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Biodiversity and ecosystem functioning in coastal marine communities
Towards predicting the consequences of extinction for ecosystem functioning in natural assemblages

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# Biodiversity and ecosystem functioning in coastal marine communities 

Towards predicting the consequences of extinction for ecosystem functioning in natural assemblages

Thomas Wynter Davies

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## Doctoral Thesis

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MATURAL
ENVIRONMENT

## RESEARCH COUNCIE



## Summary

Over a decade of research shows that the services ecosystems provide to humanity can be affected by biodiversity loss. Yet the ability to predict the consequences of species loss on ecosystem functioning has proved elusive. In part this is because conventional approaches to understanding the role of biodiversity in the maintenance of ecosystem functioning have done so in assembled communities which do not reflect natural population densities or extinction patterns. A series of empirically informed realistic biodiversity manipulations were performed in contrasting unitrophic marine communities. The aim was to test whether species contributions to community biomass can be used as surrogate measures of their contribution to ecosystem processes, as this could be used to predict the short term ('worst case scenario') consequences of species loss for ecosystem processes. The functional contribution of species was directly proportional to their contribution to community biomass in a 1:1 ratio. This relationship was consistent across three contrasting marine ecosystems and three ecosystem processes. Hence population biomass estimates can be used to predict worst case scenarios of the decline in ecosystem processes with species loss. A best case scenario was also modeled in which biomass loss associated with species extinction was fully compensated for by the extant species with the highest per capita contribution to ecosystem processes. When combined, the best and worst case scenarios provide an estimate of the maximum and minimum number of species required to maintain different levels of ecosystem processes. Such estimates can be useful for environmental managers as there is a current lack of understanding of the processes which govern compensation of ecosystem function by extinction resilient species in nature, inhibiting the generation of more realistic long term biodiversity-ecosystem function relationships.

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## Chapter 1. General Introduction

## Chapter 1 General Introduction

### 1.1 Introduction

It is now widely accepted that the anthropogenic exploitation of earth's natural resources is resulting in rapid losses of biodiversity at both regional and global scales (Sala et al. 2000a, Sala 2003, Pereira et al. 2010). In a recent assessment of ocean ecosystem health, $41 \%$ of the world's oceans were classified as suffering from medium high or high anthropogenic impacts (Halpern et al. 2008). This loss of biodiversity may seriously impinge on the goods and services which ecosystems provide to humanity by deleteriously impacting on ecosystem functions such as crop pollination (Larsen et al. 2005, Winfree and Kremen 2009), nutrient cycling (Bracken and Stachowicz 2006, Bracken et al. 2008, Solan et al. 2008) and primary production (Tilman 1999a, Bruno et al. 2005, Marquard et al. 2009).

In response to rising concerns over biodiversity loss, recent decades have witnessed the development of a rapidly expanding research agenda which attempts to evaluate the role of biodiversity in the maintenance of ecosystem functioning and hence the provision of goods and services to humanity (Solan et al. 2009). Today the Biodiversity - Ecosystem Functioning (BEF) debate has generated a wealth of research including three meta analyses (Balvanera et al. 2006, Cardinale et al. 2006, Schmid et al. 2009) which attempt to understand the mechanisms by which higher biodiversity can maintain ecosystem services. Biodiversity - Ecosystem Functioning investigations have traditionally used a
replacement series design in which species or functional richness is manipulated using randomly selected subsets of species from a larger species pool and initial densities are fixed across species richness treatments (Naeem and Li 1997, Tilman et al. 1997, Symstad et al. 1998, Hector et al. 1999, Stachowicz et al. 1999, Tilman 1999a, Hector et al. 2001, Loreau and Hector 2001, Marquard et al. 2009). Collectively these investigations have identified two principle groups of ecological mechanisms through which biodiversity may affect ecosystem functioning. Positive species interactions such as niche complementarity, facilitation and sampling effects. The theory of niche complementarity stipulates that as species richness increases competition becomes dominated by interspecific rather than intraspecfic interactions, hence because different species are adapted to exploit different aspects of the resources available to them, resource use efficiency and hence productivity increases (Hooper et al. 2005). By contrast the theory of sampling effects stipulates that one or few species contribute disproportionately to ecosystem function (Hooper et al. 2005, Stachowicz et al. 2007), and increasing biodiversity increases the probability that these species will be constituents of an assemblage. During their inception, many of the earlier biodiversityecosystem functioning experiments were criticised because their design could not identify whether positive biodiversity effects were driven by niche complementarity or sampling effects (Huston 1997), leading to the design of replacement series experiments, which compare species rich assemblages with the most productive monoculture. Where the standing biomass of a species rich community is higher than that of the best performing monoculture, this 'overyielding' is strong evidence for positive biodiversity effects on resource use efficiency (Tilman 1999b, Marquard et al. 2009). Today the sampling effect
is no longer considered a statistical artefact of improperly designed experiments, but an alternative way through which increasing species richness can influence ecosystem functioning (Wardle 1999, Srivastava and Vellend 2005).

