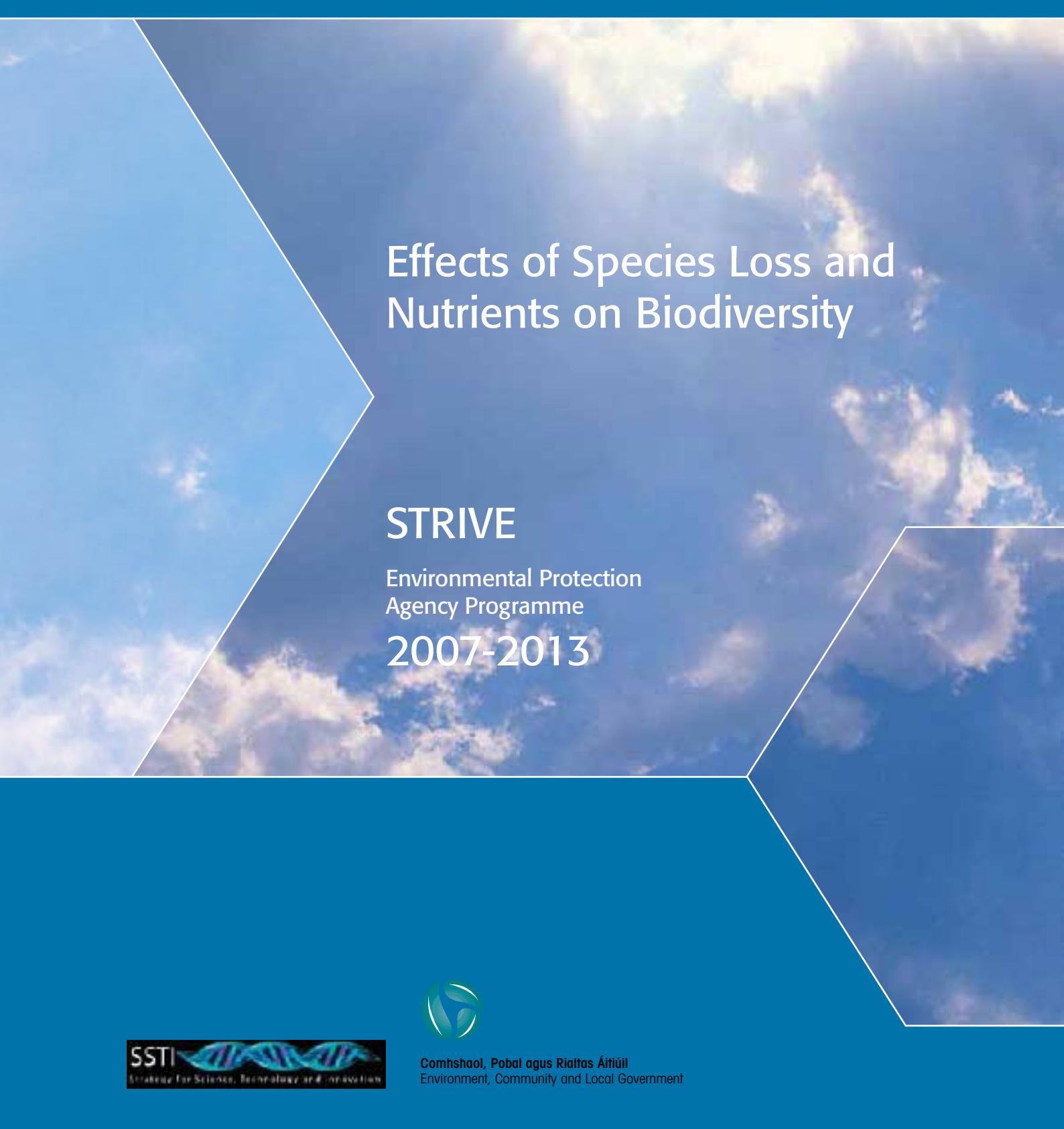


STRIVE

Report Series No.87



Effects of Species Loss and
Nutrients on Biodiversity

STRIVE
Environmental Protection
Agency Programme
2007-2013

Environmental Protection Agency

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EPA STRIVE Programme 2007–2013

Effects of Species Loss and Nutrients on Biodiversity

Anthropogenic Impacts on Marine Biodiversity: Effects of Enhanced Nutrients and Species Loss on the Biodiversity and Ecosystem Functioning of Rocky Shores

(2007-FS-B-8-M5)

STRIVE Report

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Prepared for the Environmental Protection Agency

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Executive Summary

The focus of this study was to disentangle the effects of multiple stressors on biodiversity, ecosystem functioning and stability. This project examined the effects of anthropogenic increased nutrient loads on the diversity of coastal ecosystems and the effects of loss of species on ecosystem functioning. Specifically, the direct effect of sewage outfalls on benthic communities was assessed using a fully replicated survey that incorporated spatial and temporal variation. In addition, two field experiments examined the effects of loss of species at multiple trophic levels, and tested for potential interactive effects with enhanced nutrient concentration conditions on benthic assemblage structure and ecosystem functioning. This research addressed priority issues outlined in the *Biodiversity Knowledge Programme for Ireland* (2006) and also aimed to deliver information relevant to European Union (EU) directives (the Water Framework Directive [WFD], the Habitats Directive and the Marine Strategy Framework Directive).

A sampling strategy was designed to test for the effects of sewage outfalls on rocky shores and to identify the scale of the putative impact. Benthic assemblages were compared by measuring 20 (25 x 25 cm) replicate samples from three shores with sewage outfalls, at sites proximal to the outfall (<10 m), at sites adjacent to the outfall (30–50 m) and on rocky shores without sewage outfalls (>2,000 m). All sites were moderately exposed rocky shores in north Co. Dublin and each site was sampled four times (approximately every three months). A separate sampling strategy based on the Reduced algal Species List (RSL), which is the current WFD monitoring tool for rocky shores, was also completed at each shore during the summer months, by identifying algae and measuring percent cover in 30 (50 x 50 cm) replicate samples at each shore. The findings show that while there was no effect of sewage outfalls on benthic taxon diversity or assemblage structure, the variability of assemblages was greater at sites proximal or adjacent to sewage outfalls compared to those shores without sewage outfalls. Results based

on the RSL show that algal assemblages were not affected by the presence of sewage outfalls, except when algal taxa were classed into functional groups, which showed greater variability at the sites without sewage present. A key finding of both surveys was the prevalence of spatial and temporal variation of assemblages. It is recommended that future metrics of ecological status are based on quantified sampling designs, that they incorporate changes in the variability of assemblages (indicative of community stability), that they consider shifts in assemblage structure and that they include benthic fauna and flora to assess the status of rocky shores.

A field experiment, at ambient and enhanced nutrient concentration conditions, tested for effects of loss of species (richness and identity) of grazing gastropods on primary productivity and algal assemblage structure and biomass, using a series of purpose-built experimental rock pools at Carnsore Point, Co. Wexford. Another field experiment carried out at ambient and enhanced nutrient concentration conditions tested for effects of loss of species from multiple trophic levels on algal assemblage structure and biomass, at a moderately exposed rocky reef at Rush, Co. Dublin. Both experiments ran for over 12 months and required regular maintenance. The first experiment showed that the effects of loss of species depended on the identity of the species removed and varied with nutrient concentration. In terms of total algal biomass accumulation, the effects of loss of species were negated at enhanced nutrient concentration; however, algal assemblages differed with nutrient status. The second experiment showed that the direct and indirect effects of predators and primary consumers on algae are also affected by nutrient concentration. These findings illustrate the complexity of species interactions within ecosystems and show that it is not always possible to predict the effects of loss of species from general models.

This study identified specific interactions between the effects of species loss and environmental conditions in a marine benthic system, and highlights the

importance of context-dependency. More empirical evidence is required to improve current ecological models that aim to predict the effects of loss of species on ecosystem functioning under different environmental conditions. Future studies should:

- (i) incorporate predicted environmental changes, such as sea temperature increases and ocean acidification;
- (ii) measure multiple ecosystem functions, such as nutrient cycling, decomposition rates, carbon fluxes etc.; and
- (iii) address ecosystem stability.

1 Introduction

1.1 Background

While humans depend on marine ecosystems for many valuable goods and services, we also alter these ecosystems by direct and indirect means (Millennium Ecosystem Assessment 2005). Offshore activities such as fishing and land-based activities affect the run-off of pollutants and nutrients into coastal waters and remove, alter or destroy natural habitat and change species compositions (Jackson et al. 2001; Myers and Worm 2003; Pauly et al. 2005). Coastal systems, such as rocky shores, are among the most heavily anthropogenic-impacted marine ecosystems (Halpern et al. 2007; Halpern et al. 2008b) and are also among the most productive in terms of ecosystem functioning (Odum 1983) and the services they provide, such as nutrient cycling, waste treatment, disturbance regulation, food production and recreational importance (Costanza et al. 1997). Rocky shores are, therefore, highly suitable model systems for biodiversity-ecosystem functioning (BEF) research.

As recently as 2005, it was declared that the data available from marine systems was too sparse to be included in a general synthesis of BEF relationships (Hooper et al. 2005). Since then, studies in marine systems have proliferated and priority areas for urgent research have been identified (Stachowicz et al. 2007). These include the development of a multi-trophic perspective based on more realistic experiments, designed over longer periods, against a background of natural temporal and spatial heterogeneity and the examination of the importance of biodiversity relative to other factors (e.g. consumer diversity versus nutrient resources) maintaining ecosystem services (Cardinale et al. 2006; Stachowicz et al. 2007; Gamfeldt and Hillebrand 2008). The extension of BEF research into a multi-trophic context is an emerging new field that promises to reveal how predator diversity influences ecosystems and the services they provide to humanity (Bruno and Cardinale 2008).

Evidence from experimental studies shows that ecosystem functioning can often be sustained by only a few species and that the effects of diversity may

interact with or be much weaker than other controlling factors such as disturbance, flow conditions and nutrient availability (Cardinale et al. 2000; Emmerson et al. 2001; Biles et al. 2003; Dzialowski and Smith 2008). More empirical research is required to evaluate specific mechanisms that drive ecosystem functioning, in particular, by removing one or a few targeted species (e.g. O'Connor and Crowe 2005; O'Connor et al. 2008), under different environmental conditions (Cardinale et al. 2006; Stachowicz et al. 2007; Gamfeldt and Hillebrand 2008).

The majority of BEF studies to date have been conducted in mesocosms (Crowe et al. *in press*): however, mesocosm experiments detect only a subset of possible mechanisms that operate in the field over longer time frames (Stachowicz et al. 2008a; Stachowicz et al. 2008b). Mesocosm experiments lack sufficient heterogeneity to allow the expression of niche differences and they are of insufficient duration to capture population-level responses, such as recruitment (Stachowicz et al. 2008a). Long-term field experiments are necessary to allow for the manifestation of a greater number of potential mechanisms of over-yielding in diverse communities, and thus increase the likelihood of observing a strong diversity effect (Stachowicz et al. 2008b).

The interactive effects of the changing diversity of consumer species are poorly understood but are expected to be highly important under realistic scenarios of biodiversity loss (Bruno et al. 2008; Bracken et al. 2008). Understanding real-world consequences of declining biodiversity requires addressing changes in species performance along natural diversity gradients and understanding the relationships between species' susceptibility to loss and their contributions to ecosystem functioning (Bracken et al. 2008). The next steps in predator biodiversity research are to increase experimental realism and incorporate current knowledge about the functional roles of predator richness into ecosystem management (Bruno and Cardinale 2008).

The effects of multiple anthropogenic stresses on the diversity of natural communities and how this relates

to ecosystem functioning and services is understood poorly (Crain et al. 2008). In Ireland, the economic and social benefits of biodiversity are conservatively estimated to be at least €2.6 billion per annum (The Economics of Ecosystems and Biodiversity [TEEB] 2008). However, this figure does not include significant services such as waste assimilation by aquatic biodiversity (Bullock et al. 2008). This project addresses several of the knowledge gaps identified by Ireland's National Platform for Biodiversity Research (NPBR) – for example, by providing baseline marine biodiversity data and examining how human impacts affect BEF relationships (NPBR 2006).

This study incorporated two approaches. First, to identify the potential effects of known activities on the diversity of communities requires appropriate sampling of 'impacted' and 'non-impacted' communities. In this report, the term impact is limited to describe negative effects and not used when the nature of putative effects are unknown. It is important that such studies are carefully designed, well replicated and carried out at the appropriate scale (Glasby and Underwood 1998; Bishop et al. 2002; Terlizzi et al. 2005a; Benedetti-Cecchi and Osio 2007). Second, to understand how diversity may affect ecosystem functioning and identify the causative mechanisms requires experimental manipulation (Crowe et al. 2000). Much work has been done examining BEF relationships (Hooper et al. 2005; Stachowicz et al. 2007), more recently including the effects of loss of diversity at multiple trophic levels (e.g. O'Connor and Bruno 2007; O'Connor et al. 2008; O'Connor et al. in review). This study took the next step

and examined the effects of loss of consumer diversity under different environmental conditions in response to a disturbance (eutrophication).

1.2 Project Objectives

This project aimed to disentangle multiple anthropogenic impacts on benthic marine biodiversity and ecosystem functioning. In particular, it set out to investigate (i) the effects of loss of species; (ii) effects of enhanced nutrients; and (iii) interactive effects between species loss and nutrient concentration, on the diversity and ecosystem functioning of rocky shores. Using an extensive sampling strategy and experimental manipulations, the project objectives were to:

- Test for the effects of sewage outfalls on the diversity of rocky shores, including identifying the scale of putative effects;
- Test and develop current tools for assessing the ecological status of rocky shores in line with the WFD;
- Test experimentally for the effects of loss of consumer species richness and identity on the diversity and functioning of rock pool assemblages and manipulate nutrient concentration to test if such effects interact with environmental conditions;
- Test experimentally for direct and indirect effects of the loss of benthic species from multiple trophic levels on algal assemblages and manipulate nutrient concentration to further test the context dependency of results.

2 Biodiversity of Rocky Shores: Assessing the Effect of Sewage Outfalls on Benthic Communities

2.1 Background

Globally, one of the key drivers of change in aquatic ecosystems is nutrient loading from pollution which leads to eutrophication of coastal waters (Millennium Ecosystem Assessment 2005). One of the main causes of eutrophication to coastal waters is discharge of sewage (Costanzo et al. 2001). Sewage outfalls may alter the temperature, salinity, nutrient and heavy metal concentration of the surrounding water column. This can reduce the diversity of intertidal species and lead to a dominance of a few algal species or increase the temporal and spatial variation of many species (Fairweather 1990; Gappa et al. 1990; Warwick and Clarke 1993). These effects are not, however, universal (e.g. Chapman et al. 1995). Sewage effluent discharged from municipal outfalls has been shown to directly alter patterns of benthic species composition and abundance at various spatial and temporal scales (e.g. Terlizzi et al. 2002; Guidetti et al. 2003; Terlizzi et al. 2005a). Other studies, however, show that sewage outfalls did not affect species richness of rocky shores and that recovery following decommissioning of an outfall was dependent on other activities, such as algal harvesting (Archambault et al. 2001). Moreover, the effects of sewage outfalls on rocky shore communities can be localised and unless scale is incorporated into an appropriate sampling design they may not be detected (Archambault et al. 2001; Bishop et al. 2002). The detection of the effects of sewage outfalls on natural ecosystems, therefore, depends on the development of reliable procedures that can distinguish between natural and human-induced changes (Roberts et al. 1998; Terlizzi et al. 2005a). A structured approach is essential to test for putative effects and it is accepted widely that a quantified sampling design is necessary to ensure that estimates of populations are 'representative' (true of assemblages), 'reliable' (avoiding biases), 'repeatable' (can be reproduced by other workers) and 'robust' (collected in a way that meets subsequent statistical test assumptions) (Underwood 1997).

Along with the Habitats (Council of the European Communities [CEC] 1992) and Birds Directives (CEC 1979), the Water Framework Directive (WFD) (EC 2000) is the primary legislative force that underpins the protection and management of aquatic ecosystems within the European Union (EU). The objective of the WFD is to retain 'high status' where it exists, attain at least 'good' status in all water bodies and to ensure no further deterioration by 2015. Reaching this target requires integrated management and planning based on River Basin Districts (RBDs). Ireland's Water Framework Monitoring Programme includes a series of metrics developed for the monitoring and classification of coastal and transitional waters based on macrophytes, macroalgal and angiosperm communities (Environmental Protection Agency [EPA] 2006). The Marine Ecological Tools for Reference and Classification (METRIC) project was part of the Inter-calibration Exercise of Biological Quality Elements (BQEs) aimed at harmonising ecological quality criteria for the assessment of transitional and coastal waters of Europe (Cusack et al. 2008). Under the WFD, there is a requirement to set class boundaries for the ecological quality ratios (EQRs) of all BQEs (Cusack et al. 2008). The EQR is the numerical mechanism for reporting on the quality of waters and is defined as the relationship between the reference value and the observed value after an assessment. Marine task teams have developed a number of water quality assessment tools for each BQE: however, only the macroalgal Reduced Species List (RSL) is used for monitoring rocky shores in Ireland (Orfanidis et al. 2001; Wells et al. 2007; Wilkinson et al. 2007).

