a continued decline of > 7% from present-day levels until 2100 under high CO_2 emissions scenarios (IPCC, 2013). The number of coastal hypoxic zones have also been increasing over the past 50 years and are now documented from > 500 systems (Diaz and Rosenberg, 2008) covering ~7% of ocean area. The impacts on ecosystems are complex, being associated with non-linear interactions, thresholds and hysteresis (Cardinale et al., 2012; Stachowicz et al., 2007) and take time to manifest. Thus, we need to study change over timescales that exceed decades. Synergism between ocean deoxygenation and other anthropogenic stressors, e.g. global temperature rise, ocean acidification, marine pollution and fisheries, also make it more challenging to predict and manage the impacts of deoxygenation for ecosystem health (Altieri and Gedan, 2015; Breitburg et al., 2009; Gray and Elliott, 2009).

Hypoxia has profound effects on marine organisms and often results in mass mortalities of animals that dwell on the seafloor and in the water column due to low dissolved oxygen, or indirectly due to toxic H_2S (Breitburg et al., 2009; Caddy, 2000; Falkowski et al., 1980). Significant changes may occur in terms of: organism behaviour (Gray et al., 2002; Riedel et al., 2014; Seitz et al., 2003), growth rates and body size (Caswell and Coe, 2013; Cheung et al., 2013), organism health (Keppel et al., 2015), the impairment of reproductive processes, and the contraction of the available habitat for spawning (Ekau et al., 2009; Nissling and Westin, 1997). These changes have led to 3–5-fold declines in benthic macrofaunal biomass (Hale et al., 2016; Seitz et al., 2009), and declines in secondary productivity of ~10% (Karlson et al., 2002; Sturdivant et al., 2014).

Long-term studies of the ecological impacts of ocean deoxygenation are lacking, but short-term studies (e.g. Breitburg et al., 2018; Cheung et al., 2013; Dauer et al., 1992; Gray et al., 2002; Levin et al., 2009a; Pearson and Rosenberg, 1978) indicate that the consequences of long-term deoxygenation will include decreasing biodiversity and production, changing trophic structure, decreasing size, health, fitness and reproductive capacity of organisms, and the loss of key habitats. This loss of productivity and biodiversity, and changes in the biological

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traits of taxa can profoundly constrain the ways that ecosystems function, and in coastal seas many functions are provided or mediated by benthic communities. For example, by providing food for higher trophic levels (Breitburg et al., 2009; Greenstreet et al., 1997) or stimulating decomposition and nutrient cycling which in turn drives water column primary productivity (Aller and Aller, 1998).

These ecological functions support a number of core regulating and supporting ecosystem services (e.g. nutrient cycling, waste treatment, biodiversity, biological control and habitat provision) which are threatened by deoxygenation, and approximately US$350 billion of services are lost each year to hypoxia (Diaz et al., 2012). This is in addition to other socio-economically important services such as the provision of food and recreational experiences (e.g. Carstensen et al., 2014; Hale et al., 2016). The recovery from short-term severe hypoxia can take years, but for long-term severe hypoxia recovery is hysteretic, associated with thresholds and can exceed decades (Diaz and Rosenberg, 2008). Once a system has exceeded the threshold, and turned hypoxic, it may become increasingly susceptible to repeated hypoxia (Conley et al., 2009). The increasing adoption of an 'ecosystem services' approach, following the Millennium Ecosystem Assessment (United Nations, 2005) and the increasing availability of tools for mapping ecological functioning to services (Bremner, 2008; Bremner et al., 2003, 2006; Frid et al., 2008) is shifting the basis of environmental management. There is now an explicit recognition of the underpinning of human well-being and economic activity by healthy functioning ecosystems (United Nations, 2005). It is now possible to reinterpret data on the impacts of sewage sludge disposal on sea floor communities and to assess the extent to which the changes in the taxonomic composition of the impacted communities can be used to determine past changes in ecological functioning and hence the delivery of ecosystem services. Investigation of changes in the composition and ecological functioning of natural benthic systems have shown that over decadal scales changes in the faunal composition do not result in shifts in ecosystem functioning, but rather that functioning is conserved (Clare et al., 2015; Frid, 2011). Over millennial time scales benthic functioning is also conserved through species turnover, but in periods of rapid and severe environmental change, profound shifts in species composition mean functioning is compromised (Caswell and Frid, 2013; Frid and Caswell, 2015).