Replacement series approaches have established that biodiversity can have a positive influence on productivity in ecosystems (Tilman 1999a, Marquard et al. 2009), the stability of ecosystems (Tilman et al. 2006), and multiple ecosystem processes measured simultaneously (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010). However, drawing generalised conclusions from such experiments about the consequences of biodiversity loss for natural systems is difficult. This is because despite being statistically rigorous in their approach, they often implicitly assume that patterns of species loss are random (Hooper et al. 2005, Srivastava and Vellend 2005, Bulling et al. 2006). In nature, however, species often go extinct in a deterministic order contingent on the presence of particular functional response traits (see Box 1.1) which may make them more or less resistant to a particular disturbance (Pimm et al. 1988, Roberts and Hawkins 1999, Cardillo et al. 2005). There is now an accumulating body of evidence which suggests that the consequences of deterministic species loss are markedly different from those of random species loss (Ostfeld and LoGiudice 2003, Solan et al. 2004, Zavaleta and Hulvey 2004, Gross and Cardinale 2005, Bracken et al. 2008).

In order to move towards predicting the consequences of biodiversity loss for ecosystem functioning, the second section of this thesis explores those community properties which determine the rate of decline in ecosystem processes in the real world and presents a hypothetical framework for exploring them. The final section introduces the objectives of this thesis and provides a brief outline of its contents.

## Box 1.1

## Functional Traits and Ecosystem Function

Predicting the consequences of species loss in an ecosystem requires an appreciation of what traits make species susceptible to extirpation and important for ecosystem function. Functional response traits are those aspects of an organism's morphology, physiology, and ecology which determine its response to environmental change while functional effect traits determine its impact on the functioning of wider ecosystem. In Larsen et al. 's (2005) model the consequences of species loss for ecosystem function are dependent on the relationship between functional importance and extinction susceptibility, hence they depend on whether or not functional response traits and functional effect traits are correlated. Strong correlations between functional response and effect traits result in a strong dependence of ecosystem function on patterns of community disassembly (Chapin et al. 2000, Diaz and Cabido 2001, Hooper et al. 2002, Hooper et al. 2005).

### 1.2 Incorporating realistic extinction patterns into BEF investigations

Today, investigations which attempt to understand the consequences of natural species extinctions are increasingly contributing to the BEF debate (Wardle et al. 1997, Jonsson et al. 2002, Ostfeld and LoGiudice 2003, Smith and Knapp 2003, Solan et al. 2004, Zavaleta and Hulvey 2004, Bunker et al. 2005, Gross and Cardinale 2005, Larsen et al. 2005, Schlapfer et al. 2005, Losure et al. 2007, McIntyre et al. 2007, Srinivasan et al. 2007, Zavaleta and Hulvey 2007, Bracken et al. 2008). However many of these investigations use computer simulations (Solan et al. 2004, Gross and Cardinale 2005) or predict extinction orders based on organism traits which are thought to determine extinction resilience in nature (Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007). For example Solan et al. (2004) simulated extinction in a macrobenthic invertebrate assemblage according to known correlates of extinction risk such as body size and rarity. Where extinction orders have been empirically derived, they typically rely on observational approaches which attempt to link existing patterns in community structure with known external forces such as habitat fragmentation or natural disturbance
events such as wave exposure (Zavaleta and Hulvey 2004, Larsen et al. 2005, Srinivasan et al. 2007, Bracken et al. 2008). While this approach is capable of quantifying patterns in community structure at large geographical scales, it assumes a causal link between the existing pattern of community structure and some large scale disturbance event known to be taking place. Hence this approach lacks the ability to empirically relate patterns of community composition to specific disturbance events limiting its ability to draw conclusions about the effect of different disturbances on ecosystem structure and functioning. For example Zavaleta and Hulvey (2004) employed a nested subset analysis which allowed for the determination of a rank extinction order for vascular plants in an experimental grassland ecosystem. The nested subset approach quantifies the order of species extinction across gradients of species richness by quantifying patterns of nestedness in community structure (Wright and Reeves 1992, Atmar and Patterson 1993). Where communities of differing species richness are highly nested, extinction susceptible species will be present only in areas with the highest species richness, while resilient species will persist in regions where species richness is at its lowest. This approach however, assumes that the pattern of species richness observed is caused by some disturbance on the ecosystem which varies spatially in the impact it has. Zavaleta and Hulvey (2004) could not demonstrated a causal link between the richness pattern observed and the disturbances proposed to be responsible, as is often the case where authors quantify patterns of species loss using observational data. Recent developments in this nested subset approach have now provided analyses which can weight patterns of nestedness according to known disturbance gradients (Ulrich et al. 2009), however the reliability of these approaches is so far untested. Bracken et al. (2008) manipulated the
diversity of a macroalgal community to represent changes in community structure across a gradient of wave exposure. However no causal relationship between the two was empirically demonstrated. Larsen et al. (2005), quantified the extinction patterns of dung beetles and bee species using observed changes in community composition across recently created islands of differing size and a gradient of agricultural intensification respectively. Although the observed compositional patterns are likely to be strongly driven by the proposed disturbance regimes in these cases, this observational approach to quantifying extinction patterns does not provide data which can reliably inform us of the context of BEF relationships under different disturbance scenarios. This is particularly important as a number of investigations have highlighted how the rate of decline in ecosystem functioning is dependent on the order of species extinction (Solan et al. 2004, Larsen et al. 2005). For example Larsen et al. (2005) found that because large bodied dung beetle and bee species were both most efficient at performing their respective ecosystem functions, and most prone to extinction, dung burial and pollination rates declined rapidly with species loss.