The RSL was developed originally to test the ecological status of Mediterranean rocky shores and is based on the premise that macroalgae are sensitive indicators of changes in aquatic environments (Orfanidis et al. 2001). This metric is based on the model that under increasing levels of eutrophication late successional perennial algae, such as *Cystoseira spp.*, *Fucus spp.*, are replaced by opportunistic species, such as

Ulva spp. (Fletcher 1996; Nienhuis 1996; Schramm and Nienhuis 1996; Arevalo et al. 2007). The metric further classifies algal taxa based on their functional groups to indicate shifts from a pristine ecosystem state with late successional species ('Ecological Status Group I') to a degraded state with opportunistic species ('Ecological Status Group II'). Ideally, under the WFD a list of sensitive algal species indicative of pristine shores should be compiled; however, there are several difficulties with this. First, there is no accepted list of sensitive algal species and those that may be sensitive at one location may not be so at another. In addition, rocky shores are dynamic systems and natural successions can result in very large abundances of several dominant species – for example, shores may shift from fucoid algal dominance to barnacle dominance without any change in 'ecological quality'. It has been argued that it is the algal *numerical species richness* – not the identity of the actual species present – that is broadly constant in the absence of disturbance, and it was proposed that species richness, on a defined length of shore, be used as a criterion of ecological quality (Wells et al. 2007). In general, a shore description (based on the number of suitable habitats available for algae, wave exposure and natural turbidity) is recorded and the total algal species richness is recorded as the number of taxa present on a reduced species checklist (approx. 90 taxa). From these data the ratio of early to late successional species is calculated, and the proportion of red and green algae compared with the total and the proportion of opportunistic algae compared with the total number of algae. Based on these metrics EQRs are calculated for rocky shores (Cusack et al. 2008).

Although water quality in the majority of Irish coastal waters is high, some areas are seriously affected by direct municipal discharges and elevated nutrient inputs, and one of the main shortcomings in managing Irish coastal biodiversity is a lack of baseline data (EPA 2008). The primary aim of this study was to test for effects of sewage outfalls on the diversity of benthic assemblages. This study also aimed to identify the scale of the effect of municipal sewage outfalls on benthic assemblages and tested the sensitivity of current WFD monitoring tools to sewage-affected rocky shores. These results also provide baseline data that contribute to the description of the diversity of benthic communities on Irish rocky shores.

2.2 Methodology

To test for the effects of municipal sewage outfalls on the diversity of rocky shores and to identify the scale of a putative impact, benthic assemblages were sampled (i) proximate to an outfall (<10 m from outfall), (ii) adjacent to an outfall (30–50 m from outfall) and (iii) at 'control' locations (>2 km from outfall). Following consultation with Fingal County Council and extensive field inspections, six locations in north Co. Dublin were selected for this study ([Fig. 2.1](#)). Rocky shore assemblages were sampled proximate and adjacent to sewage outfalls at Rush, Loughshinney and Portrane and at control shores at Bremore (north of Balbriggan), Barnageeragh (Skerries) and Portmarnock.

International protocols for sampling biodiversity in coastal communities (e.g. NaGISA 2007) were incorporated into this sampling design. To test for the effects of the presence of sewage outfalls (and for the scale of the effect) and spatial variation on benthic communities of rocky shores, each of the nine selected sites was assessed four times (approximately every three months for a year) to incorporate potential effects of temporal variation. The aim of this 12-month study was not to assess long-term trends in natural variation but to include potential variation owing to seasonality implicitly within the design. Sampling was carried out in March 2009, August 2009, November 2009 and February 2010. It is important to note that temporal variability was incorporated but there was no replication for seasonal effects: therefore, the term 'time' not 'season' is used to interpret the findings. On each sampling occasion, double-strung quadrats of 25 x 25 cm area were used to estimate the percentage cover of sessile species (e.g. algae, mussels, barnacles) and the abundance of individuals of species such as gastropods. Double-strung grid quadrats were used to estimate the percentage cover of sessile species (Foster et al. 1991), and species that were observed within the quadrat but did not match any intersection point were assigned a value of 1%. Quadrats were placed randomly within the low-mid shore on a relatively flat substrate and avoided rock pools and deep crevices. There were three factors in a balanced nested design: (i) distance from outfall (fixed, three levels), (ii) location (random, nested in [i], three levels), (iii) time (random, four levels) with 20 replicate samples for each treatment, yielding a total of 720 sampling units (quadrats).



Figure 2.1. Map showing sampling locations: Bremore, Barnageeragh and Portmarnock (open icons = no sewage outfall) and Loughshinney, Rush and Portrane (closed icons = sewage outfall).

To test if the presence of sewage affects the structure or diversity of algal assemblages on rocky shores using a quantified sampling design based on the RSL, each of the three shores with sewage outfalls and the three shores without sewage outfalls were also sampled again during summer months (2009) using a double-strung quadrat (50 x 50 cm) placed randomly on the shores. Quadrats were thrown randomly among high-, mid- and low-shore and included rock pools, crevices, and emergent rock. All algae were identified and the percentage cover of each was estimated. The two factors in these analyses were: (i) sewage outfall (fixed, two levels); and (ii) location (random, nested in [i]), with 30 replicate samples for each treatment, yielding 180 algal assemblage samples (quadrats). The EQRs were also calculated for each shore based on species richness, proportion of red algae, ecological status groups (ESG) ratio, proportion of green algae, proportion of 'opportunist' algae and shore description.

Non-metric multi-dimensional scaling (MDS) was used to produce two-dimensional ordinations to compare assemblages among different distances to an outfall, location and time (Field et al. 1982; Clarke 1993). MDS plots allow for the visualisation of each replicate assemblage in terms of its relative similarity, based on taxon composition and assemblage structure, estimated in multi-dimensional space. Permutational analysis of variance (PERMANOVA) was used to test for differences among benthic communities and algal assemblages, with pairwise post hoc tests among levels of significant terms, based on Bray-Curtis similarity matrices with 9999 permutations. Distance-based tests for homogeneity of multivariate dispersions (PERMDISP) were used to test for differences in taxon dispersion among assemblages based on similar Bray Curtis similarity matrices. To assess the influence of the less dominant taxa, analyses were performed on untransformed data and transformed data with varying degrees of transformation severity (square root, fourth

root, $\log[x+1]$, presence/absence) (Clarke and Warwick 2001a). To test for general effects of functional diversity, all taxa were also classed into functional groups (e.g. all barnacle species were grouped together and algal taxa were classed into their functional groups based on morphology (Steneck and Dethier 1994)) and re-analysed. Analysis (SIMPER) technique was used to identify which species (taxa or functional group) were important in identifying significant differences in assemblages. Taxon richness (S), Shannon diversity (H' (\log_e)) and Pielou's evenness (J') indices were also calculated and compared with analysis of variance (ANOVA).

2.3 Results

2.3.1 Effects of sewage outfalls on benthic communities incorporating tests for spatial scale and temporal variation

In total, 43 taxa (benthic invertebrates and algae) were identified. The presence of a sewage outfall had no effect on species richness, S , ($F_{2,711} = 3.9$, $P > 0.70$) but did vary among locations ($F_{6,711} = 11.83$, $P < 0.01$). Taxon richness was greater at the site proximate to an outfall at Loughshinney and at Portmarnock (no outfall) than at all other sites. Taxon diversity (H' (\log_e)) was not affected by the presence of a sewage outfall ($F_{2,711} = 3.9$, $P > 0.70$) but did vary among locations ($F_{6,711} = 6.94$, $P < 0.01$). Portmarnock had greater diversity than all other sites. Neither the presence of sewage ($F_{2,711} = 0.78$, $P > 0.50$) nor location ($F_{6,711} = 1.56$, $P > 0.16$) affected taxon evenness (J').

Proximity to a sewage outfall, location and sampling period all appeared to affect the assemblage structure of benthic communities in some way but these effects were not consistent (Fig. 2.2). Significant interactions between distance from the outfall and time, and between location and time suggest that benthic assemblages differed depending on the distance from the outfall during certain sampling periods and also varied among locations and certain times (Table 2.1). Pairwise tests could not identify an effect of distance from an outfall on assemblage structure (Appendix 1), suggesting that the effect of sewage outfalls was minimal. Contrastingly, assemblages differed considerably among locations and with time (Appendix 2). Although these were random factors in the current analyses, it is interesting to note that all locations differed from each other at each sampling period except once (winter) when two of the locations without sewage outfalls (Barnageeragh and Portmarnock) had similar assemblages ($t = 1.18$, $P > 0.22$). The effect of sampling time differed at different locations – at Rush close to an outfall, assemblages differed on each sampling time whereas at Loughshinney close to an outfall, assemblages were similar on all but one sampling time (summer) (Appendix 3). These effects were consistent under all but the most severe transformation. Analyses on presence/absence data showed that assemblages differed interactively among location and time ($F_{18,684} = 5.8$, $P < 0.01$) but distance from a sewage outfall was not significant ($F_{2,684} = 0.9$, $P > 0.6$), indicating that differences in assemblages are not just driven by a few dominant species but reflect a difference in overall assemblage structure.

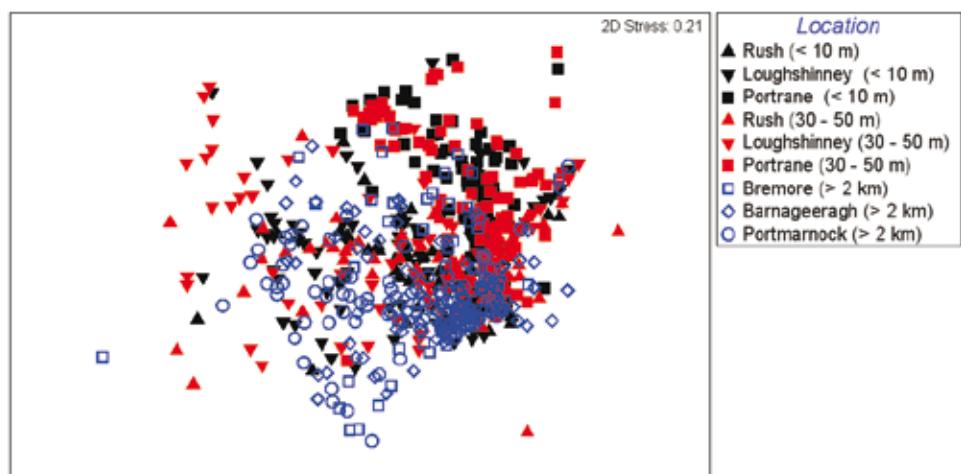


Figure 2.2. Multi-dimension scaling plot (MDS) of benthic assemblages at sites proximate to a sewage outfall (black icons), adjacent to a sewage outfall (red icons) and on shores without a sewage outfall (blue icons).

Table 2.1. PERMANOVA to test for effects of distance to sewage outfall, time and location on the assemblage structure of rocky shores, n = 30. Significant P values are in bold.

Source	Df	MS	F	P
Distance	2	56050	1.0341	0.418
Time	3	39935	4.9618	0.001
Location (Distance)	6	49630	6.1663	0.001
Distance x Time	6	12353	1.5349	0.024
Location (Distance) x Time	18	8048.5	4.4094	0.001
Residual	684	1825.3		

PERMANOVA = Permutational analysis of variance; Df = Degrees of freedom; MS = Mean squares; F = pseudo F value; P = P (permutational).

SIMPER analyses show that the key contributors to any differences in assemblage owing to the presence of sewage outfalls result from a reduction in abundance of species such as *Semibalanus balinoides* (barnacles), *Fucus vesiculosus* (brown algae), *Lithothamnion spp.* (red algae), *Fucus serratus* (brown algae), *Osmundae pinnatifida* (red algae) and *Ceramium rubrum* (red algae) and an increase in species such as *Mytilus edulis* (mussels), *Ulva lactua* (green algae), *Chondrus crispus* (red algae), *Patella vulgata* (limpet) and *Ulva intestinalis* (green algae) (Appendix 4). Identification of the key species that determine assemblage structure with space and time was not the focus of this study; however, details of these SIMPER analyses are available. SIMPER analyses also show that the average similarity of assemblages close to an outfall was 34.5%, adjacent to an outfall was 32.6% and at sites > 2 km from an outfall was 38.5%. This is consistent with the PERMDISP results that show that distance from a sewage outfall affected the dispersion of taxa within assemblages ($F_{2,717} = 8.44$, $P < 0.01$), which was indicative of an overall increase in assemblage structure variability. Pairwise tests show that assemblages proximate or adjacent to a

sewage outfall had similar dispersion patterns ($t = 1.5$, $P > 0.22$) and were both more variable than sites without a sewage outfall ($t = 2.68$, $P < 0.03$; $t = 3.9$; $P < 0.01$). This shows that the presence of a sewage outfall increased assemblage variability and also identified the scale of the effect. The random factors 'Time' and 'Location' also affected overall assemblage variability and are detailed in Appendix 5.

When species/taxa were classed into functional groups, assemblages differed depending on the Time sampled and Location but there was no effect of distance to a sewage outfall on assemblage structure (Fig. 2.3; Table 2.2). There was a significant interaction between Time and Location and pairwise tests show again that this was because assemblages at all locations differed from each other at each sampling period except once (winter) when two of the locations without sewage outfalls (Barnageeragh and Portmarnock) had similar assemblages ($t = 1.3$; $P > 0.16$). The effect of sampling time also differed at different locations following a similar pattern to the raw data results. These effects were consistent under all data transformations, indicating that they were not driven by differences in a few dominant functional groups, but by an overall shift in assemblage structure. The functional groups that determined the different assemblages at different locations and during different time periods have been identified and details of these SIMPER analyses are available; however, they are not the focus of this report. Similar to the previous analyses, the distance from a sewage outfall had a significant effect on functional group dispersal with assemblages ($F_{2,717} = 27.42$, $P < 0.001$). Pairwise tests show that assemblages proximate or adjacent to a sewage outfall had similar functional group dispersion patterns ($t = 1.53$, $P > 0.21$) and were both more variable than sites with a sewage outfall ($t = 5.63$, $P < 0.001$; $t = 6.8$; $P < 0.001$). Functional group dispersal was also affected by the random factors Time ($F_{3,716} = 26.63$, $P < 0.01$) and Location ($F_{8,711} = 13.12$, $P < 0.01$) and pairwise tests show a similar pattern as the raw data.

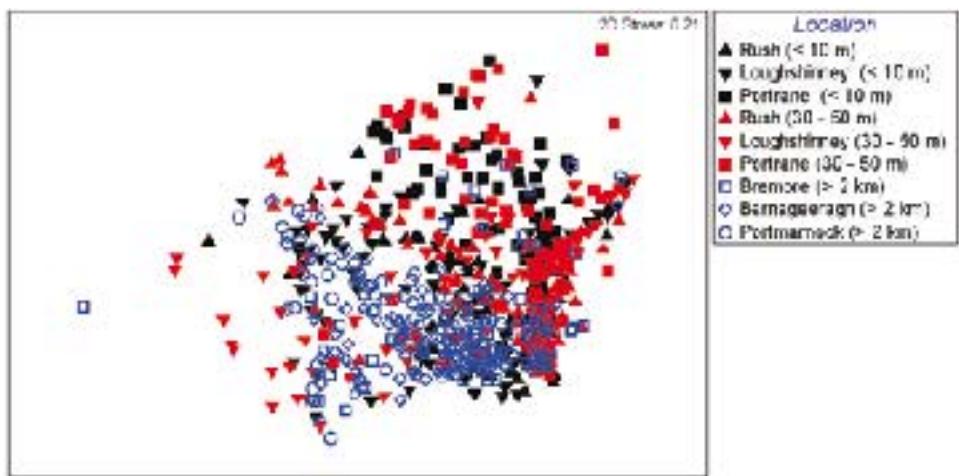


Figure 2.3. Multi-dimensional scaling plot (MDS) of benthic assemblages classed into functional groups at sites proximate to a sewage outfall (black icons), adjacent to a sewage outfall (red icons) and on shores without a sewage outfall (blue icons).

Table 2.2. PERMANOVA on benthic taxa classed into functional groups to test for effects of distance to sewage outfall, time and location on the assemblage structure of rocky shores, n = 30. Significant P values are in bold.

Source	Df	MS	F	P
Distance	2	59316	1.137	0.319
Time	3	41645	6.4929	0.001
Location (distance)	6	49284	7.6839	0.001
Distance x time	6	8526.6	1.3294	0.151
Location (distance) x time	18	6413.9	3.9617	0.001
Residual	684	1619		

PERMANOVA = Permutational analysis of variance; Df = Degrees of freedom; MS = Mean squares; F = pseudo F value; P = P (permutational).

2.3.2 Effects of sewage outfalls on algal assemblages based on quantification of WFD RSL metrics

In total, 37 algal taxa were identified. The presence of a sewage outfall did not affect algal taxa richness ($F_{1,174} = 0.0, P > 0.97$) or diversity ($F_{1,174} = 0.13, P > 0.73$) but there was an effect of location on algal richness ($F_{4,174} = 17.32, P < 0.001$) and diversity ($F_{4,174} = 9.94, P < 0.001$). Portmarnock had greater algal taxon richness and diversity than all other locations. Algal taxon evenness was not affected by sewage ($F_{1,174} = 0.37, P > 0.58$) or location ($F_{4,174} = 2.05, P > 0.09$).

There was no difference in algal assemblage structure between shores with and without sewage outfalls ($F_{1,178} = 2.18, P > 0.9$) but there was an effect of location ($F_{4,178} = 6.9, P < 0.001$) (Fig. 2.4). In addition, there was no effect of a sewage outfall on the algal species dispersal within assemblages (PERMDISP: $F_{1,178} = 1.41, P > 0.29$), which did differ among locations (PERMDISP: $F_{5,178} = 4.94, P < 0.002$). These effects were consistent on all data transformations.