In 1986 Pearson and Rosenberg developed a conceptual model of the ecological structure and functioning of benthic systems, which placed the availability of food, in the form of organic matter, at its heart. This model was partially developed from the observed impacts of organic pollution on marine benthic communities, in terms of their species richness, abundance and biomass (Pearson and Rosenberg, 1978), and has since been validated in many coastal systems (Diaz and Rosenberg, 1995; Gray et al., 2002). The core concepts of these ideas have underpinned marine benthic ecology since the 1970s and may also function as a generalised model of disturbance (e.g. Connell and Slatyer, 1977). In this paper we revisit one of the classic benthic macrofaunal data sets from which the Pearson and Rosenberg model was derived, the Garroch Head sewage sludge disposal site and ask the questions (i) to what extent do the benthic macrofaunal changes caused by enrichment and deoxygenation drive functional changes, (ii) did the changes in functioning correspond to the change in taxonomic composition, (iii) what was the nature of the recovery, and (iii) what are the consequences of functional changes for the delivery of ecosystem services derived from the benthos?

From 1979 to 1998 Garroch Head in the Firth of Clyde was used as a disposal site for sewage sludge (the solid components of sewage). The site received on average $1.67 \pm 0.06 \times 10^{6}\,\mathrm{t\,year^{-1}}$ sludge from primary treatment plants in the Strathclyde region, surrounding the city of Glasgow, Scotland and was deposited on the seafloor for five days each week throughout the year. The sludge contained organic material with elevated heavy metals and organochlorine compounds (e.g. Pearson and Blackstock, 1987), and at this time its disposal at sea was considered an acceptable disposal option because the large dilution reduced chemical contamination and natural processes reduced the biological oxygen demand of the wastes (Frid and Caswell, 2017). Sewage sludge was disposed offshore from a series of sites around the UK and was regulated under the Dumping at Sea Act (1974) and the Food and Environmental Protection Act (1985), which was accompanied by regular sampling at these sites to monitor the environmental impacts. By 1998 the sludge disposal ceased with the adoption of the EU Urban Waste Water Directive (European Economic Community, 1991). Using benthic macrofaunal data from eight sampling stations situated in 3 km radius from the Garroch Head sewage sludge disposal site (plus one reference station at 8.5 km) this study aims to quantify changes in the biological characteristics or 'traits' of macrobenthos along a gradient of organic enrichment and deoxygenation over 26 years. The biological traits of organisms have considerable impacts on the magnitude of ecosystem functioning (Cardinale et al., 2012; Crowe and Frid, 2015), and we anticipate that the considerable ecological changes that occur in enriched and deoxygenated systems will profoundly affect ecosystem functioning and in turn the delivery of ecosystem services. The Garroch Head data are of very high quality, despite some changes in sampling procedures, and are used to explore changes in the ecological functioning of the benthos through time. The wide spatial extent of the Garroch Head sampling programme meant that differing levels of anthropogenic organic enrichment and hypoxia could be explored over the 19 years of sewage sludge disposal and the seven years post-disposal (Pearson and Stanley, 1980; SEAS, 1999). These data represent a unique opportunity to investigate the decade long ecological impacts of varying levels of organic enrichment and hypoxia on benthic ecosystem functioning.

2. Materials and methods

2.1. The Garroch Head dataset

Environmental monitoring at Garroch Head was conducted by the Scottish Association for Marine Sciences (SAMS) and the Scottish Environmental Advisory Services Ltd. (SEAS), on behalf of the Department of Agriculture and Fisheries for Scotland, which began in 1979 and sampling occurred every year until disposal ceased in 1998 (Coates and Pearson, 1997, 1999; Pearson, 1981, 1983, 1991, 1992, 1993, 1994; Pearson and Blackstock, 1982, 1983, 1985, 1986, 1987, 1988, 1989; Pearson et al., 1990; Pearson and Coates, 1995, 1998; Pearson et al., 1992; Pearson and Stanley, 1980; SEAS, 1999) when the disposal of sewage sludge at sea was banned. Monitoring at Garroch Head incorporated biological sampling of sediment microbes, benthic macrofauna and demersal fish assemblages plus a suite of environmental variables and the concentrations of notable pollutants (Supplementary Table S1). In 2000, 2004 and 2005 follow up environmental surveys were conducted by the Scottish Environmental Protection Agency (SEPA) and SAMS in order to assess the recovery of the site after sewage sludge disposal had ceased (Duncan, 2005; Scottish Environment Protection Agency, 2000; Scottish Environmental Protection Agency, 2004).

The centre of the disposal site was located 6 km south of Garroch Head on the Isle of Bute (station P7, Fig. 1), Firth of Clyde, Scotland. This site replaced an earlier sewage sludge disposal site located 4 km to the north that received Strathclyde's sewage from 1904 to 1974. This site was found to be an accumulating site with low current speeds < $10\,\mathrm{cm\,s^{-1}}$ and so in 1974 was relocated 2 km further south (Fig. 1; Dooley, 1979; Midgley et al., 2001).

Samples were collected from 40 different sampling stations throughout the 26 years, and of these eight stations were sampled near annually for biotic and abiotic factors. These eight stations plus the reference station, 8.5 km to the north, were used in this study to achieve the maximum temporal duration and the full spectrum of organic enrichment (Fig. 1). The number of sampling points totalled 184 over the