Empirically determining patterns of community disassembly under different disturbance scenarios is a necessary prerequisite if ecologists are to identify whether BEF relationships may be generalised across multiple systems and disturbance types or whether they are context dependent (Zavaleta et al. 2009). Integral to moving towards such generalizations should be approaches in which established communities can be exposed to different types and intensities of disturbance. In adopting such approaches, investigators can contribute data to the research community which is directly applicable to policy makers and conservationists. Many of the above investigations have provided
solid foundations on which the next generation of BEF investigations may be built. However in doing so researchers should strive to achieve designs which are as close to reality as possible. Only by combining observational and manipulative experimental designs which can empirically relate realistic disturbance to changes in biodiversity and ecosystem function can such applied studies fulfil their full potential and identify the principle mechanisms through which biodiversity loss will affect ecosystem functioning in nature.

### 1.3 A framework for predicting the consequences of species loss for

 ecosystem functioning in nature.
### 1.3.1 The role of biomass in determining short term BEF relationships.

Current consensus suggests that the relationship between biodiversity and ecosystem functioning is dependent on whether functional effect traits which determine the contribution of species to ecosystem function are correlated with functional response traits which determine their susceptibility to extinction (Diaz and Cabido 2001) (Box 1). Thus the BEF relationship is dependent on the order of species extinction with respect to their contribution to ecosystem functioning (the functional extinction order) (Larsen et al. 2005). The way in which biomass is allowed to vary with declining species richness has been a fundamental issue in the design of BEF experiments (Huston 1997, Byrnes and Stachowicz 2009). Intuition suggests that in the short term, changes in community biomass resulting from species extinctions are likely to drive changes in ecosystem processes. The 'mass - ratio' hypothesis (Grime 1998) suggests that dominant species control the majority of ecosystem processes in natural assemblages because they are the
most numerically abundant. By contrast differences in organism level traits and positive species interactions (i.e. complimentary resource use and facilitation) could be of negligible importance for ecosystem processes. This theory is a kin to The Metabolic Theory of Ecology which predicts that the turnover of energy by a population will be proportional to the biomass of that population because species metabolic rates scale positively with individual biomass in the same ratio as population density scales negatively with individual biomass (Ernest et al. 2003, Brown et al. 2004). A number of studies have identified biomass-dominant species as being major contributors to ecosystem functioning (Smith and Knapp 2003, Solan et al. 2004, Grman et al. 2010, Sasaki and Lauenroth 2011), suggesting that loss of ecosystem function will be dependent on the position of such species in the extinction order of natural assemblages (Schwartz et al. 2000, Raffaelli 2004, Gross and Cardinale 2005, Losure et al. 2007). Replacement series design experiments have been unable to identify the importance of dominant species for ecosystem functioning, because they generate artificially uniform assemblages where all species are planted at similar fixed densities. By contrast the biomass of natural assemblages is often dominated by one or few species (Whittaker 1975, Gaston 2010). Hence in order to test the prevalence of mass-ratio theory in natural ecosystems, researchers need to conduct in situ biodiversity manipulations in which species are removed from natural assemblages and the associated decline in ecosystem processes is quantified and related to their population biomass. This substractive design is becoming more commonly employed to quantify the long term impacts of species removal on ecosystem functioning (Wootton 2004, Cross and Harte 2007, Munson and Lauenroth 2009, Grman et al. 2010, Wootton 2010).

Previously Larsen et al. (2005) presented a hypothetical model which described how extinction order and functional effect traits interact to describe BEF relationships in nature. In their model Larsen et al. (2005) identify that the shape of the biodiversity ecosystem function relationship is dependent on the order of species extinction with respect to their functional contribution. Figure. 1.3.1 presents an extension of this model which demonstrates how different dominance patterns and functional extinction orders interact to produce BEF relationships where biomass is assumed to drive the functional contribution of species. Where biomass is distributed evenly across the community (Figure. 1.3.1. A), the removal of any species results in an equitable loss of functioning; hence the BEF relationship is linear regardless of extinction order (Larsen et al. 2005). Where species display inequitable contributions to community biomass, the BEF relationship is dependent on the magnitude of dominance (Schwartz et al. 2000, Adler and Bradford 2002) and the position of dominant species within the extinction order (Figure. 1.3.1 B and C). Exponentially decaying rank - population biomass distributions (Figure 1.3.1 C) result in ecosystem functioning being more sensitive or more redundant to species loss than predicted by linear distributions (Figure. 1.3.1 B). This model suggests that predictions can be made about BEF relationships in nature provided that population biomass determines the contribution of species to ecosystem function; the distribution of biomass across an assemblage is known; and the order of species loss with respect to their population biomass is known or predictable. Such predictions would be 'precautionary' in that they do not account for recovery of ecosystem function as a result of density compensation. Demonstrating the applicability of this synthetic model in the