Similarly, when data were classed into algal functional groups, there was no effect of sewage on algal functional group assemblages ($F_{1,178} = 4.89, P > 0.1$) but there was an effect of location ($F_{4,178} = 6.44, P < 0.001$) (Fig. 2.5), and these effects were consistent on all data transformations. There was an interactive effect of sewage and location on the dispersal of alga functional groups (PERMDISP: $F_{5,178} = 18.41, P < 0.001$). PERMDISP pairwise tests show that dispersion of algal functional groups was greater at all three of the shores with a sewage outfall than the shores without and also that, among the shores without a sewage outfall, dispersion was greater at Portmarnock than Bremore and Barnageeragh (Appendix 6).

Following the RSL method (sampling during summer months), no difference was detected between shores with sewage outfalls present compared to those

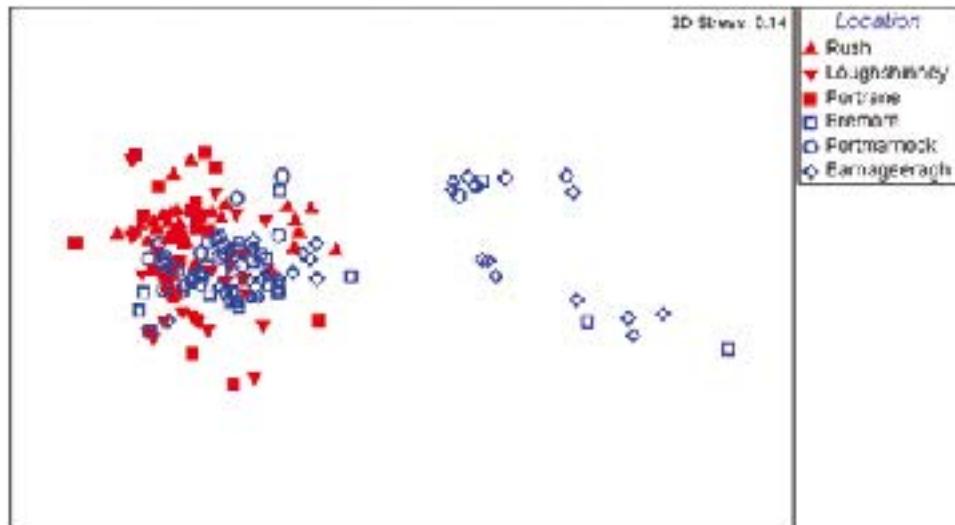


Figure 2.4. Multi-dimensional scaling plot (MDS) of algal assemblages on shores with a sewage outfall (red icons) and on shores without a sewage outfall (blue icons), based on Reduced algal Species List (RSL).

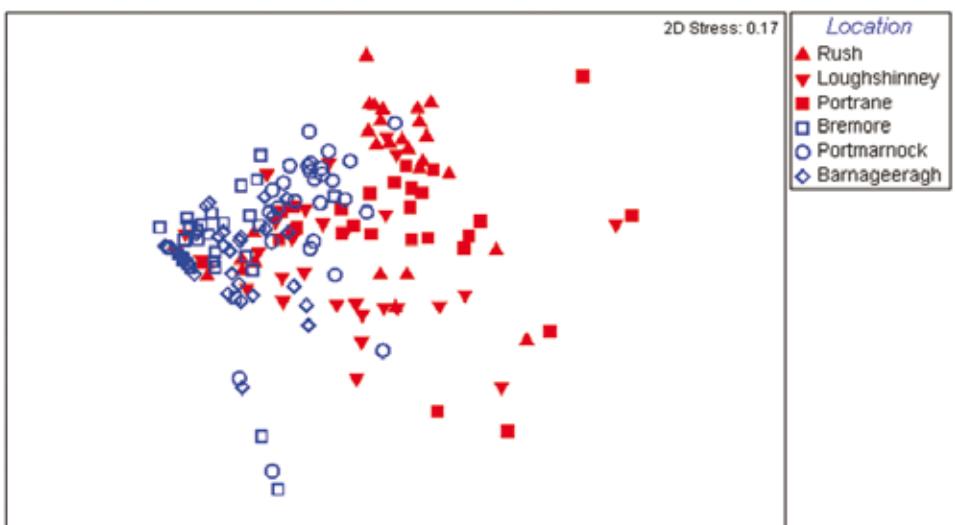


Figure 2.5. Multi-dimensional scaling plot (MDS) of algal functional group assemblages on shores with a sewage outfall (red icons) and on shores without a sewage outfall (blue icons), based on Reduced algal Species List (RSL).

without ($F_{1,4} = 0.1, P > 0.77$). The shores with sewage outfalls had a mean EQR final score of 0.70 (± 0.01 SE [standard error]) ranked as 'Good', compared to

the shores without sewage outfalls, which had a mean EQR final score of 0.68 (± 0.07 SE) and were ranked as 'Good'/ 'Moderate' ([Table 2.3](#)).

Table 2.3. Metrics calculated for Water Framework Directive (WFD) classification at three sites with a sewage outfall and three sites without a sewage outfall.

	Sewage Outfall			No Sewage Outfall		
	Rush	Loughshinney	Portrane	Bremore	Barnageeragh	Portmarnock
Number of green species	3	3	3	2	2	5
Number of brown species	5	4	7	8	6	6
Number of red species	17	13	17	13	6	19
Number of opportunists	4	4	4	2	2	3
ESG1 perennial	14	8	15	11	9	14
ESG2 opportunist	10	10	11	10	4	12
Summary						
Species richness	25	20	27	23	14	30
Proportion of greens	0.12	0.15	0.11	0.09	0.14	0.17
Proportion of reds	0.68	0.65	0.63	0.57	0.43	0.63
ESG ratio	0.71	1.25	0.73	0.91	0.44	0.86
Proportion of opportunists	0.16	0.2	0.15	0.09	0.14	0.1
Shore description	15	15	15	15	15	15
De-shoring factor	1	1	1	1	1	1
Corrected species richness	25	20	27	23	14	30
Scores (EQRs)						
Species richness	0.500	0.640	0.560	0.380	0.700	0.640
Proportion of rhodophyta	0.844	0.835	0.807	0.514	0.837	0.835
ESG ratio	1.050	0.547	0.709	0.340	0.657	0.547
Proportion of chlorophyta	0.800	0.852	0.884	0.810	0.733	0.852
Proportion of opportunists	0.500	0.607	0.826	0.629	0.800	0.607
Final score	0.500	0.640	0.560	0.380	0.700	0.640
Classification	Good	Good	Good	Moderate	Good	Good

ESG = ecological status group; EQR = ecological quality ratio.

2.4 Discussion

The findings show that although some evidence of effects of the presence of sewage on benthic assemblage structure was detected, these were not consistent or predictable. There was weak evidence that benthic assemblages at locations with sewage included greater abundances of mussels, limpets and green algae and less fucoid and red algal species compared to shores without sewage outfalls, but this is not a robust conclusion. Moreover, spatial (among locations) and

temporal (throughout the year) variation of assemblage structure was far greater than the effect of sewage. Further, even the identified patterns of variability through time were not consistent among locations. For example, assemblage structure differed among all locations during each sampling period except once (winter), when two of the locations without sewage (Barnageeragh and Portmarnock) did not differ from each other. Also, at Rush (sewage present), assemblage structure was different at each sampling period, while assemblages

at Loughshinney (also sewage present) were similar for most of the year, diverging only in the summer. A generally similar pattern emerged when data were classed into functional groups: however, the interaction between distance from an outfall and time was no longer detected. Some information was, therefore, lost when species were grouped, highlighting that greater taxonomic resolution is required for assessments of impacts on benthic assemblage structures.

It is clear, however, that the variability of benthic assemblage structure was affected by the presence of sewage. Assemblages at sites proximate (< 10 m) or adjacent (30–50 m) to sewage outfalls showed greater variability than sites far (> 2,000 m) from an outfall. These results indicate that the scale of the effect of sewage on variability of assemblages was between 50 and 2,000 m. Assemblage structure variability also varied significantly through time and among locations, making it difficult to make general predictions about the effects of sewage on the overall stability of benthic assemblages, which are inherently variable. A similar pattern emerged when taxa were classed into functional groups: therefore, there would be no benefit in attempting to generalise or compare functional traits (e.g. fucoid algae) across locations.

Using a quantified approach based on the RSL, algal assemblage structure and variability did not differ on shores with or without sewage outfalls but assemblage structure did vary among locations. When algal taxa were classed into functional groups, no effect of sewage on assemblage structure remained: however, variability of algal assemblages was greater on shores without sewage outfalls. This contrasts to the previous results, based on the different sampling strategy (i.e. flora and fauna on emergent rock), which showed the opposite trend of greater assemblage variability on shores with sewage outfalls. Based on the findings of both sampling strategies, it is clear that changes in variability of assemblages (indicative of community stability) should be considered together with shifts in assemblage structure and that whole assemblages should be included to accurately assess putative impacts on rocky shores.

Using the EQRs, no difference between shores with and without sewage outfalls was found. In fact, all but one location were classed as 'good' with only Bre more (no

sewage outfall) classed as 'moderate'. This suggests that either: (a) EQRs are not sensitive to detecting differences in rocky shore assemblages driven by the addition of sewage or (b) the effects of sewage determining these assemblages are not as important as the background variation in space and time. Rocky shores are known to be highly dynamic systems and may persist with several alternative stable states (Petraitis and Dudgeon 1999; Petraitis et al. 2009; Petraitis and Hoffman 2010). This brings into question the need to define a 'pristine' set of conditions for marine waters. This concept may underpin the application of both the WFD and MSFD (Borja et al. 2012): however, it may not be the most useful method of environmental management, in particular for the protection of marine biodiversity. Pristine marine environments are extremely rare and defining such conditions for the application of these directives has proven difficult (Hering et al. 2010; Van Hoey et al. 2010), largely because of a lack of knowledge of natural variability of 'reference' conditions (Duarte 2009).

Several EU regions are currently developing their own WFD metrics with the overall aim of harmonisation. Catalonia, Italy and France use different macroalgal indices based on sensitivity of communities to human impacts drawn from expert-opinion derived classifications of 'good' and 'bad' species (e.g. methods using spatial databases and GIS, such as CARtography of LITToral and sublittoral communities [CARLIT]). Greece and the Mediterranean regions of Spain use the Ecological Evaluation Index (EEI). This is based on a classification of algae into groups based on their morphology (Ballesteros et al. 2007; Orfanidis 2007; Asnaghi et al. 2009). In Ireland, the RSL index is based on algal species richness measured as presence/absence, contrasting with other metrics being developed in the North East Atlantic region that quantify relative abundance (e.g. quality of rocky bottoms [CFR] [Juanes et al. 2008]). It has been argued that for this reason the RSL is less sensitive but more robust and precise than other metrics (Guinda et al. 2008; Bermejo et al. 2012) but this remains to be tested. An assessment of the RSL on Atlantic shores in southern Spain concluded that although this index showed consistent results with analytical water-quality monitoring it did not discriminate between good and high-quality status (Bermejo et al. 2012). Moreover, there are several differences in the

application of the modified metrics employed in different regions (Guinda et al. 2008; Juanes et al. 2008; Bermejo et al. 2012). For example, some algal species are assigned to different ESGs depending on the variation of the metric being used (e.g. *Corallina spp.*, ESG-I by Orfanis et al. 2001 and ESG-II by Ballesteros et al. 2007) or assigned a different opportunistic character (e.g. *Ceramium spp.* considered opportunist by Guinda et al. 2008 and non-opportunist by Wells et al. 2007).

The merits of the different approaches are difficult to assess because of inconsistencies in the experimental design of several studies. It is well documented that spatial and temporal variation must be estimated to identify a human impact and that multiple reference sites are essential to test for a putative effect at the appropriate spatial scale (Underwood 1992; Archambault et al. 2001; Bishop et al. 2002; Benedetti-Cecchi and Osio 2007). Nevertheless, several studies attempting to test WFD metrics have failed to adhere to correct experimental design (Arevalo et al. 2007).

It has been reported that high loads of domestic and industrial waste water result in a shift from algal-dominated assemblages to invertebrate-dominated assemblages (Díez et al. 2012). If such a shift in assemblage structure is indicative of an 'impacted' state then flora and fauna should be assessed simultaneously (Underwood 1996; Archambault et al. 2001; Bishop et al. 2002), in particular when invertebrate taxa can be correlated with a disturbance gradient (Hiscock et al. 2005; Goodsell et al. 2009). This is not currently done in Ireland and presently only one published study has assessed algal and invertebrate assemblages on rocky shores to estimate BQE_s. The Rocky Intertidal Community Quality Index (RICQI), was developed for the Atlantic coasts of Spain and is based on indicator species, morphologically complex algal cover, species richness and faunal cover (Díez et al. 2012). Díez et al. (2012) have developed a conceptual model for this region based on benthic assemblages following the introduction of enhanced sewage treatment along a distance gradient. They concluded that the derived metric, RICQI, was more accurate than others at identifying degrees of disturbance. While this study was limited to the Basque region and further tests are required to test the generality of their findings, the concept could be developed for other regions.

Caution is warranted if the concept of 'bio-indicators' is to be further developed for marine benthic systems (Goodsell et al. 2009). The selection of an indicator taxon must be based on substantial evidence of (i) a strong correlation between levels of an environmental variable of interest and the taxon; (ii) a causal relationship between the variable and the response of the indicator over multiple scales; and (iii) a direct relationship that has been proven over multiple spatial and temporal scales (Goodsell et al. 2009). This information is often lacking in marine systems, in particular for rocky shores, where a range of taxa are suggested to be indicative of different levels of environmental stresses (Hawkins et al. 1994). It is important to remember that the use of indicator taxa to represent environmental change is meaningless when the change itself is more easily measured (Goodsell et al. 2009).

Moreover, the usefulness of metrics, such as species richness, to quantify the effects of anthropogenic disturbances is unclear (Harper and Hawksworth 1995; Magurran 2004). For example, fluctuations in species richness can be confounded by natural environmental variation, meaning that a decline in species richness may not be representative of a decline in ecosystem health (Hawkins et al. 1986; Warwick and Clarke 1998; Blanchard and Bourget 1999). Moreover, such indices are often affected by sampling effort (Clarke and Warwick 2001b). This has important implications for WFD metrics because most do not use a quantified sampling strategy. Alternatives to species-richness metrics include the examination of the taxonomic distinctness of organisms within an assemblage to assess functional diversity (Warwick and Clarke 2001). Some studies have found that indices of taxonomic distinctness are more sensitive to anthropogenic disturbances than traditional diversity indices (Warwick and Clarke 1995; Terlizzi et al. 2005b; Roberts et al. 2008), while others found contrasting results (Salas et al. 2006; Costa et al. 2010). This concept remains to be tested fully but appears worthy of consideration.

In terms of integrating WFD estimates of ecological status with the context of ecosystem functioning and services, a limitation of many metrics is an over-reliance on species richness (a subset of diversity),

which rarely relates to the functioning of marine ecosystems that tend to be dominated by species-identity effects (Emmerson et al. 2001; O'Connor and Crowe 2005). Also, the relative abundances of different species can significantly alter the functioning of an ecosystem (Benedetti-Cecchi 2004; Maggi et al. 2009) and changes in assemblage structure are

not identified by metrics based on species richness. Furthermore, very little is known about the functional role of most benthic species and if metrics are to be indicative of ecosystem functioning, more work is required to develop tools that assess the structural and functional aspects of marine benthic communities (Van Hoey et al. 2010).

3 Quantification of the Effects of Eutrophication and Species Loss on the Diversity and Functioning of Rock Pool Assemblages

3.1 Background

Natural systems are almost always subjected to a myriad of anthropogenic stressors (Halpern et al. 2008a; Halpern et al. 2008b). Eutrophication and the loss of species are two of the key drivers of change in marine ecosystems (Worm et al. 2002; Millennium Ecosystem Assessment 2005), yet it is not known how multiple anthropogenic impacts interact and affect ecosystem functioning (Crain et al. 2008). The development and application of ecosystem-based approaches to marine resource management have highlighted the need to understand the impacts of multiple anthropogenic stressors (Rosenberg and McLeod 2005; Leslie and McLeod 2007). Conceptually, the cumulative effects of multiple stressors may be additive, antagonistic or synergistic (Breitburg et al. 1998; Folt et al. 1999). Findings of recent meta-analyses suggest that the cumulative effects of activities such as fishing, eutrophication, pollution, etc. are most likely synergistic, thus warranting urgent research attention (Burkepile and Hay 2006; Crain et al. 2008; Gruner et al. 2008).

Predicting the consequences of species loss remains an elusive goal of critical importance for the maintenance of ecosystem functioning and services (Loreau et al. 2001; Hooper et al. 2005; Burkepile and Hay 2008; O'Gorman and Emmerson 2009). Although the relationship between biodiversity and ecosystem functioning has been the focus of much research since the 1990s (Hooper et al. 2005; Stachowicz et al. 2007), relatively little is known about the effects of loss of consumer diversity on lower trophic levels (Worm et al. 2002; Duffy et al. 2005; Byrnes et al. 2007; Duffy et al. 2007; Bruno and Cardinale 2008; Burkepile and Hay 2008). Moreover, few studies have been done at appropriate experimental scales to capture a realism that would enable current knowledge of functional

roles of consumers to be incorporated into ecosystem management (Bracken et al. 2008; Bruno and Cardinale 2008; Naeem 2008). In addition, the magnitude and direction of the effects of loss of consumers are highly variable and may depend on environmental context (Boyer et al. 2009; O'Connor and Bruno 2009).