Figure 1.3.1 The influence of dominance structure on biodiversity - ecosystem function
relationships. A. Equitable distributions of biomass across assemblages result in an equitable distribution of Ecosystem Functioning (A1). Hence the functional contribution of species does not vary with increasing extinction susceptibility (A2) and the relationship between Species Richness and Ecosystem Function is linear irrespective of the extinction order (A3) (modified from Larsen et al.., 2005). B. Modified from Larsen et al.. (2005). Linear rank biomass curves (B1) result in linear rank functional contribution curves (B2). Hence the relationship between species richness and ecosystem function is dependent on the functional extinction order (B2). Where functional contribution is positively related to extinction susceptibility, ecosystem function declines exponentially with decreasing species richness (solid lines, B2 and B3). The inverse is true where functional contribution and extinction susceptibility are negatively correlated (dashed lines, B2 and B3). Humped backed relationships between functional contribution and extinction susceptibility result in sigmoidal relationships between species richness and ecosystem function (dotted lines, B2 and B3). C. Exponentially decaying rank biomass distributions (C1) result in exponentially decaying rank functional contribution curves (C2). This results in exponentially rising (dashed lines) and decaying (solid lines) relationships between functional contribution and extinction susceptibility (C2). Hence ecosystem function becomes highly sensitive (dashed lines) or redundant (solid lines) to species loss respectively (C3). Humped back distributions between functional contribution and extinction susceptibility in B2 become a Gaussian distribution in C 2 , resulting in a more pronounced step in the sigmoidal relationship between species richness and ecosystem function (dotted lines, C3).
real world could be an important step towards developing useful predictive tools for ecosystem function conservation in line with the 'precautionary principle'.

### 1.3.2 The role of compensation in ameliorating the short term impacts of biodiversity loss

At the centre of the BEF paradigm is the notion that increasing species richness increases an ecosystem's resilience to disturbance. The word resilience is used here to refer to the ability of an ecosystem to maintain its functional integrity under adverse environmental conditions. This is opposed to the term resistant which is used here to describe the vulnerability of a species to a particular disturbance event. While short-term declines in ecosystem functioning may be predicted from the order of species loss with respect to their population biomass, in the long term extinction resistant species may compensate for the loss of their competitors by increasing their resource use (functional compensation) and abundance (numerical compensation) (Gonzalez and Loreau 2009). The ability of species to compensate for each other however depends firstly on species performing similar roles in ecosystem functioning (i.e. species possess similar functional effect traits) so that one species can compensate for declines in the abundance of another. Secondly species which are similar in their functional roles must display different responses to adverse environmental conditions (i.e. a high diversity of functional response traits), a property of ecosystems known as biological insurance (Yachi and Loreau 1999, Loreau 2000). Where this is the case many species within an ecosystem may be 'redundant' in the roles they perform, because extinction resistant species can offset declines in ecosystem functioning associated with species loss (Walker 1992, Walker et al. 1999).

Figure 1.3.2 explores how density compensation can ameliorate the impacts of short term biodiversity loss on ecosystem functioning in natural assemblages. Where the first species to
be lost are the most functionally important (Figure 1.3.2, B), ecosystem function declines rapidly with species loss (Figure 1.3.2, C, curves b) in the absence of compensatory responses. However where compensation does occur it can ensure the provision of ecosystem functioning resulting in more saturating long term relationships between species richness and ecosystem function (Figure 1.3.2, C curves a). Where the most functionally