This study aimed to disentangle the effects of loss of species and of eutrophication and test for an interaction between nutrient concentration and effects of loss of consumer species in a marine benthic system. Species loss and nutrient concentration were manipulated experimentally in rock pools, to test for effects on assemblages (structure and biomass) and ecosystem functioning (primary productivity). Previously, it was shown that the effects of loss of a key grazer species, *Patella ulyssiponensis*, determined the total biomass of algae in rock pools while other species of grazing gastropods could not compensate for the loss of *P. ulyssiponensis* even at increased densities (O'Connor and Crowe 2005). Such idiosyncratic effects of species loss are prevalent in marine systems and arguably more important than species diversity *per se* (Emmerson et al. 2001; Stachowicz et al. 2007). More recently, the need to examine consumer species richness and composition (identity) effects in the context of ecosystem development (succession) has been stressed (Griffin et al. 2010). This study aimed to test the context dependency of previous findings and to examine the effects of loss of species on ecosystem functioning and successional assemblages. It tested the model that in rock pools the loss of a key consumer species (*P. ulyssiponensis*), but not the loss of other species (*L. littorea*, *G. umbilicalis*) (i.e. species identity not richness) affects: (i) rates of primary productivity; (ii) total algal biomass; and (iii) algal assemblage structure. It was also tested whether these effects interacted with water column nutrient concentrations (ambient and enhanced).

3.2 Methodology

Natural rock pools differ in shape, size, shore height and colonisation history, making it difficult to compare them without confounding other factors (Underwood and Skilleter 1996). To solve this, experimental pools (30 cm diameter, 10 cm depth) were constructed by drilling with a diamond tipped corer on an exposed rocky shore at Carnsore Point, Co. Wexford, Ireland ($52^{\circ} 10.3'N$, $6^{\circ} 21.8'W$). This site is composed largely of granite and contains a network of patches of cleared rock, mussels, barnacles and algae (O'Connor and Crowe 2008). The mid-shore comprises a network of emergent rock and shallow rock pools dominated by macroalgae (e.g. *Lithothamnion* spp., *Corallina officianalis*, *Chondrus crispus*, *Ulva* spp., *Scytoniphon lomentaria* and *Fucus vesiculosus*) and a suite of grazing gastropods (e.g. *P. ulyssiponensis*, *Gibbula umbilicalis* and *L. littorea*) that is typical of exposed shores in this region (O'Connor and Crowe 2005). Forty experimental pools were created at sites placed randomly along approximately 20 m of the mid shore each at least 1 m apart. Construction was carried out over several weeks in May 2009, experimental treatments were established the following month and ran from June 2009 to July 2010.

To test for the effects of the loss of grazer species (richness and identity) on benthic assemblages, the presence of the three most abundant grazing gastropod species (mean density in rock pools) (< 10 cm depth): *P. ulyssiponensis* 28 (\pm SE 7) individuals m^{-2} , *G. 38* (\pm SE 8) individuals m^{-2} and *L. littorea* 22 (\pm SE 6) individuals m^{-2}) was manipulated. Five grazer manipulation treatments were established involving the removal of all three species, removal of each species individually and with all three present at ambient densities (Table 3.1). To test for an interaction between the effects of loss of species and different levels of nutrient concentration, another set of these treatments was established and nutrient concentration was artificially enhanced.

Experimental treatments were established a few weeks after the construction of the rock pools to allow the substrate to settle. Treatments were allocated randomly to each pool and it was necessary to cover each pool to maintain grazer manipulations with stainless steel mesh lids (0.9 mm wire diameter, 4.17 mm aperture, 67% open area). The lids were attached to the shore with screws

and washers using a hammer action drill. Previous studies have shown that this size mesh did not affect algal assemblage structure or biomass (O'Connor and Crowe 2005). Experimental treatments were checked regularly (approximately monthly) and maintained. The experiment ran for 13 months to allow algal recruitment and succession to occur.

Table 3.1. Experimental treatments to test for effects of loss of species of grazing gastropod and effects of nutrient additions on benthic assemblages and productivity.

Treatments	
Grazer manipulation	Nutrient additions
All grazers present *	+/-
Loss of one grazer species (<i>Patella</i>)	+/-
Loss of one grazer species (<i>Littorina</i>)	+/-
Loss of one grazer species (<i>Gibbula</i>)	+/-
Loss of three grazer species (<i>Patella</i> , <i>Littorina</i> <i>Gibbula</i>)	+/-

*Based on natural densities scaled to the surface area of the experimental rock pools: five *Patella*, four *Littorina* and six *Gibbula*.

Nutrient concentrations were enhanced in appropriate treatments by the addition of slow-release fertiliser pellets (Osmocote®) in plastic mesh cases (10 cm x 10 cm), following previous recommendations (Worm et al. 2000; Atalha and Crowe 2010). Mesh cases were added to each experimental pool to control for any experimental artefacts caused by the case rather than the nutrients. Initially, 160 g of fertiliser was added to each plot with enhanced nutrient treatments and after six weeks water samples were taken during low tide to test if this method was effective. Water samples from experimental pools with added fertiliser had much greater concentrations of phosphate (MRP) ($MS = 257.86$, $F_{1,24} = 9980.75$, $P < 0.001$) and dissolved inorganic nitrogen (DIN) ($MS = 237.77$, $F_{1,24} = 1106.90$, $P < 0.001$) than treatments at ambient conditions. Following this, fertiliser pellets were replaced every 8–12 weeks to sustain greater concentrations of nutrients in appropriate treatments for the duration of the experiment.

Gross primary productivity was estimated by measuring dissolved oxygen concentrations in rock pool seawater, using an optical probe (HQ20 Hatch Lange portable LDO™, Loveland USA) after a period of artificially

induced darkness (community respiration) and a similar period of sunlight (net primary productivity). Measurements were taken several times during the experiment. However, there were some technical difficulties and following an updated protocol only the measurements taken after 13 months are reported. These readings were taken at saturating irradiance on sunny days and stable weather conditions and followed recommendations for the incubation method as a tool examining ecosystem functioning relationships (Noël et al. 2010). To further increase accuracy, all readings were taken, each of three consecutive days and their means were used in the analyses (even though variability among days was negligible). Destructive samples were taken at the end of the experiment when all algae were identified and biomass (dry weight) of each alga was measured in the laboratory.

Analysis of variance (ANOVA) was used to test hypotheses involving primary productivity, total algal biomass and grazer biomass. Prior to analyses, Cochran's test was used to test for homogeneity of variances and data were transformed when necessary. Permutational analysis of variance (PERMANOVA) was used to test hypotheses involving assemblage structure based on a Bray-Curtis similarity matrix with 9999 permutations. All analyses had two fixed factors: (i) nutrient concentration (two levels) and (ii) grazer treatment (five levels) and were tested for an interaction between the two factors, $n = 4$. Post hoc tests were used to compare significant terms.

3.3 Results

Primary productivity rates were greater in rock pools at enhanced nutrient concentration than ambient conditions, but there was no consistent effect of loss of species (including the loss of all three grazer species) on primary productivity ([Table 3.2](#); [Fig. 3.1](#)). The loss of grazers did affect total algal biomass accumulation; however, there was a significant interaction between nutrient concentration and loss of species ([Table 3.2](#); [Fig. 3.1](#)). At enhanced nutrient concentration, there was no effect of loss of grazer species on algal biomass, while at ambient conditions the loss of certain species had a positive effect on algal biomass. Specifically, the loss of *P. ulyssiponensis* alone, or the loss of *L. littorea* alone, led to an increase in algal biomass. Nevertheless, the loss of all three grazer species did not affect algal biomass (i.e. algal biomass in treatments with all three grazers present did not differ from treatments that had all three species removed). This shows that the effects of species loss were identity dependent (depending on which species was removed) and determined by the presence of other grazer species, and also varied with environmental context (nutrient concentration).

Algal assemblage structure was affected by nutrient concentration ($MS = 328.8$, $F_{1,30} = 3.35$, $P < 0.01$; [Fig. 3.2](#)) but not grazer species diversity ($MS = 1042.0$, $F_{4,30} = 1.09$, $P > 0.36$; [Fig. 3.2](#)) and there was no interaction between the loss of species and nutrient concentration ($MS = 1276.5$, $F_{4,30} = 1.33$, $P > 0.17$; [Fig. 3.2](#)). Algal assemblages in rock pools with

Table 3.2. ANOVA to test the effects of enhanced nutrient concentration and the loss of diversity of grazers on primary productivity (square-root transformed data), total algal biomass (untransformed data) and algal taxa richness (untransformed data) in rock pools after 13 months, $n = 4$. Significant P values are in bold.

Source of variation	Df	Primary productivity			Total algal biomass			Algal taxa richness		
		MS	F	P	MS	F	P	MS	F	P
Nutrient concentration (N)	1	9.69	9.59	<0.00	11.41	0.16	0.69	0.23	0.08	0.77
Grazer species diversity (G)	4	2.50	2.48	0.06	110.78	1.53	0.22	5.09	1.89	0.14
N x G	4	0.99	0.99	0.43	202.62	2.80	0.04	8.66	3.22	0.03
Residual	30	1.01			72.27			2.69		

PERMANOVA = Permutational analysis of variance; Df = Degrees of freedom; MS = Mean squares; F = pseudo F value; P = P (permutational).

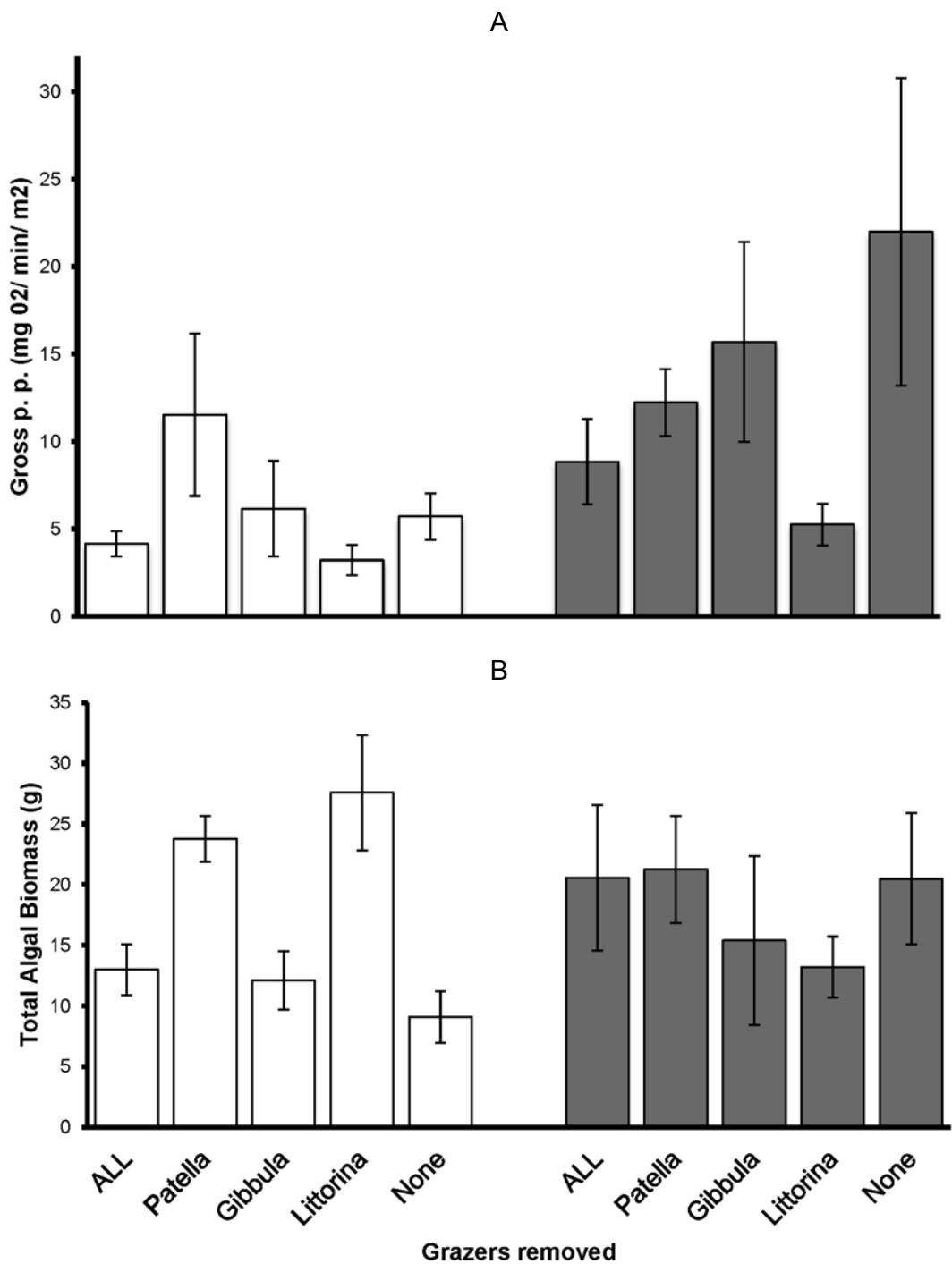


Figure 3.1. (A) Mean primary productivity (p.p.) rates (\pm SE) and (B) Mean total algal biomass (\pm SE), in rock pools with experimental treatments of different richness and identities of species of grazers present, after 13 months. Open bars are at ambient nutrient concentration and grey bars have enhanced nutrient concentration.

enhanced nutrient concentration contained a greater proportion of *Ulva spp.*, *Porphyra umbilicalis*, *Chondrus crispus*, *Punctaria latiflora*, *Gelidium sesquipedale* and *Ectocarpus spp.* and less of *Scytoniphon lomentaria*, *Fucus vesiculosus*, *Ceramium rubrum*, *Palmaria palmata* and *Polysiphonia spp.* (Table 3.3). There was a significant interaction between an effect of loss of species and nutrient on algal taxon richness

($MS = 8.7$, $F_{4,30} = 3.22$, $P < 0.03$; Fig. 3.3). Post hoc tests showed that at ambient conditions there was no difference among grazer diversity treatments, however, at enhanced nutrient concentration the treatment from which all three grazers were removed had greater algal taxon richness than other treatments (Fig. 3.3).

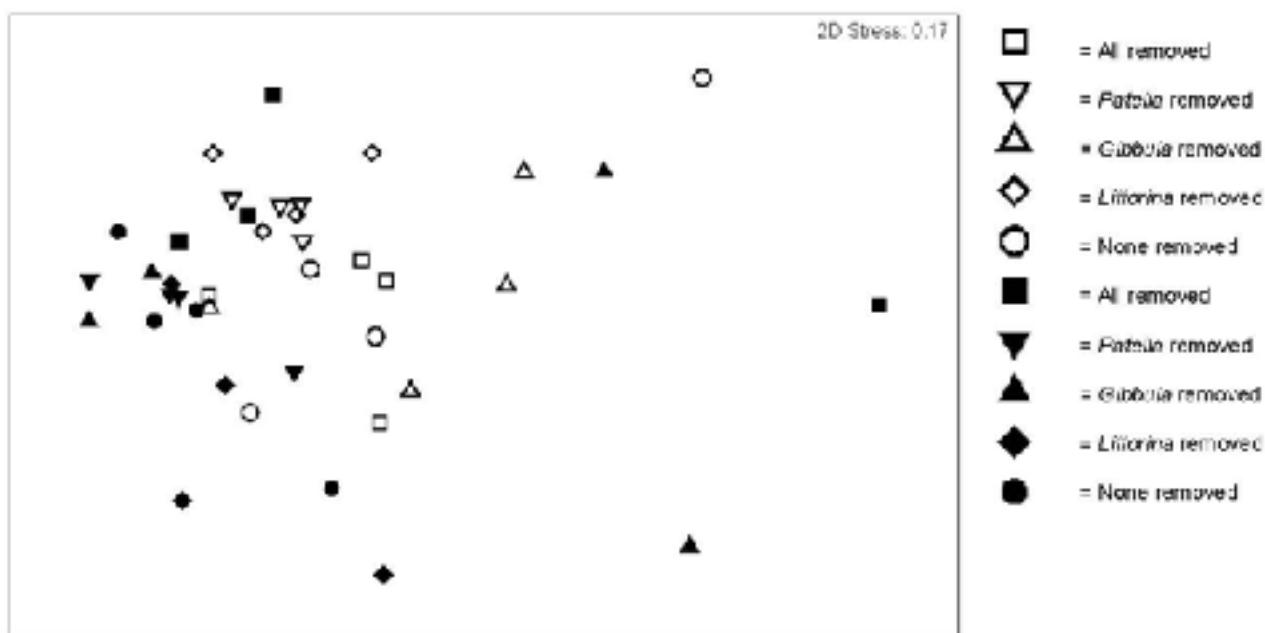


Figure 3.2. Multidimensional scaling plot (MDS) showing algal assemblage structure in rock pools under different experimental treatments (species loss), after 13 months. Data are square-root transformed. Open symbols are at ambient nutrient concentration and black symbols have enhanced nutrient concentration.