Figure 1.3.2 A hypothetical framework for exploring the consequences of species loss for ecosystem functioning. A. Deterioration in ecosystem function with species loss (C) is determined by the relationship between functional importance and extinction susceptibility (B), whether or not density compensation occurs, and the distribution of functionality across the species pool. In A follow arrows from left to right to see how these factors interact to produce the curves in C .
important species are the most resistant to extinction (Figure 1.3.2, B) ecosystem function does not decline rapidly with species loss in the short term regardless of density compensation (Figure 1.3.2, C, curves a). During simulations of macroinvertebrate
extinction, Solan et al. (2004) recognized that when extinction was ordered according to population density, density compensation caused no notable change in community bioturbation following the loss of extinction susceptible rare species, because the proportional change in bioturbation following their loss was small. Where species display similar contributions to ecosystem function (Figure 1.3.2 B), ecosystem functioning declines in a negative linear fashion with species loss in the short term (Figure 1.3.2 C, curve C), however compensation by extinction resistant species can offset the loss of functioning resulting in a saturating BEF relationship in the long term (Figure 1.3.2, curves a). Figure 1.3.2 demonstrates the importance of understanding how compensation alters the form of short term BEF relationships in natural ecosystems. If the potential of species to compensate for declines in ecosystem function associated with species loss can be predicted then, when combined with a mass-ratio rule, more accurate long range forecasts of deterioration in ecosystem functioning during biodiversity loss can be made. However current consensus on the prevalence of compensatory dynamics is conflicting (Houlahan et al. 2007, Gonzalez and Loreau 2009). While some investigations have found evidence that compensation can ameliorate loss of functioning in ecosystems undergoing species loss (Peres and Dolman 2000, Cross and Harte 2007, Peters et al. 2009) large scale observational studies have found that compensatory dynamics are not a common feature of all natural communities (Houlahan et al. 2007). It seems intuitive that the potential for an assemblage to compensate for biodiversity loss and the rate at which such compensation occurs will depend to some degree on environmental context. For example a number of studies have highlighted how the rate and scale of compensatory responses can be affected by nutrient availability (Zhang and Zhang 2006, Cross and Harte 2007), precipitation (Munson and Lauenroth 2009), and the identity of species following species loss (Walker et al. 1999, Solan et al. 2004). Density compensation is therefore not necessarily a stabilizing mechanism against loss of biodiversity
in ecosystems in general. This is fundamentally important as many previous large scale biodiversity experiments have fixed the initial densities of assemblages across species richness treatments therefore assuming a priori that density compensation is a common feature of natural ecosystems (Hector et al. 1999, Tilman 1999a, Marquard et al. 2009). Forecasting the decline in ecosystem services with species loss requires that researchers conduct in situ investigations to establish the processes which govern whether extinction resistant species compensate for biodiversity loss in nature. In the absence of being able to predict whether compensation is likely to occur, conservation managers could predict the short term consequences of species loss for ecosystem functioning using community biomass data, and model a range of theoretical compensation scenarios to illustrate the potential long term impacts of a specific extinction event.

### 1.4 Thesis outline

The primary aim of this study was to determine common properties of natural ecosystems which may be used to predict the consequences of biodiversity loss for ecosystem processes in natural assemblages. Specifically it was hypothesised that a mass-ratio rule exists in natural assemblages whereby species contributions to ecosystem processes are directly proportional to their contributions to community biomass. Hence in the short term, the decline in an ecosystem process with species loss will be dependent on the order of species extinction with respect to their population biomass. Demonstrating the validity of this theory could provide an elegant tool for conservation mangers to predict the short term or 'worst case scenario' consequences of species loss for ecosystem functioning using only community biomass data where the order of species extinction is known or predictable.

In order to achieve this aim, four natural assemblages (salt marsh plants, two contrasting assemblages of fouling invertebrates and macroalgae turfs) were manipulated to simulate
empirically derived extinction orders in response to realistic anthropogenically accelerated disturbance events. In chapter 2 salt marsh plants were manipulated to simulate extinction in response to an increase algal mat deposition, in chapter 3 macroalgae turfs were manipulated to simulate an increase in wave exposure, and in chapter 4 sessile invertebrate communities were manipulated to simulate extinction in response to hypoxia. Ecosystem processes were measured across the resulting gradients of species richness, individual species contributions to each process were quantified and then related to contributions to community biomass. Each of chapters 2-4 addresses a different question. For example Chapter 3 (macroalgae) focuses on testing whether different ecosystem processes, primary production and nutrient uptake, are affected similarly by species loss as a result of the mass-ratio relationship. Chapter 4 tests the validity of the mass-ratio relationship in fouling invertebrate assemblages as its extension outside of autotrophic assemblages has previously not been explored. Chapter 5 combines data from chapters 2, 3 and 4 to test the application of the mass-ratio rule across multiple ecosystems and ecosystem processes. In addition, chapter 5 presents worst and best case scenario predictions of the biodiversity ecosystem process relationship in each of the ecosystems studied. The worst case scenario is predicted using the mass-ratio relationship (i.e. in the absence of compensation) while the best case scenario is predicted by simulating full compensation by the extant species with the highest per capita contribution to ecosystem processes. Together these predictions represent the boundaries of the envelope of possible biodiversity-ecosystem function relationships. It was recognized that the best case scenario makes a number of assumptions about density compensation in nature. Hence in order to explore whether extinction resistant species can compensate for declines in ecosystem function associated with realistic species extinction, in chapter 2 the manipulation of salt marsh plants was maintained over two growing seasons and compensatory responses monitored over time.

## Chapter 2. Do extinction resistant species

compensate for loss of function associated with
extinction in a salt marsh plant assemblage?


# Chapter 2 Do extinction resistant species compensate for loss of function associated with extinction in a salt marsh plant assemblage? 

### 2.1 Abstract

Numerous studies have investigated the consequences of loosing biodiversity for the processes and stability of ecosystems. However, in adopting rigorous statistical approaches many of these investigations fix initial densities of artificially assembled communities across species richness treatments, and hence make an a priori assumption that in nature extinction resistant species will compensate for the loss of their competitors numerically and consequently functionally. Surprisingly few investigations have assessed whether extinction resistant species compensate for the loss of their competitors during realistic extinction events in nature. In this investigation, a salt marsh plant assemblage was manipulated to simulate an empirically derived realistic extinction sequence of species. Both numerical (community biomass) and functional (primary production) compensation by extinction resistant species was subsequently monitored over two growing seasons in 2009 and 2010. While limited compensation of primary production was observed in 2009, this was not attributable to compensation of community biomass by extinction resistant plants, and was more likely due to increases in the abundance of the mat forming green algae Rhizoclonium sp . No compensation of either community biomass or productivity was observed over the 2010 growing season. These results indicate that compensation by extinction resistant species is not a rapid process in the salt marsh plant assemblage studied, and is likely dependent on the structure of the ecosystem undergoing species loss, and the environment in which it is situated. These results suggest that caution should be exercised when making assumptions about the role of compensation dynamics in ameliorating the impact of species loss on the structure and processes of natural ecosystems.

### 2.2 Introduction

Current projections suggest that biodiversity will continue to decline in both terrestrial and aquatic environments over the $21^{\text {st }}$ century (Sala et al. 2000b, Pereira et al. 2010). This has prompted a rapidly expanding research agenda which endeavours to understand the consequences of losing biodiversity for the functioning of natural ecosystems (Hooper et al. 2005, Solan et al. 2009). While many studies have attempted to determine whether decreasing biodiversity results in a decline in the stability and processes of natural ecosystems, they have typically generated artificial assemblages in which initial densities are fixed across species richness treatments (Hector et al. 1999, Tilman 1999a, Hector and Bagchi 2007, Marquard et al. 2009). Hence these investigations make an a priori assumption that extinction resistant species will compensate both numerically and functionally for the loss of their competitors in natural ecosystems. Such compensatory interactions are however little studied in natural ecosystems (Gonzalez and Loreau 2009), and the potential for them to ameliorate the impact of biodiversity loss on ecosystem functioning is not well understood.

Theory predicts that higher species richness in natural communities stabilizes aggregate variability in key ecosystem functions such as productivity and nutrient cycling in face of environmental perturbations (Tilman 1999b, Hooper et al. 2005). One mechanism through which this can occur is the density compensation effect whereby declines in the abundance of one species are compensated for by increases in the abundance of others (Micheli et al. 1999, Tilman 1999b, Gonzalez and Loreau 2009). Density compensation is typically measured as the negative covariance in abundance between species (Micheli et al. 1999). Where species co-vary positively they are synchronous in their response to environmental perturbations, hence declines in ecosystem processes associated with the loss of one species cannot be offset by increases in the abundance of another species (Micheli et al. 1999). Where species co-
vary negatively, species which are resistant to an environmental perturbation can compensate numerically for declines in the abundance of species which are more susceptible by increasing their abundance (density compensation) (Micheli et al. 1999, Gonzalez and Loreau 2009). In order for this compensation to be possible, firstly species must display different responses to environmental disturbances. This is contingent on a high diversity of functional traits which determine resilience or susceptibility to disturbance (functional response traits)(Diaz and Cabido 2001). Secondly species need to be able to succeed each other in the ecosystem functions they perform by possessing similar fundamental niches. This property of ecosystems is known as the Insurance Hypothesis (Walker et al. 1999, Yachi and Loreau 1999).

A number of investigations have explored the prevalence of density compensation in both natural and artificial communities exposed to environmental perturbations (Wardle et al. 1999, Klug et al. 2000, Fischer et al. 2001, Steiner 2005, Steiner et al. 2005, Tilman et al. 2006, Zhang and Zhang 2006, Cross and Harte 2007, Houlahan et al. 2007, Valone and Barber 2008, Peters et al. 2009, Winfree and Kremen 2009, Grman et al. 2010, Sasaki and Lauenroth 2011). The evidence in support of the existence of compensatory dynamics in natural communities is, however, conflicting (Gonzalez and Loreau 2009). Studies which artificially generate assemblages of varying species richness have found little evidence of compensatory stabilization of community biomass over time, instead finding that alternative mechanisms increase community stability at high species richness, such as the portfolio effect (Doak et al. 1998, Tilman 1999b) in which aggregate community biomass is stabilized by the statistical averaging of the variance in component species (Tilman et al. 2006). Similarly, observations of species co-variances in many natural communities has yielded conflicting evidence of compensation influencing community stability (Houlahan et al. 2007, Valone and Barber 2008, Winfree and Kremen 2009). In a comparison of 41 natural communities
including plants, mammals, fish, insects and reptiles, Houlahan et al.. (2007) found that in general species abundance tended to co-vary positively indicating synchronous responses to environmental fluctuations and hence low potential for compensatory stabilization of community biomass during species loss. Research conducted in freshwater zooplankton communities suggests that stability is driven by portfolio effects (Steiner 2005), and where compensatory dynamics are observed they are limited to groups of species which were both functionally similar and displayed different tolerances to acidification (Klug et al. 2000, Fischer et al. 2001). Some observational studies have highlighted that compensatory dynamics are occurring between populations in at least some natural communities experiencing species loss (Peres and Dolman 2000, Peters et al. 2009) while others have indicated that species removal can result in cascading changes in whole ecosystem structure (Estes et al. 1998, Terborgh et al. 2001, Springer et al. 2003). For example two populations of swarm-raiding army ants were found to display strong compensatory dynamics in response to rain-forest fragmentation both in terms of abundance and functioning in the form of swarm-raiding predation on detritivorous arthropods. Similarly, in a study of neotropical rainforest primates, Peres and Dolman (2000) found evidence that medium sized species offset declines in the density of larger more intensely hunted species. In order to understand whether compensatory dynamics are a common feature of ecosystems undergoing extinction, researchers need to compliment observational studies of compensation in nature with in situ experimental manipulations of natural assemblages of animals and plants which aim to monitor compensatory responses through time (Wardle et al. 1999, Cross and Harte 2007, Grman et al. 2010, Sasaki and Lauenroth 2011).