Figure 3.3. Mean number of algal taxa (\pm SE) in rock pools with experimental treatments, of different richness and identities of species of grazers present, after 13 months. Open bars are at ambient nutrient concentration and grey bars have enhanced nutrient concentration.

Table 3.3. SIMPER analysis of taxa contributing to differences in algal assemblages in response to the enhancement of nutrient concentration in rock pools, after 13 months, $n = 4$. Average Bray-Curtis dissimilarity = 44.02%.

Taxa	Average abundance				
	Ambient	Enhanced nutrients	Avg. Diss.	Contrib. (%)	Cum. (%)
<i>Ulva spp.</i>	3.45	3.67	14.04	31.89	31.89
<i>Scytoniphon lomentaria</i>	1.32	0.37	9.15	20.77	52.67
<i>Fucus vesiculosus</i>	0.65	0.44	5.3	12.03	64.70
<i>Porphyra umbilicalis</i>	0.24	0.45	4.05	9.2	73.90
<i>Chondrus crispus</i>	0.19	0.26	2.92	6.64	80.54
<i>Punctaria latifloa</i>	0.1	0.18	1.94	4.41	84.95
<i>Ceramium rubrum</i>	0.12	0.11	1.63	3.71	88.66
<i>Palmaria palmata</i>	0.15	0.07	1.44	3.27	91.93
<i>Gelidium sesquipedale</i>	0.02	0.13	1.13	2.56	94.49
<i>Polysiphonia spp.</i>	0.07	0.05	0.88	2.00	96.48
<i>Ectocarpus spp.</i>	0.01	0.1	0.87	1.97	98.45
<i>Osmundae osmunda</i>	0.03	0.03	0.4	0.91	99.36

Avg Diss. = Average dissimilarity; Contrib. (%) = % that taxa contributed to overall dissimilarity; Cum. (%) = Cumulative percentage dissimilarity.

3.4 Discussion

Enhanced nutrient concentration, not the loss of grazers, led to an increase in primary productivity rates in rock pools. This contrasts with the response of accumulated algal biomass, which showed that the loss of certain grazer species (*P. ulyssiponensis* and *L. littorea*) led to an increase in total algal biomass but only at ambient conditions. As predicted, under ambient conditions, the loss of *P. ulyssiponensis* led to an increased algal biomass; however, the loss of *L. littorea* also led an increase in algal biomass. Interestingly, when all three grazer species are removed there was no effect on algal biomass, indicating that the effects of loss of *P. ulyssiponensis* or *L. littorea* are mediated by the presence of the remaining species. This is a key point because previous studies based on the removal of all grazer species concluded that the effects of eutrophication override the effects of loss of grazers (e.g. Worm et al. 2002; Worm and Lotze 2006). The results show that the effects of loss of species are identity dependent, and so determined by the identity of the species removed and of those remaining. This has important management implications – for example, when harvesting strategies are focused on one species, such as the exploitation of *L. littorea*. Another key point

is that these effects of species loss were negated at enhanced nutrient concentration, further highlighting the context dependency of these interactions. In short, different species are performing differently and how they perform is also determined by the presence of other species in their functional group. Moreover, environmental context determines the effect of loss of consumers on algal biomass, making it extremely difficult to predict the effects of loss of species without detailed knowledge of a system.

The disparity between response of primary productivity rates and accumulated biomass may be caused by the sampling method (Tait and Schiel 2010). Nonetheless, it should be noted that although such processes are linked there may not be a direct positive correlation (Hawkins et al. 1992; Waide et al. 1999). For example, if rates of primary productivity and of consumption are both great, such as is predicted on exposed shores (Hawkins and Hartnoll 1983), there may be no difference in accumulated algal biomass (standing stock) even when primary productivity increases, illustrating that primary productivity and algal biomass accumulation can be decoupled (Hector 1998; Waide et al. 1999). It is therefore important to measure both accumulated algal biomass and primary productivity

rates because they provide unique information that is essential for understanding the functional dynamics of ecosystems (Griffin et al. 2010).

The increase in algal biomass in response to the loss of grazers (at ambient conditions) was not driven by a shift in algal assemblage structure but an increase in similar algal assemblages. This is consistent with previous studies and indicates that gastropod grazers may not exert a preference for certain algal species (O'Connor and Crowe 2005; Griffin et al. 2010). All algal assemblages were affected by enhanced nutrient conditions, which led to an increase in ephemeral algae as would be expected (Worm et al. 2002; Worm and Lotze 2006). This shows that although the effects of loss of species on total algal biomass appear negated at enhanced nutrient concentration, these are in fact different algal assemblages in terms of composition and structure. This has important implications for the interpretation of the current research findings because although the rock pools with enhanced nutrients may have similar total algal biomass and appear to be robust to the loss of grazer species, these are different algal assemblages, which may differ in terms of ecosystem processes and functioning (Bruno et al. 2005; Stachowicz et al. 2008b; Bracken et al. 2011). For example, rock pools with enhanced nutrient concentration were dominated by algae, which are more palatable to grazers, such as *Ulva* spp. (Hawkins and Hartnoll 1983). This potentially affects secondary production and trophic dynamics. Ambient rock pools, on the other hand, were dominated by algal species that are thought to be key contributors to total primary productivity rates, such as *Fucus* spp. (Odum 1958; Mann 1973; Tait and Schiel 2011).

An unexpected result was the interactive effect of the loss of grazers with nutrient concentration on algal taxon richness. Counter to classical theory, at enhanced nutrients when all three grazers were removed, thus releasing dominant algae from grazing pressure, the greatest algal taxon richness was recorded. A comparable study of rock pools in South-West England found that algal taxon richness was correlated to algal biomass and both were determined by the presence of *P. ulyssiponensis* (Griffin et al. 2010). The current study found that both *P. ulyssiponensis* and *L. littorina* affected algal biomass and no correlation between algal taxon richness and total algal biomass was found. This shows that current ecological theories are inadequate for understanding the mechanisms that drive biodiversity patterns and that predictions based on general models are not useful for local effects at the scale relevant to management decisions.

This study has identified specific interactions between the effects of species loss and environmental conditions in a marine benthic system. It highlights the importance of context-dependency when designing and interpreting BEF experiments, in particular in terms of multiple human impacts (Crain et al. 2008). Much more empirical research is required to provide accurate data that is essential to develop BEF models that incorporate interactions under different environmental conditions (Godbolt and Solan 2009). Future studies should, therefore, examine realistic species-loss scenarios under predicted and current levels of anthropogenic stresses at appropriate scales to yield findings that can be better incorporated into ecosystem management (Bracken et al. 2008; Naeem 2008; Crowe et al. in press).

4 Quantification of the Effects of Eutrophication and the Loss of Species from Multiple Trophic Levels on the Diversity and Functioning of a Benthic Community

4.1 Background

Understanding the consequences of biodiversity loss in complex, natural ecosystems requires that we move beyond simple systems of competing species to incorporating processes that occur within and among trophic levels (Duffy et al. 2007; Stachowicz et al. 2007). Field-based experiments that simulate the loss of species from different trophic levels are an essential tool for furthering our understanding of the functional roles of consumers in ecosystems and for revealing the mechanisms by which biodiversity affects ecosystem functioning in nature (Bracken et al. 2008; Stachowicz et al. 2008a; Stachowicz et al. 2008b; Edwards et al. 2010; Crowe et al. in press).

Recent work has yielded important insights into the direct and indirect effects of loss of species from multiple trophic levels on the functioning and stability of benthic communities (O'Connor and Bruno 2007; O'Connor et al. 2008; Donohue et al. in review). This study follows from a previous experiment by O'Connor et al. (in review) that tested the separate and combined effects of loss of two predators (crabs and whelks) and two groups of their prey (mussels and gastropod grazers) on primary producers (algal cover and assemblage structure). This experiment ran for six months before any effect of treatments was detected. After twelve months, the loss of predators affected algal cover negatively: however, this effect was mediated by the presence of their prey. Moreover, the identity of their prey determined algal assemblage structure. Specifically, the loss of mussels led to a dominance in red turfing algae and the loss of grazers led to a dominance of brown fucoid algae, whereas when all consumers were present algal assemblages were more variable – shown by greater algal taxa dispersion. Donohue et al. (in review) examined further the effects of the loss of these species on several distinct aspects of stability of the algal assemblages. It was shown that each species contributed in different ways to different

forms of stability, determined by both their identity and trophic position, with their loss triggering a range of cascading effects and consistently driving distinct shifts in the structure of assemblages. For example, observed rates of secondary extinctions were up to an order of magnitude greater than predicted by current theory and were caused by the loss of predators rather than by species from intermediate trophic levels.

These findings could not have been predicted from current theoretical frameworks, highlighting the need for more long-term field experiments to develop a multi-trophic perspective of species loss based on realistic estimates of diversity change at local scales. Furthermore, it is essential that the context-dependency of such responses is tested by manipulating environmental conditions as well as species diversity with robust experimental designs. This study tested the effects of loss of a benthic predator (whelks) and their prey (mussels, grazing gastropods), in a factorial design, under ambient conditions and at artificially enhanced nutrient concentrations, to test for interactions between effects of loss of species and increased nutrients, using a similar experimental set-up as the previously described studies. The models tested include: (i) at ambient and enhanced nutrient concentrations, total algal biomass will decrease with the loss of whelks and increase with the loss of grazers; (ii) at ambient and enhanced nutrient concentrations, algal assemblage structure will be determined by the identity of primary consumers; (iii) total algal biomass will be greater in all treatments at enhanced nutrient concentrations; (iv) algal assemblage structure will differ between ambient conditions and enhanced nutrient concentrations. To distinguish between direct and indirect effects on algal populations and to identify the mechanisms driving species interactions, the effects of experimental treatments on the intermediate trophic level (mussels and grazers) were also examined.

4.2 Methodology

The experimental site was located at Rush, Co. Dublin ($53^{\circ} 31.4'N$, $6^{\circ} 04.9'W$) on the east coast of Ireland, a moderately exposed intertidal rocky reef containing a network of patches of bare rock, mussels beds and macroalgal stands, typical of rocky shores in this region (O'Connor and Crowe 2008). A fully factorial experimental design was balanced and had three crossed factors: (i) 'loss of predators' (two levels: with whelk, without whelk); (ii) 'loss of primary consumers' (three levels: no primary consumers removed, grazers removed, mussels removed); and (iii) nutrient concentration (two levels; ambient conditions, enhanced nutrient concentrations). Mussels were considered as primary consumers in this design because the ingestion of algal spores is an important component of the mussel diet (Santelices and Martinez 1988). Mussels are also important ecosystem engineers as they modify the physical environment on rocky shores (Jones et al. 1997) and are particularly strong drivers of non-trophic interactions arising primarily from competition for space on rock surfaces (Lubchenco and Menge 1978). The experiment ran for 14 months from June 2009 till August 2010 and all 12 treatments were replicated four times (48 experimental units).

Experimental plots were established within the mid to low shore. Each plot contained approximately 50% mussel cover prior to the random allocation of treatments (range 45–55%). It was necessary to use cages to control the presence of mobile predators and molluscan grazers. The cages consisted of square fences measuring $35 \times 35 \times 12$ cm made of stainless steel mesh (0.9 mm diameter, 3.33 mm aperture, 61% open area), allowing immigration and recruitment of primary producers and many epibenthic consumers (including primary consumers and small predators, e.g. amphipods, polychaetes and Nemertea). The experimental design used in the current research, therefore, caused the local extinction of key components of a larger intertidal community in an open experimental system without removing entire trophic levels. To test for any experimental artefacts of the cages, algal and mussel cover and grazer biomass in experimental plots without cages were compared to the caged treatment within which all manipulated consumers were present. No difference was found in any of these variables between the caged treatments and un-caged plots

(algal biomass: $MS = 1.94$, $F_{1,6} = 0.03$, $P > 0.86$; mussel biomass: $MS = 87.58$, $F_{1,6} = 0.00$, $P > 0.97$; grazer biomass: $MS = 1.72$, $F_{1,6} = 0.01$, $P > 0.94$).

Experimental manipulations mimicked as closely as possible natural patterns at the experimental site. Mussels and molluscan grazers were removed manually from the treatments to simulate loss of these species. Predators were added to the plots if required for the treatment at a density initially of one individual per plot. Cages and treatments were checked regularly (approximately every two weeks) and maintained during the experiment. Throughout the experiment algal cover and assemblage structure were quantified using a 64-point double-strung quadrat (25 x 25 cm), which was placed in each plot and all taxa under each intersection point were recorded. Destructive samples were taken at the end of the experiment and all species were identified and their biomass (constant dry weight after several days in an oven at 60°C) was recorded.

Nutrient concentrations were enhanced in appropriate treatments by the addition of slow-release fertiliser pellets (Osmocote®) in plastic mesh cases (10 cm x 10 cm) (following Worm et al. 2000; Atalha and Crowe 2010). Mesh cases were added to each experimental plot to control for any experimental artefacts caused by the case rather than the nutrients. Initially, 160 g of fertilizer was added to each plot with enhanced nutrient treatments and after four weeks samples were taken from the water column directly above each plot on an ebbing tide to test if this method was effective. Water samples from experimental plots with added fertiliser had significantly greater concentrations of dissolved inorganic nitrogen (DIN) than treatments at ambient conditions ($MS = 12.11$, $F_{1,46} = 42.03$, $P < 0.001$). Following this, fertiliser pellets were replaced every 8–12 weeks to sustain greater concentrations of nutrients in appropriate treatments for the duration of the experiment.

Analysis of variance (ANOVA) was used to test all hypotheses involving algal, mussel and grazer biomass after first testing for homogeneity of variances with Cochran's test. Variables were transformed where necessary to homogenise variances. Total algal biomass data were log ($x + 1$) transformed, mussel biomass data were square-root transformed and grazer biomass data were not transformed prior to analyses. The Student-Newman-Keuls procedure was used to make post-

hoc comparisons among levels of significant terms. PERMANOVA (Permutational multivariate analysis of variance; Anderson 2001; McArdle and Anderson 2001) was used to test hypotheses about algal assemblage structure. SIMPER (Similarity of Percentages) (Clarke and Warwick 2001a) analyses were used to identify which algal taxa contributed most to pairwise dissimilarities between treatments. Multivariate analyses were based on Bray-Curtis similarity matrices, calculated from square-root-transformed algal biomass data and were done with 9999 permutations of the residuals under a reduced model with PRIMER Version 6.1.10 (PRIMER-E Ltd, Plymouth, UK).

4.3 Results

Total algal biomass was affected by the loss of several species depending on the combination of species removed: however, these effects were determined by nutrient concentration. Specifically, there were significant interactions between the loss of the predator (whelk) and nutrient concentration and between loss of primary consumers (mussels, grazers) and nutrient concentration (Table 4.1). At ambient conditions, the removal of grazers alone led to a dramatic increase in algal biomass, while the removal of whelk alone

or together with grazers led to a decrease in algal biomass (Fig. 4.1). Contrastingly, at enhanced nutrient concentration, there was no effect of loss of any of the species or functional groups removed on total algal biomass. Algal biomass was not greater at enhanced nutrient concentration but the effects of loss of species were negated.

Table 4.1. ANOVA to test the effect of enhanced nutrient concentration and for effects of loss of predators and primary consumers on total algal biomass ($\log(x+1)$ transformed data) after 14 months, $n = 4$. Significant P values are in bold.

Source of variation	Df	MS	F	P
Nutrient conc. (N)	1	0.77	1.25	0.27
Predator (P)	1	15.50	24.93	<0.00
Primary consumer (C)	2	1.18	1.9	0.16
N x P	1	2.97	4.78	0.03
N x C	2	1.03	1.65	0.21
P x C	2	2.97	4.78	0.01
N x P x C	2	1.18	1.90	0.16
Residual	36	0.62		

PERMANOVA = Permutational analysis of variance; Df = Degrees of freedom; MS = Mean squares; F = pseudo F value; P = P (permutational).

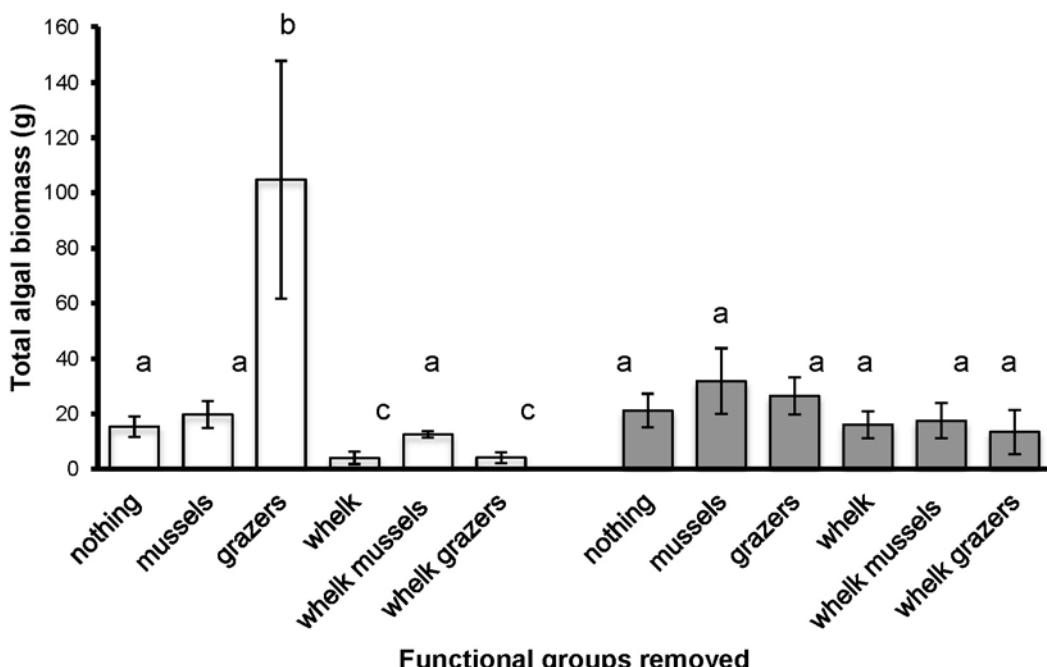


Figure 4.1. Total algal biomass (mean +/- S. E.) in treatments containing different functional groups of consumers in ambient (open bars) and enhanced nutrient concentrations (grey bars) after 13 months, $n = 4$. Letters (a, b, c) denote means that are indistinguishable ($P < 0.05$).