Few investigations have sought to understand whether extinction resistant species can compensate for the loss of their competitors by conducting in situ manipulations of natural assemblages in which species are removed. (although see Wardle et al. 1999, Smith and

Knapp 2003, O'Connor and Crowe 2005, Cross and Harte 2007). Where in situ manipulations have been conducted they often focus on removing whole functional groups (Smith and Knapp 2003, O'Connor and Crowe 2005, Cross and Harte 2007). For example Cross and Harte (2007) removed shallow rooted forb species from a sub alpine meadow while Smith and Knapp (2003) removed only the number of rare and uncommon plant species while reducing the abundance of dominants in a grassland ecosystem. However recent studies have highlighted how the impact of species loss on ecosystem functioning can be markedly different when simulating realistic patterns of extinction comparative to more unrealistic approaches (Solan et al. 2004, Zavaleta and Hulvey 2004, McIntyre et al. 2007, Bracken et al. 2008). However they have either generated artificial communities to represent realistic extinction scenarios (Zavaleta and Hulvey 2004, Bracken et al. 2008) or present results based on theoretical modelling approaches (Solan et al. 2004, McIntyre et al. 2007). Few studies to date have manipulated natural assemblages to simulate an empirically derived extinction order and monitored compensatory responses through time. Such approaches can provide researchers with opportunities to test how ecosystem functioning is likely to respond to disturbances in the real world.

The aim of this investigation was to establish whether numerical compensation can offset declines in ecosystem processes (functional compensation) associated with species loss across a realistic extinction gradient in a natural ecosystem. Firstly an extinction order of salt marsh plants was empirically derived in response to a climate driven disturbance event. Secondly the natural assemblage was manipulated to simulate the observed extinction order of species. Finally the rate of functional and numerical compensation by extinction resistant species was quantified. In doing so, this investigation tested whether compensation occurs in natural assemblages undergoing realistic extinctions, and hence whether it is a strong stabilizing mechanism against the impacts of species loss on ecosystem processes. It was
envisaged that over time species poor plots community biomass and ecosystem processes would increase through time due to release from competition. Hence the amount of community biomass and hence ecosystem functioning would approach that of the natural assemblage over time. However in species rich plots competition amongst constituent species remains high so the rate at which community biomass and ecosystem processes recovers to control values would be slower.

### 2.3 Methods

### 2.3.1 Overview

This study is presented in two phases, a disturbance phase in which a realistic extinction order of salt marsh plants is quantified, and a community disassembly and compensation phase in which natural plant communities were manipulated to simulate the empirically derived extinction order and compensatory responses monitored over time. In the Disturbance Phase the order of plant species loss was determined in response to algal mat deposition. Mat deposits (accumulated algal debris detached during periods of high storm intensity and deposited at the land/sea interface) can alter the structure of salt marshes and other intertidal communities (van Hulzen et al. 2006). Such deposits are likely to increase in both volume and frequency with predicted increases in the frequency and severity of storm events in the North Atlantic resulting from climate change (Ulbrich and Christoph 1999, Holland and Webster 2007). In the community disassembly and compensation phase, the natural assemblage was manipulated to simulate the empirically derived extinction order and plant productivity and biomass were monitored over two growing seasons. The aim was to establish whether compensation would offset the impact of species loss on community biomass or BM (numerical compensation) and Gross Community Productivity or GCP (functional compensation).

### 2.3.2 Experimental field site

Ninety $1 \mathrm{~m}^{2}$ experimental plots were established in an area of transitional low salt marsh vegetation located in the Cefni estuary, Anglesey, Wales, UK ( $53^{\circ} 10^{\prime} 12^{\prime \prime} \mathrm{N}: 4^{\circ} 23^{\prime} 39^{\prime \prime} \mathrm{W}$ ) on $10 / 06 / 08$. Plots were spaced $\sim 3 \mathrm{~m}$ apart and marked using bamboo canes. A preliminary survey revealed the assemblage consisted of the halophytic vascular plants Plantago maritima, Armeria maritima, Limonium humile, Salicornia ramosissima, Puccinellia maritima, Triglochin maritima, Aster tripolium, Atriplex portulacoides, Spergularia media and the mat forming green algae Rhizoclonium riparium (hereafter referred to by genus only).