Table 4.2. PERMANOVA to test the effect of enhanced nutrient concentration and for effects of loss of predators and primary consumers on algal assemblage structure (square-root transformed data) after 14 months, n = 4. Significant P values are in bold.

Source of variation	Df	MS	Pseudo-F	P (perm.)
Nutrient conc. (N)	1	4389.9	3.00	0.014
Predator (P)	1	10788	7.37	<0.00
Primary consumer (C)	2	13579	9.27	<0.00
N x P	1	2239.7	1.53	0.20
N x C	2	2186.9	1.49	0.15
P x C	2	2315.7	1.58	0.12
N x P x C	2	2229.4	1.52	0.14
Residual	36	1464.5		

PERMANOVA = Permutational analysis of variance; Df = Degrees of freedom; MS = Mean squares; F = pseudo F value; P = P (permutational).

Algal assemblage structure was affected by all of the factors manipulated and there were no interactions, showing that nutrient concentration had a direct effect in algal assemblage structure, independent of the effects of loss of whelk, loss of mussels and loss of grazers (Table 4.2; Fig. 4.2). Pairwise tests confirmed that the loss of mussels had a significant effect on algal assemblages ($t = 2.17, P < 0.001$), as did the loss of grazers ($t = 2.86, P < 0.001$), and also showed that these assemblages were also different

from each other ($t = 4.46, P < 0.001$), indicating that the loss of either group of primary consumers affected algal assemblage structure differently. At enhanced nutrient concentration algal assemblages comprised of a greater biomass of *Osmundea pinnatifida*, *Porphyra umbilicalis* and *Ulva lactua* and less *Fucus spiralis* and *Chondrus crispus* compared to assemblages in other experimental plots (Table 4.3.A). Algal assemblages from which whelk had been removed comprised of a greater biomass of *P. umbilicalis* and less *F. spiralis*,

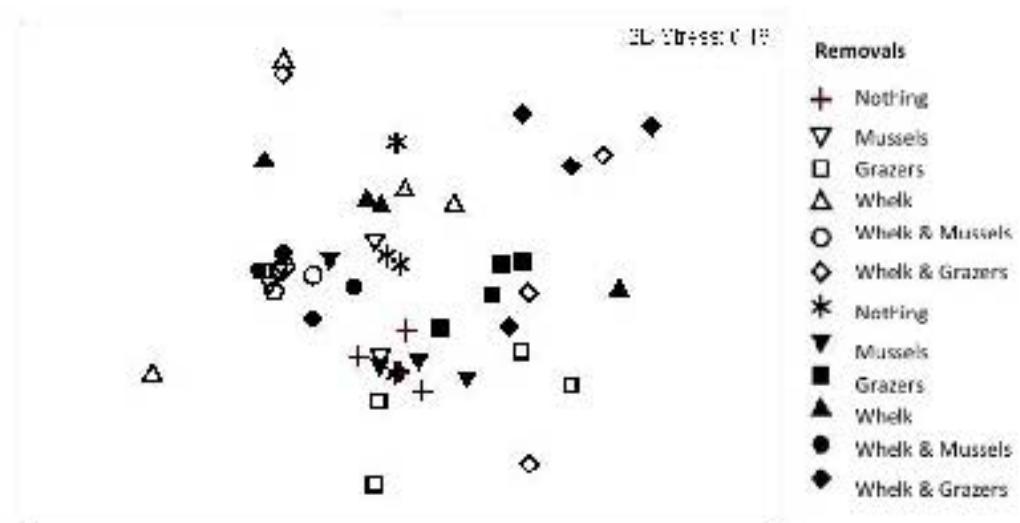


Figure 4.2. Multi-dimensional scaling plot (MDS) showing algal assemblage structure under different treatments (loss of predators and consumers) after 14 months, n = 4. Data are square-root transformed. Open symbols are at ambient conditions and black symbols have enhanced nutrient concentration.

C. crispus, *O. pinnatifida* and *U. lactua* compared to other assemblages (Table 4.3.B). Algal assemblages from which mussels had been removed comprised of a greater biomass of *O. pinnatifida*, *C. crispus*, *U. lactua* and *Ceramium rubrum* and less *F. spiralis* and *P. umbilicalis* compared to other assemblages (Table 4.3.C). Algal assemblages from which grazers had been removed comprised of a greater biomass of *F. spiralis*, *P. umbilicalis*, *U. lactua* and *Cladophora rupestris* and the less biomass of *C. crispus* and *O. pinnatifida* (Table 4.3.D). Hence, assemblages from which mussels and grazers were removed also differed from each other – largely driven by greater biomasses of *F. spiralis*, *P.*

umbilicalis, *U. lactua* in treatments without grazers and greater biomasses of *C. crispus* and *O. pinnatifida* in treatments without mussels (Table 4.3.E).

The removal of whelks led to an increase in total mussel biomass (Fig. 4.3 A; MS = 1268.6, $F_{1,24} = 13.63$, $P < 0.001$), however, mussel biomass was not affected by increased nutrient concentrations (Fig. 4.3. B; MS = 353.89, $F_{1,24} = 3.8$, $P > 0.06$), nor by removal of grazers (that may compete with mussels for space or clear space for mussels by removing algae) (Fig. 4.3. B; MS = 160.66, $F_{1,24} = 1.73$, $P > 0.2$) and there were no significant interactions.

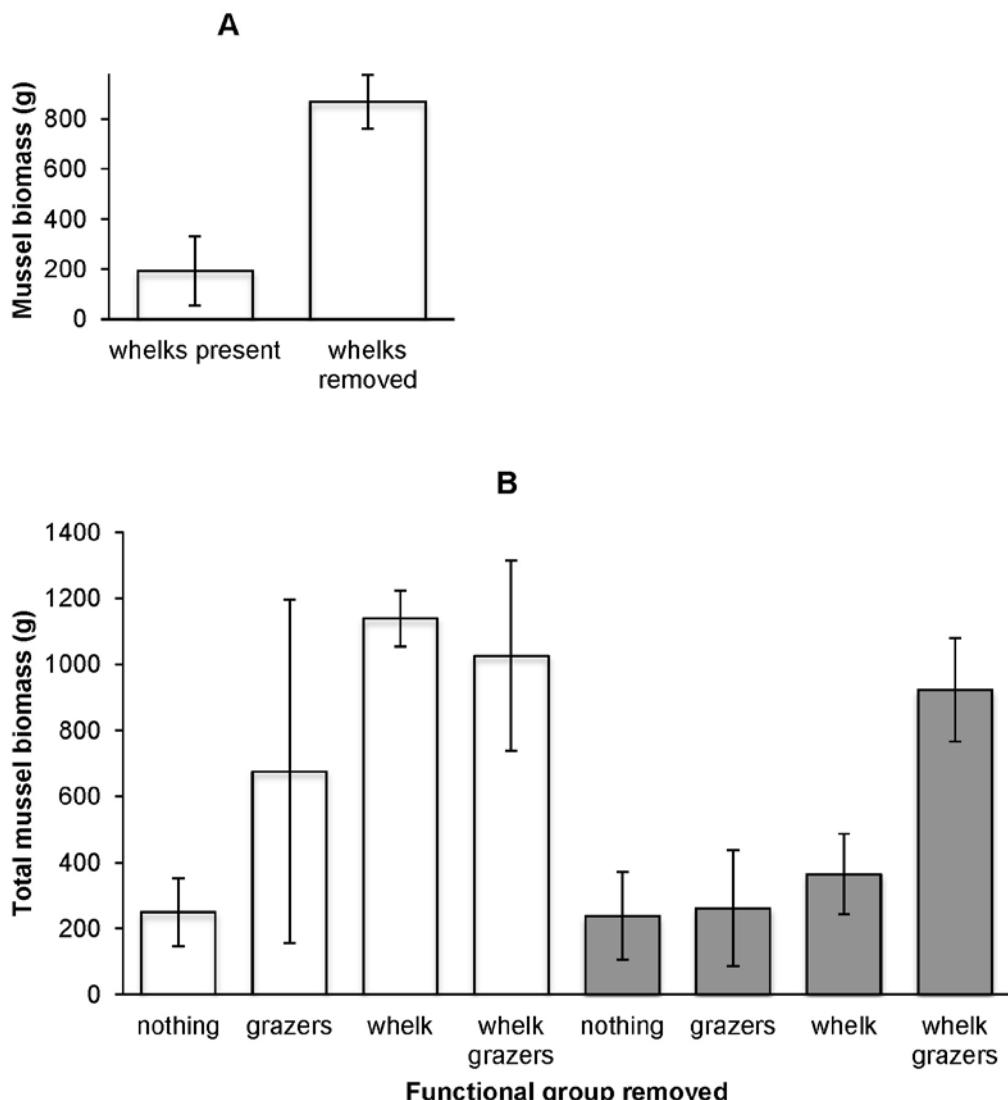


Figure 4.3. Total mussel biomass (mean +/- S. E.): A. Treatments containing different combinations of functional groups of consumers in ambient (open bars) and enhanced nutrient concentrations (grey bars); B. Mean of all treatments that contained whelks compared to mean of treatments that had whelks removed. After 13 months, $n = 4$.

Table 4.3. Similarity percentages analysis (SIMPER) of algal species contributing to differences in compared assemblages in response to experimental treatments after 14 months, n = 4. Average dissimilarity between assemblages with and without: A. Enhanced nutrients = 65.43; B. Predators = 67.83; C. Mussels = 58.01; D. Grazers = 71.88 and E. Comparison of treatments without mussels and without grazers = 76.46. Based on Bray-Curtis similarity matrices.

Species		Average biomass				
A.		Ambient	Enhanced nutrients	Avg. diss.	Diss/SD	Contrib. (%)
<i>Fucus spiralis</i>		2.15	1.71	18.04	1.15	27.57
<i>Chondrus crispus</i>		1.96	1.49	13.19	1.14	20.15
<i>Osmundea pinnatifida</i>		1.11	1.44	12.17	1.06	18.59
<i>Porphyra umbilicalis</i>		0.66	0.93	9.92	0.83	15.17
<i>Ulva lactua</i>		0.31	1.34	9.87	1.09	15.08
<i>Ceramium rubrum</i>		0.16	0	1.29	0.41	1.97
<i>Cladophora rupestris</i>		0.08	0.08	0.96	0.35	1.47
B.		Predator present	Predators removed	Avg. diss	Diss/SD	Contrib. (%)
<i>Fucus spiralis</i>		3.36	0.51	22.62	1.37	33.35
<i>Chondrus crispus</i>		2.11	1.33	12.87	1.24	18.98
<i>Osmundea pinnatifida</i>		1.36	1.19	11.54	1.14	17.01
<i>Ulva lactua</i>		1.18	0.46	9.69	1.03	14.28
<i>Porphyra umbilicalis</i>		0.78	0.81	8.77	0.89	12.93
<i>Ceramium rubrum</i>		0.08	0.08	1.22	0.39	1.8
<i>Cladophora rupestris</i>		0.16	0	1.12	0.36	1.66
C.		Mussels present	Mussels removed	Avg. Diss	Diss/SD	Contrib. (%)
<i>Fucus spiralis</i>		1.32	1.3	14.86	1.02	25.62
<i>Osmundea pinnatifida</i>		1.51	2	14.77	1.45	25.46
<i>Chondrus crispus</i>		1.36	2.53	14.05	1.22	24.22
<i>Ulva lactua</i>		0.42	0.89	7.71	0.95	13.28
<i>Porphyra umbilicalis</i>		0.56	0.08	4.71	0.76	8.12
<i>Ceramium rubrum</i>		0.07	0.17	1.92	0.5	3.3
D.		Grazers present	Grazers removed	Avg. Diss	Diss/SD	Contrib. (%)
<i>Fucus spiralis</i>		1.32	3.18	21.2	1.25	29.5
<i>Porphyra umbilicalis</i>		0.56	1.75	14.16	1.01	19.7
<i>Chondrus crispus</i>		1.36	1.28	12.57	1.12	17.49
<i>Osmundea pinnatifida</i>		1.51	0.31	11.86	0.91	16.5
<i>Ulva lactua</i>		0.42	1.16	9.86	1	13.72
<i>Cladophora rupestris</i>		0	0.24	1.6	0.45	2.22
<i>Ceramium rubrum</i>		0.07	0	0.62	0.23	0.87
E.		Mussels removed	Grazers removed	Avg. Diss	Diss/SD	Contrib. (%)
<i>Fucus spiralis</i>		1.3	3.18	19.17	1.27	25.08
<i>Chondrus crispus</i>		2.53	1.28	18.42	1.47	24.09
<i>Osmundea pinnatifida</i>		2	0.31	14.67	1.43	19.19
<i>Porphyra umbilicalis</i>		0.08	1.75	12.51	1.18	16.36
<i>Ulva lactua</i>		0.89	1.16	8.93	1.15	11.68
<i>Cladophora rupestris</i>		0	0.24	1.42	0.46	1.85
<i>Ceramium rubrum</i>		0.17	0	1.34	0.42	1.75

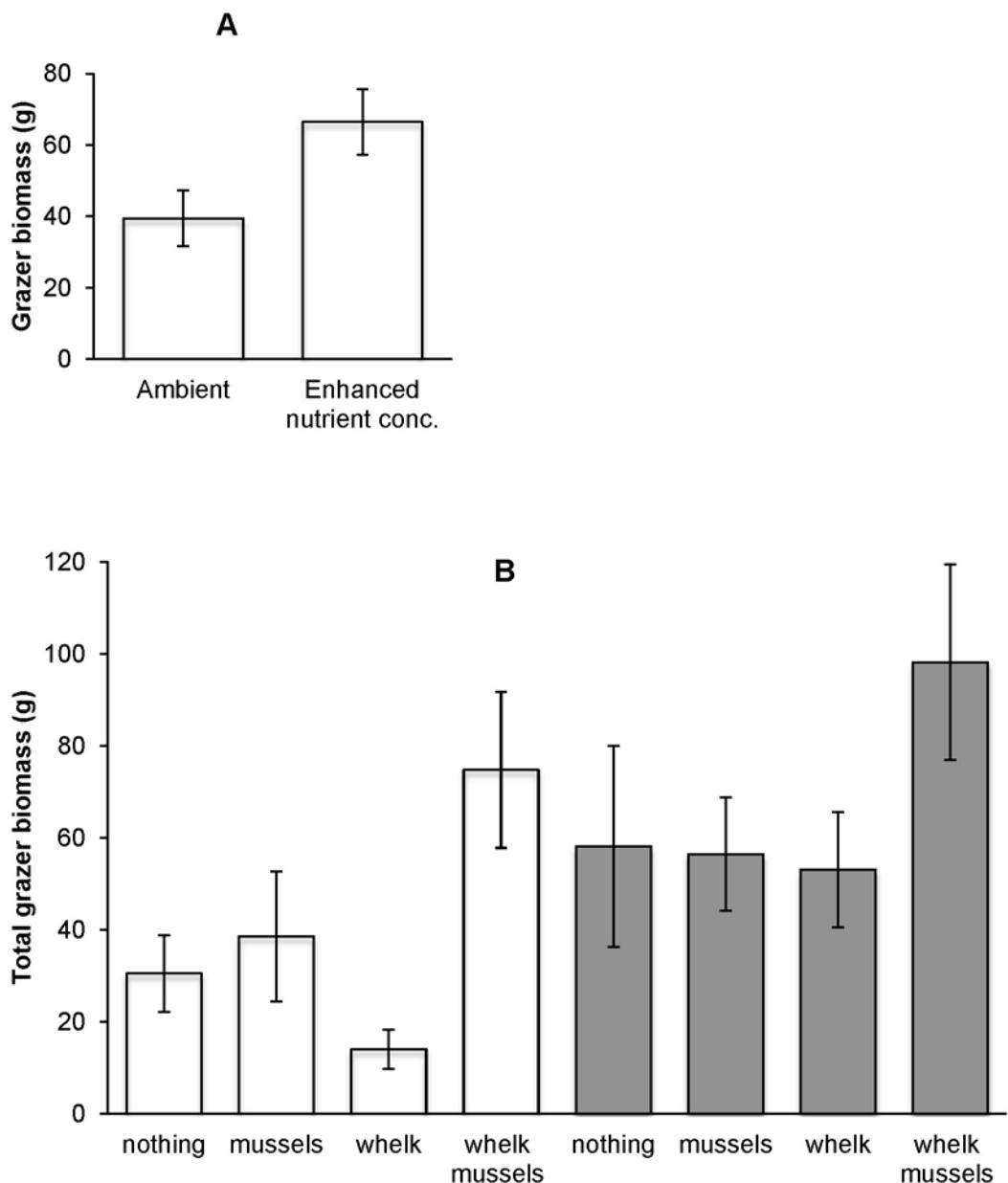


Figure 4.4. Total grazer biomass (mean +/- S. E.): A. Mean of all treatments at ambient conditions compared to mean of treatments at enhanced nutrient concentrations. After 13 months, $n = 4$. B. Treatments containing different combinations of functional groups of consumers in ambient (open bars) and enhanced nutrient concentrations (grey bars);

Total grazer biomass was greater in treatments with enhanced nutrient concentrations compared to treatments at ambient conditions ([Fig. 4.4](#); [Table 4.4](#)). A significant interaction occurred between the removal of primary consumers and the removal of whelks

([Table 4.4](#)) and post hoc tests show that the loss of mussels and whelks together led to an increase in grazer biomass regardless of nutrient concentration ([Fig. 4.4.B](#); $P < 0.05$).

Table 4.4. ANOVA to test the effect of enhanced nutrient concentration and for effects of loss of a predator and of mussels on total grazer biomass, after 14 months, n = 4. Significant P values are in bold.

Source of variation	Df	MS	F	P
Nutrient conc., N	1	5835.24	6.44	0.018
Predator, P	1	1586.23	1.75	0.198
Primary consumer, C	1	6289.93	6.95	0.014
N x P	1	143.91	0.16	0.694
N x C	1	323.09	0.36	0.556
P x C	1	4946.63	5.46	0.028
N x P x C	1	17.49	0.02	0.891
Residual	24	905.55		

PERMANOVA = Permutational analysis of variance; Df = Degrees of freedom; MS = Mean squares; F = pseudo F value; P = P (permutational).

4.4 Discussion

These findings show that total algal biomass was affected by the loss of a predator (whelks) and primary consumers (grazers). However, these effects were interactive and determined by environmental conditions. In contrast to a previous experiment (O'Connor et al. in review), at ambient conditions, the loss of grazers led to an increase in total algal biomass, whereas the loss of whelks alone or together with grazers led to a reduction in algal biomass. This indicates that the effect of loss of grazers on algal biomass was dependent on the presence of whelks. Enhanced nutrient concentration negated all effects of loss of species on total algal biomass, highlighting the necessity of incorporating environmental conditions when attempting to predict the effects of loss of species.

Algal assemblage structure was affected by the loss of whelks, mussels, grazers and nutrient concentration and this must be considered when interpreting the effects of loss of species on algal biomass. Consistent with the previous study (O'Connor et al. in review), the loss of mussels again led to an increase in the dominance of red-turfing algae and the loss of grazers led to an increase in fucoid algae. In contrast to the previous study, this experiment found that the loss of whelk also led to a shift in algal assemblage structure that included greater biomass of species, such as *P. umbilicalis*, which are commonly associated with mussel beds,

suggesting that this shift was driven by an increase in mussels resulting from a reduction in predation. Similar to the findings of Section 3, it is important to note that algal assemblages at enhanced nutrients differ from those at ambient conditions. The former are dominated by ephemeral species and caution is warranted against considering these assemblages as resistant to the effects of species loss based on total algal biomass because it is likely that these assemblages perform differently in terms of ecosystem functioning (Bruno et al. 2005; Stachowicz et al. 2008b; Bracken et al. 2011) and so they should not be considered as comparable for ecosystem services.

The identification of the direct and indirect effects of loss of mussels, grazers and whelks on algal biomass and assemblage structure is necessary for understanding the mechanisms driving interactions among functional groups at different trophic levels and for examining how these interactions vary with nutrient concentration. Several direct negative effects were identified between predators and primary consumers, including the effect of whelks on mussel biomass and the combined effects of whelks and mussels on grazer biomass. Both these effects were independent of nutrient concentration, although grazer biomass in general was greater at enhanced nutrients. Therefore, the effect of loss of grazers on total algal biomass is likely a direct effect resulting from a reduction in grazing pressure because there was no associated increase in mussel biomass, and algal assemblages shifted to the dominance of *F. vesiculosus*, *P. umbilicalis* and *U. lactua* (the preferred species of grazing gastropods; Hawkins 1983; Hawkins et al. 1992). The lack of effect of grazers on algal biomass at enhanced nutrients could be explained by the compensatory shift in algal assemblage structure that maintained the total algal biomass.

Indirect effects of predators on algal biomass (so-called trophic cascades) were also identified at ambient conditions. The effect of the loss of whelks on algal biomass was mediated by an increase in mussel biomass. This is clear because the removal of whelks led to an increase in mussel biomass and a reduction in algal biomass, as both mussels and algae have different predatory pressures but compete directly for space as a primary resource (Lubchenco and Menge 1978). Moreover, algal assemblages in plots without whelks shifted towards a dominance of

species, such as *O. pinnatifida*, *C. crispus*, *U. lactua* and *P. umbilicalis*, which are found commonly growing attached epiphytically to mussels (O'Connor and Crowe 2008). In addition, total algal biomass did not decrease when both whelks and mussels were removed – most likely because of the increase in grazer biomass, which may have increased grazing pressure and compensated for the positive effect of removing their competitor for space.

This study identified several direct and indirect effects of predators and primary consumers on primary producers. Some effects were consistent with previous studies (e.g. primary consumer identity affected algal assemblage structure) and others were not (e.g. predators also indirectly affected algal assemblage structure). Furthermore, many direct and indirect effects of consumers on primary producers were determined by environmental context. It is clear, therefore, that current models of the effects of loss of species are inadequate for predicting the effects of loss of species from multiple trophic levels in marine ecosystems.

Detailed information of the effects of loss of species derived from empirical evidence under different environmental conditions is required to improve current ecological models that aim to predict the effects of loss of species on ecosystem functioning. Future studies should address this paucity of data and also address the relationship between species loss and ecosystem stability. The findings of this study, combined with a previous experiment part-funded by the EPA and the Irish Research Council for Science, Engineering and Technology (IRCSET) (O'Connor et al. in review), has yielded valuable data that are currently being used to develop new models exploring the relationship between species loss and ecosystem stability under changing environmental conditions. A recently established working group will use these data to develop new models and includes partners at Queen's University Belfast (Nessa O'Connor and Mark Emmerson), Trinity College, Dublin (Ian Donohue and Andrew Jackson), University of Zurich (Owen Petchey) and Universitat Pompeu Fabra, Barcelona (José Montoya).

5 Recommendations

The robust benthic sampling strategies employed in this study did not identify clear effects of sewage outfalls on benthic assemblage structure or diversity. However, they did show that sewage outfalls affect the variability of benthic assemblages, which has important consequences in terms of ecosystem stability. The scale of this impact was identified as between 50 and 2,000 m from a point source (municipal outfall in Dublin area). The current findings highlight the variability of dynamic rocky shore communities and illustrate clearly the importance of incorporating spatial and temporal variation, at appropriate scales for putative impacts, into quantified monitoring programmes. It is also clear that changes in variability of assemblages (indicative of community stability) need to be considered together with shifts in assemblage structure and that whole benthic assemblages (not just algae) should be included to assess the ecological status of rocky shores accurately. An over-reliance on metrics based on species richness should be avoided and the development of other tools such as taxonomic distinctness indices or rocky intertidal community quality indices should be considered for future WFD monitoring programmes – in particular, surveillance monitoring.

Water Framework Directive (WFD) metrics are based on a comparison to a defined set of pristine conditions that may not be possible to define for rocky shores in a meaningful way. Moreover, the implementation of any ecological assessment tool may be hampered by the chronic lack of baseline data describing current biodiversity patterns of Irish shores and this should also be addressed in particular with regard to biosecurity and global change scenarios (Sweeney et al. 2003; Coll et al. 2009). The MarClim study of British coasts indicated that climate change is already having a profound impact on seashore indicator species (Laffoley et al. 2005), however, there are no long-term datasets available in Ireland with which to examine patterns of marine environmental change over time (Sweeney et al. 2003). It is considered likely that there will be changes in the relative distributions between southern and northern species assemblages (Coll et al. 2009) and the arrival of invasive species in coastal habitats is expected to have further implications, not least since the wider changes

in climate may favour their increased establishment (Sweeney et al. 2003). Biodiversity is certain to be affected, although changes in assemblage structure may be more likely than changes in the numbers of species (Boelens et al. 2005), and this should be reflected in monitoring programmes.

This study tested general ecological models and showed that the effects of loss of consumer species on ecosystem functioning cannot be predicted based on current species richness models. It also provided useful information for the management of marine resources: for example, it was shown that the effects of removal, for example, of some harvested species (mussels, littorinids) can vary with environmental conditions. Several direct and indirect effects of predators and primary consumers on primary producers were identified. Some effects were consistent with previous studies (e.g. primary consumer identity affected algal assemblage structure) and others were not (e.g. predators also indirectly affected algal assemblage structure). Furthermore, many direct and indirect effects of consumers on primary producers were shown to be determined by environmental conditions. It is clear that current models of the effects of loss of species are inadequate for predicting the effects of loss of species from multiple trophic levels in marine ecosystems. Detailed information of the effects of loss of species derived from empirical evidence under different environmental conditions is required to improve current ecological models that aim to predict the effects of loss of species on ecosystem functioning. Future studies should address this paucity of data and also address the relationship between species loss and ecosystem stability, specifically examining the multiple facets of ecosystem stability (Donohue et al. in review). The findings of this study are currently being used to develop new models exploring the relationship between species loss and ecosystem stability under changing environmental conditions.

This study identified specific interactions between effects of species loss and environmental conditions in a marine benthic system, and it highlights the importance of context-dependency when designing and interpreting

BEF experiments. Much more empirical research is needed to examine realistic species-loss scenarios under different environmental conditions, preferably under predicted and current levels of anthropogenic stresses to yield findings that can be better incorporated into ecosystem management (Bracken et al. 2008; Naeem 2008; Godbold and Solan 2009; Crowe et al. in press). It has been shown how enhanced nutrient concentration changed the effects of loss of species. Future work should incorporate other predicted environmental changes, such as sea temperature increases, ocean acidification and potentially the predicted arrival invasive species. Primary productivity rates and biomass accumulation (standing stock), which are indicative of changes in the functioning of a system, were measured. To further incorporate the multi-functionality of natural ecosystems, future studies

should also aim to measure multiple ecosystem functions (Hector and Bagchi 2007; Gamfeldt et al. 2008), such as nutrient cycling, decomposition rates, carbon fluxes, etc. It is also recommended that future empirical studies are supplemented by theoretical modelling approaches (possibly collaborative), to facilitate an optimal platform for the development and testing of new ecological models.

The lack of knowledge regarding how ecosystems function and how biodiversity contributes to that function remains a key challenge for scientists and should remain a priority area for research, principally, because the loss of biodiversity is likely to have a variety of effects on ecosystem functioning, resilience to change, the provision of goods and services and human well-being (NPBR 2006; Ferris 2007).

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Acronyms and Annotations

ANOVA	Analysis of variance
BEF	Biodiversity-ecosystem functioning
BQE	Biological quality element
CARLIT	CARtography of LITToral and sublittoral communities
CEC	Council of the European Communities
CFR	Quality of Rocky Bottoms Index
EEI	Ecological Evaluation Index
EPA	Environmental Protection Agency
ESG	Ecological status group
EQR	Ecological quality ratio
EU	European Union
H' (log_e)	Shannon diversity index
J'	Pielou's evenness index
MDS	Multi-dimensional scaling
METRIC	Marine Ecological Tools for Reference, Intercalibration and Classification
MSFD	Marine Strategy Framework Directive
NaGISA	Natural Geography In near Shore Areas
NPBR	National Platform for Biodiversity Research
PERMANOVA	Permutational analysis of variance
PERMDISP	Permutational analysis of multivariate dispersions
S	Taxon richness
SIMPER	Similarity of Percentages
RBD	River Basin District
RICQI	Rocky Intertidal Community Quality Index
RSL	Reduced algal Species List
TEEB	The Economics of Ecosystems and Biodiversity
WFD	Water Framework Directive

Appendix 1

Pairwise tests for ‘Distance x Time’ for pairs of levels of factor ‘Distance’ on benthic assemblage structure based on benthic taxa.

Groups	t	P (perm)
<i>Within level ‘Spring’ of factor ‘Time’</i>		
Proximate, Adjacent	0.63263	0.693
Proximate, None	0.96507	0.622
Adjacent, None	1.2182	0.181
<i>Within level ‘Summer’ of factor ‘Time’</i>		
Proximate, Adjacent	0.72574	0.773
Proximate, None	1.9377	0.104
Adjacent, None	1.4913	0.114
<i>Within level ‘Autumn’ of factor ‘Time’</i>		
Proximate, Adjacent	0.75586	0.71
Proximate, None	1.1877	0.407
Adjacent, None	1.3814	0.171
<i>Within level ‘Winter’ of factor ‘Time’</i>		
Proximate, Adjacent	0.53218	1
Proximate, None	1.2152	0.213
Adjacent, None	1.0725	0.528

Appendix 2

Pairwise tests of term ‘Location (Distance) x Time’ for pairs of levels of factor ‘Location’ on benthic assemblage structure based on benthic taxa. Significant P values are in bold.

Groups	t	P (perm)
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Spring’ of factor ‘Time’</i>		
Rush (proximate), Loughshinney (proximate)	3.3114	0.001
Rush (proximate), Portrane (proximate)	4.5879	0.001
Loughshinney (proximate), Portrane (proximate)	4.1674	0.001
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Summer’ of factor ‘Time’</i>		
Rush (proximate), Loughshinney (proximate)	2.1807	0.001
Rush (proximate), Portrane (proximate)	4.3872	0.001
Loughshinney (proximate), Portrane (proximate)	3.6694	0.001
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Autumn’ of factor ‘Time’</i>		
Rush (proximate), Loughshinney (proximate)	2.2535	0.003
Rush (proximate), Portrane (proximate)	5.2597	0.001
Loughshinney (proximate), Portrane (proximate)	4.0172	0.001
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Winter’ of factor ‘Time’</i>		
Rush (proximate), Loughshinney (proximate)	2.7724	0.001
Rush (proximate), Portrane (proximate)	4.1593	0.001
Loughshinney (proximate), Portrane (proximate)	3.7805	0.001
<i>Within level ‘Adjacent’ of factor ‘Distance’</i>		
<i>Within level ‘Spring’ of factor ‘Time’</i>		
Rush (adjacent), Loughshinney (adjacent)	1.5887	0.039
Rush (adjacent), Portrane (adjacent)	3.8825	0.001
Loughshinney (adjacent), Portrane (adjacent)	3.5703	0.001
<i>Within level ‘Adjacent’ of factor ‘Distance’</i>		
<i>Within level ‘Summer’ of factor ‘Time’</i>		
Rush (adjacent), Loughshinney (adjacent)	4.3659	0.001
Rush (adjacent), Portrane (adjacent)	3.7055	0.001
Loughshinney (adjacent), Portrane (adjacent)	3.9878	0.001
<i>Within level ‘Adjacent’ of factor ‘Distance’</i>		
<i>Within level ‘Autumn’ of factor ‘Time’</i>		
Rush (adjacent), Loughshinney (adjacent)	2.3084	0.001
Rush (adjacent), Portrane (adjacent)	3.7253	0.001
Loughshinney (adjacent), Portrane (adjacent)	3.389	0.001

Groups	t	P (perm)
<i>Within level 'Adjacent' of factor 'Distance'</i>		
<i>Within level 'Winter' of factor 'Time'</i>		
Rush (adjacent), Loughshinney (adjacent)	2.7755	0.001
Rush (adjacent), Portrane (adjacent)	3.0242	0.001
Loughshinney (adjacent), Portrane (adjacent)	3.2481	0.001
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Spring' of factor 'Time'</i>		
Bremore, Barnageeragh	2.9915	0.001
Bremore, Portmarnock	2.386	0.002
Barnageeragh, Portmarnock	2.4804	0.001
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Summer' of factor 'Time'</i>		
Bremore, Barnageeragh	2.1237	0.003
Bremore, Portmarnock	2.7312	0.001
Barnageeragh, Portmarnock	2.3732	0.002
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Autumn' of factor 'Time'</i>		
Bremore, Barnageeragh	2.6477	0.003
Bremore, Portmarnock	2.7164	0.001
Barnageeragh, Portmarnock	2.5164	0.001
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Winter' of factor 'Time'</i>		
Bremore, Barnageeragh	1.6419	0.021
Bremore, Portmarnock	2.129	0.003
Barnageeragh, Portmarnock	1.1879	0.223

Appendix 3

Pairwise tests of term ‘Location (Distance) x Time’ for pairs of levels of factor ‘Time’ on benthic assemblage structure based on benthic taxa. Significant *P* values are in bold.

Groups	t	P (perm)
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Rush (proximate)’ of factor ‘Location’</i>		
Spring, Summer	2.2578	0.002
Spring, Autumn	3.0626	0.001
Spring, Winter	2.3251	0.001
Summer, Autumn	4.0838	0.001
Summer, Winter	3.7214	0.001
Autumn, Winter	3.1834	0.001
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Loughshinney (proximate)’ of factor ‘Location’</i>		
Spring, Summer	2.8937	0.001
Spring, Autumn	1.1433	0.249
Spring, Winter	1.1085	0.255
Summer, Autumn	2.9381	0.001
Summer, Winter	2.7568	0.001
Autumn, Winter	0.88205	0.527
<i>Within level ‘Proximate’ of factor ‘Distance’</i>		
<i>Within level ‘Portrane (proximate)’ of factor ‘Location’</i>		
Spring, Summer	3.9716	0.001
Spring, Autumn	3.1389	0.001
Spring, Winter	3.0681	0.001
Summer, Autumn	2.768	0.002
Summer, Winter	2.1593	0.007
Autumn, Winter	1.5497	0.070
<i>Within level ‘Adjacent’ of factor ‘Distance’</i>		
<i>Within level ‘Rush (adjacent)’ of factor ‘Location’</i>		
Spring, Summer	3.2023	0.001
Spring, Autumn	2.3512	0.001
Spring, Winter	2.623	0.001
Summer, Autumn	2.815	0.001
Summer, Winter	2.5864	0.001
Autumn, Winter	2.7514	0.001

Groups	t	P (perm)
<i>Within level 'Adjacent' of factor 'Distance'</i>		
<i>Within level 'Loughshinney (adjacent)' of factor 'Location'</i>		
Spring, Summer	3.9958	0.001
Spring, Autumn	1.3459	0.093
Spring, Winter	1.8332	0.007
Summer, Autumn	4.338	0.001
Summer, Winter	4.8805	0.001
Autumn, Winter	2.3045	0.001
<i>Within level 'Adjacent' of factor 'Distance'</i>		
<i>Within level 'Portrane (adjacent)' of factor 'Location'</i>		
Spring, Summer	3.9941	0.001
Spring, Autumn	3.3341	0.001
Spring, Winter	2.7847	0.001
Summer, Autumn	2.2305	0.004
Summer, Winter	2.23	0.003
Autumn, Winter	1.3695	0.125
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Bremore' of factor 'Location'</i>		
Spring, Summer	2.4121	0.001
Spring, Autumn	2.1386	0.001
Spring, Winter	2.4008	0.001
Summer, Autumn	2.3223	0.001
Summer, Winter	1.6943	0.021
Autumn, Winter	1.2124	0.216
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Barnageeragh' of factor 'Location'</i>		
Spring, Summer	4.2692	0.001
Spring, Autumn	3.1219	0.001
Spring, Winter	2.7441	0.001
Summer, Autumn	2.947	0.001
Summer, Winter	1.8722	0.010
Autumn, Winter	1.9126	0.017
<i>Within level 'No sewage outfall' of factor 'Distance'</i>		
<i>Within level 'Portmarnock' of factor 'Location'</i>		
Spring, Summer	2.5624	0.002
Spring, Autumn	1.2645	0.190
Spring, Winter	1.5945	0.049
Summer, Autumn	1.7667	0.024
Summer, Winter	1.5577	0.036
Autumn, Winter	1.1538	0.221

Appendix 4

SIMPER analyses of benthic taxa contributing to difference in assemblages at shores with sewage (< 10 m from outfall) and shores without sewage outfalls. DIss./ SD = measure of the variation in contribution to dissimilarity (Clarke 1993). Contrib. % = average percentage contribution to the overall Bray-Curtis dissimilarity between assemblages with and without sewage (71.87%). The taxa listed account for > 99% of the dissimilarity. n = 90.

Algal taxa	Average cover (%)/individual				
	Outfall (proximate)	No outfall	Diss./SD	Contrib.%	Cum.%
<i>Semibalanus balanoides</i>	37.64	43.2	1.25	23.54	23.54
<i>Fucus vesiculosus</i>	2.75	29.33	0.89	17.56	41.1
<i>Mytilus edulis</i>	13.04	7.67	0.65	11.08	52.18
<i>Lithophamnion spp.</i>	11.96	13.08	0.8	10.98	63.15
<i>Fucus serratus</i>	4.80	10.57	0.48	7.72	70.87
<i>Osmundea pinnatifida</i>	3.95	8.13	0.58	5.97	76.84
<i>Ulva lactua</i>	9.18	1.23	0.51	5.11	81.95
<i>Chondrus crispus</i>	5.22	1.63	0.51	3.29	85.24
<i>Patella vulgata</i>	4.15	1.71	0.8	2.77	88.00
<i>Ceramium spp.</i>	1.07	2.63	0.38	1.61	89.61
<i>Ulva intestinalis</i>	1.60	1.1	0.31	1.52	91.13
<i>Fucus spiralis</i>	0.18	1.69	0.19	1.28	92.41
<i>Hilena brandia spp.</i>	0.65	1.32	0.26	1.27	93.69
<i>Chthamalus montagui</i>	1.25	0.17	0.23	1.05	94.74
<i>Polysiphonia fucoides</i>	0.36	1.65	0.3	0.97	95.71
<i>Rhodothamniella floridula</i>	0.65	0.27	0.13	0.5	96.21
<i>Ulothrix sp.</i>	0.70	0	0.17	0.47	96.68
<i>F. vesiculosus evesiculosus</i>	0.28	0.48	0.11	0.46	97.14
<i>Odonthalia dentata</i>	0	0.73	0.15	0.41	97.55
<i>Littorina littorea</i>	0.33	0.22	0.42	0.34	97.90
<i>Ectocarpus sp.</i>	0.67	0	0.16	0.33	98.23
<i>Littorina neritoides</i>	0.17	0.15	0.16	0.21	98.43
<i>Palmaria palmata</i>	0.13	0.26	0.21	0.20	98.64
<i>Gibbula umbilicalis</i>	0.29	0.03	0.25	0.19	98.83
<i>Gelidium pucillum</i>	0.08	0.30	0.20	0.16	98.99
<i>Elachista fucicola</i>	0.03	0.25	0.15	0.16	99.16
<i>Lomentaria articulata</i>	0.19	0.13	0.17	0.14	99.3

Appendix 5

Pairwise tests each level of the term A. ‘Time’ and B. ‘Location’ on dispersion of taxa in benthic assemblages. Significant *P* values are in bold.

A.	t	P (perm)
Groups		
(Spring, Summer)	7.5352	0.001
(Spring, Autumn)	3.4519	0.004
(Spring, Winter)	4.5984	0.002
(Summer, Autumn)	4.9661	0.001
(Summer, Winter)	2.8606	0.021
(Autumn, Winter)	1.6192	0.160

B.	t	P (perm)
Groups		
(Rush [proximate], Loughshinney [proximate])	7.3658	0.001
(Rush [proximate], Portrane [proximate])	3.51E-02	0.982
(Rush [proximate], Rush [adjacent])	2.0174	0.109
(Rush [proximate], Loughshinney [adjacent])	6.3192	0.001
(Rush [proximate], Portrane [adjacent])	4.2017	0.001
(Rush [proximate], Bremore)	1.256	0.318
(Rush [proximate], Barnageeragh)	3.1274	0.010
(Rush [proximate], Portmarnock)	3.6437	0.001
(Loughshinney [proximate], Portrane [proximate])	7.5865	0.001
(Loughshinney [proximate], Rush [adjacent])	4.1237	0.001
(Loughshinney [proximate], Loughshinney [adjacent])	0.25043	0.846
(Loughshinney [proximate], Portrane [adjacent])	3.3517	0.003
(Loughshinney [proximate], Bremore)	5.1352	0.001
(Loughshinney [proximate], Barnageeragh)	4.1151	0.001
(Loughshinney [proximate], Portmarnock)	3.5711	0.001
(Portrane [proximate], Rush [adjacent])	2.0773	0.089
(Portrane [proximate], Loughshinney [adjacent])	6.4757	0.001
(Portrane [proximate], Portrane [adjacent])	4.33	0.001
(Portrane [proximate], Bremore)	1.3064	0.265
(Portrane [proximate], Barnageeragh)	3.2237	0.006
(Portrane [proximate], Portmarnock)	3.7513	0.001
(Rush [adjacent], Loughshinney [adjacent])	3.5655	0.005
(Rush [adjacent], Portrane [adjacent])	1.5293	0.202
(Rush [adjacent], Bremore)	0.73099	0.564
(Rush [adjacent], Barnageeragh)	0.70269	0.554
(Rush [adjacent], Portmarnock)	1.1457	0.365

B.	t	P (perm)
Groups		
(Loughshinney [adjacent], Bremore)	4.4633	0.001
(Loughshinney [adjacent], Barnageeragh)	3.3713	0.007
(Loughshinney [adjacent], Portmarnock)	2.8856	0.021
(Portrane [adjacent], Bremore)	2.4302	0.032
(Portrane [adjacent], Barnageeragh)	0.95378	0.424
(Portrane [adjacent], Portmarnock)	0.41274	0.717
(Bremore, Barnageeragh)	1.5465	0.206
(Bremore, Portmarnock)	2.0041	0.088
(Barnageeragh, Portmarnock)	0.51767	0.632

Appendix 6

PERMDISP pairwise test of each level of the term Sewage Outfall X Location, on dispersion of functional groups within algal assemblages.
Significant *P* values are in bold.

Groups	t	P (perm)
(Outfall Rush, Outfall Loughshinney)	1.3558	0.241
(Outfall Rush, Outfall Portrane)	1.3809	0.261
(Outfall Rush, No outfall Bremore)	5.7935	0.001
(Outfall Rush, No outfall Barnageeragh)	7.3068	0.001
(Outfall Rush, No outfall Portmarnock)	3.8472	0.002
(Outfall Loughshinney, Outfall Portrane)	2.4144	0.048
(Outfall Loughshinney, No outfall Bremore)	4.0951	0.001
(Outfall Loughshinney, No outfall Barnageeragh)	4.6973	0.001
(Outfall Loughshinney, No outfall Portmarnock)	2.1352	0.077
(Outfall Portrane, No outfall Bremore)	6.6118	0.001
(Outfall Portrane, No outfall Barnageeragh)	8.2723	0.001
(Outfall Portrane, No outfall Portmarnock)	4.8224	0.002
(No outfall Bremore, No outfall Barnageeragh)	0.30832	0.814
(No outfall Bremore, No outfall Portmarnock)	2.1687	0.081

An Gníomhaireacht um Chaomhnú Comhshaoil

Is í an Gníomhaireacht um Chaomhnú Comhshaoil (EPA) comhlactha reachtúil a chosnaíonn an comhshaol do mhuintir na tíre go léir. Rialáimid agus déanaimid maoirsiú ar ghníomhaíochtaí a d'fhéadfadh truailliú a chruthú murach sin. Cinntímid go bhfuil eolas cruinn ann ar threochtaí comhshaoil ionas go nglactar aon chéim is gá. Is iad na príomh-nithe a bhfuilimid gníomhach leo ná comhshaol na hÉireann a chosaint agus cinntí go bhfuil forbairt inbhuanaithe.

Is comhlacht poiblí neamhspleách í an Gníomhaireacht um Chaomhnú Comhshaoil (EPA) a bunaíodh i mí Iúil 1993 faoin Acht fán nGníomhaireacht um Chaomhnú Comhshaoil 1992. Ó thaobh an Rialtais, is í an Roinn Comhshaoil, Pobal agus Rialtais Áitiúil.

ÁR bhFREAGRACHTAÍ

CEADÚNÚ

Bíonn ceadúnais á n-eisiúint againn i gcomhair na nithe seo a leanas chun a chinntí nach mbíonn astuithe uathu ag cur sláinte an phobail ná an comhshaol i mbaol:

- áiseanna dramhaíola (m.sh., líonadh talún, loisceoirí, stáisiúin aistrithe dramhaíola);
- gníomhaíochtaí tionsclaíocha ar scála mór (m.sh., déantúsaiocht cágaisíochta, déantúsaiocht stroighne, stáisiúin chumhactha);
- diantalmhaíocht;
- úsáid faoi shrian agus scaoileadh smachtaithe Órgánach Génathraithe (GMO);
- mór-áiseanna stórais peitreibl;
- scardadh dramhuisce.

FEIDHMIÚ COMHSHAOIL NÁISIÚNTA

- Stiúradh os cionn 2,000 iniúchadh agus cigireacht de áiseanna a fuair ceadúnas ón nGníomhaireacht gach bliain.
- Maoirsíú freagrachaí cosanta comhshaoil údarás áitiúla thar sé earnáil - aer, fuaim, dramhaíl, dramhuisce agus caighdeán uisce.
- Obair le húdaráis áitiúla agus leis na Gardaí chun stop a chur le gníomhaíocht mhídhleathach dramhaíola trí comhordú a dhéanamh ar líonra forfheidhmithe náisiúnta, díriú isteach ar chiontóirí, stiúradh fiosrúcháin agus maoirsíú leigheas na bhfadhbanna.
- An dlí a chur orthu siúd a bhriseann dlí comhshaoil agus a dhéanann dochar don chomhshaol mar thoradh ar a ngníomhaíochtaí.

MONATÓIREACHT, ANAILÍS AGUS TUAIRISCIÚ AR AN GCOMHSHAOIL

- Monatóireacht ar chaighdeán aeir agus caighdeán aibhneacha, locha, uiscí taoide agus uiscí talaimh; leibhéal agus sruth aibhneacha a thomhas.
- Tuairisciú neamhspleách chun cabhrú le rialtais náisiúnta agus áitiúla cinntí a dhéanamh.

RIALÚ ASTUITHE GÁIS CEAptha TEASA NA HÉIREANN

- Cainníochtú astuithe gáis ceaptha teasa na hÉireann i gcomhthéacs ár dtiomantas Kyoto.
- Cur i bhfeidhm na Treorach um Thrádáil Astuithe, a bhfuil baint aige le hos cionn 100 cuideachta atá ina mór-ghineadóirí dé-ocsáid charbóin in Éirinn.

TAIGHDE AGUS FORBAIRT COMHSHAOIL

- Taighde ar shaincheisteanna comhshaoil a chomhordú (cosúil le caighdéan aeir agus uisce, athrú aeráide, bithéagsúlacht, teicneolaíochtaí comhshaoil).

MEASÚNÚ STRAITÉISEACH COMHSHAOIL

- Ag déanamh measúnú ar thionchar phleananna agus chláracha ar chomhshaol na hÉireann (cosúil le pleannanna bainistíochta dramhaíola agus forbartha).

PLEANÁIL, OIDEACHAS AGUS TREOIR CHOMHSHAOIL

- Treoir a thabhairt don phobal agus do thionscal ar cheisteanna comhshaoil éagsúla (m.sh., iarratais ar cheadúnais, seachaint dramhaíola agus rialacháin chomhshaoil).
- Eolas níos fearr ar an gcomhshaol a scaipeadh (trí cláracha teilifise comhshaoil agus pacáistí acmhainne do bhunscoileanna agus do mheánscoileanna).

BAINISTÍOCHT DRAMHAÍOLA FHORGHNÍOMHACH

- Cur chun cinn seachaint agus laghdú dramhaíola trí comhordú An Chláir Náisiúnta um Chosc Dramhaíola, lena n-áirítear cur i bhfeidhm na dTionscnamh Freagrachta Táirgeoirí.
- Cur i bhfeidhm Rialachán ar nós na treoracha maidir le Trealamh Leictreach agus Leictreonach Caite agus le Srianadh Substaíntí Guaiseachá agus substaintí a dhéanann ídiú ar an grios ózón.
- Plean Náisiúnta Bainistíochta um Dramhaíl Ghuaiseach a fhorbairt chun dramhaíl ghuaiseach a sheachaint agus a bainistiú.

STRUCHTÚR NA GNÍOMHAIREACHTA

Bunaíodh an Gníomhaireacht i 1993 chun comhshaol na hÉireann a chosaint. Tá an eagraíocht á bhainiú ag Bord lánaimseartha, ar a bhfuil Príomhstiúrthóir agus ceithre Stiúrthóir.

Tá obair na Gníomhaireachta ar siúl trí ceithre Oifig:

- An Oifig Aeráide, Ceadúnaithe agus Úsáide Acmhainní
- An Oifig um Fhorfheidhmiúchán Comhshaoil
- An Oifig um Measúnacht Comhshaoil
- An Oifig Cumarsáide agus Seirbhísí Corparáide

Tá Coiste Comhairleach ag an nGníomhaireacht le cabhrú léi. Tá dáréag ball air agus tagann siad le chéile cúpla uair in aghaidh na bliana le plé a dhéanamh ar cheisteanna ar ábhar imní iad agus le comhairle a thabhairt don Bhord.

Science, Technology, Research and Innovation for the Environment (STRIVE) 2007-2013

The Science, Technology, Research and Innovation for the Environment (STRIVE) programme covers the period 2007 to 2013.

The programme comprises three key measures: Sustainable Development, Cleaner Production and Environmental Technologies, and A Healthy Environment; together with two supporting measures: EPA Environmental Research Centre (ERC) and Capacity & Capability Building. The seven principal thematic areas for the programme are Climate Change; Waste, Resource Management and Chemicals; Water Quality and the Aquatic Environment; Air Quality, Atmospheric Deposition and Noise; Impacts on Biodiversity; Soils and Land-use; and Socio-economic Considerations. In addition, other emerging issues will be addressed as the need arises.

The funding for the programme (approximately €100 million) comes from the Environmental Research Sub-Programme of the National Development Plan (NDP), the Inter-Departmental Committee for the Strategy for Science, Technology and Innovation (IDC-SSTI); and EPA core funding and co-funding by economic sectors.

The EPA has a statutory role to co-ordinate environmental research in Ireland and is organising and administering the STRIVE programme on behalf of the Department of the Environment, Heritage and Local Government.



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