### 2.2.3 Disturbance Phase

Thirty of $90 \mathrm{1m}^{2}$ plots were randomly assigned to one of six experimental treatments ( $\mathrm{n}=5$ per treatment). The fucoid algae Fucus serratus was collected from a nearby rocky shore on $17 / 06 / 08$, spread over a $1 \mathrm{~m}^{2}$ area of each plot in one of four treatment volumes ( $141,281,42$ 1 and 56 1) (see Figure 2.3.1) and fixed in place using a 1.5 cm mesh net. Netting alone was also applied to five procedural control plots to assess whether it had an inhibitory affect on plant growth. The remaining five plots were left as an untouched control treatment. Due to the rapid desiccation and decay of $F$. serratus a further deposition event was simulated 36 days after the initial treatment application using the same approach. Algae and netting were removed from the plots 61 days after initial treatment application. Plots were then left for 10 days during which they were immersed by high spring tides which removed decaying organic matter. In order to quantify the response of each species to algal mat deposition, the $\%$ cover of each species was quantified 71 days after the initial treatment application using a $0.5 \times 0.5 \mathrm{~m}$ quadrat divided into 49 point intersections placed centrally within each $1 \mathrm{~m}^{2}$ plot to avoid edge effects. In order to obtain a comparable measure of extinction susceptibility for


Figure 2.3.1 Mimicking disturbance by algae mat deposition on the Cefni salt marsh, Anglesey. Left Column: Algae ( $F$. serratus) was deposited in five different volumes on five replicate $1 \mathrm{~m}^{2}$ plots per treatments in June of 2008. Algae was re-applied 36 days later. Right Column: The visual impact of different algae mat treatments on salt marsh vegetation following the removal of mats in August 2008, 61 days after initiall treatment application.
each species their respective \% cover values were standardised to relative \% cover using [Relative \% cover $=(\%$ cover/mean control $\%$ cover $)-1]$. Extinction susceptibility of each species was then estimated as the slope value obtained from OLS regression (forced through 0 ) of relative $\%$ cover against volume of algae applied per unit time. This was performed independently for each species using averaged treatment responses. Netting did not affect \% cover (see results text) in all species used in the analysis. Hence the procedural control and true control data were pooled (total $\mathrm{n}=10$ ) to provide a more accurate measure of natural population density. In cases where complete loss of a species was observed during applications of algae at a level lower than the maximum applied (Salicornia only), the higher application responses were excluded from the analysis to prevent further $0 \%$ cover measurements underestimating the regression slope estimate and hence extinction susceptibility.

### 2.3.4 Plot manipulation and density compensation

The extinction order resulting from the disturbance phase was used to generate a gradient of species richness across 36 of the remaining undisturbed plots (4 replicates to each treatment level) which was representative of community disassembly in response to algal mat deposition. Nine treatments were established representing a richness gradient from 0 to 8 species (see Figure 2.3.2). Species were removed in a subtractive fashion so that four plots contained only the most extinction resistant species, four contained the two most extinction resistant species and so on. This was conducted in a $40 \times 40 \mathrm{~cm}$ area central to each plot. The 8 (or 'ALL’) species treatment represented the control where no species were removed. The lowest species richness plots ( 0 species) had all vascular plant vegetation removed but still contained the alga Rhizoclonium on the soil surface. Some species were too patchy in their distribution for reliable estimates of extinction susceptibility and/or functional contribution to be made (i.e. the $95 \%$ confidence limits of their mean abundance overlapped


Figure 2.3.2 A salt marsh plant community is manipulated to simulate species extinction in response to deposition of Fucoid algae mats. Each image represents the removal of a species sequentially during community disassembly. Hence where Triglochin is removed (bottom right) no plant species remain, while the image labelled 'All' contains all species. Refer to text for explanations of plot manipulation.
with 0 ) hence these species were removed in all treatments except the controls. An additional treatment in which only these species were removed was used as the maximum richness
treatment in the analysis. In order to avoid disrupting soil properties, species were removed by breaking off the above ground biomass just below the soil surface as opposed to weeding. Community composition and primary productivity were quantified immediately following plant species removal in June 2009 and re-quantified in July and September of 2009 and May, June and July of 2010 to monitor compensatory responses of extinction resistant species. Light levels and hence productivity and rates of plant growth were insufficient in winter months to warrant continued year round measurements of community composition and productivity. Manipulations, however, were conducted on a monthly basis throughout all months of the year from June 2009 to August 2010 to ensure that the number and identity of species in each treatment remained constant. Community composition in each plot was assessed as \% cover using a $0.3 \times 0.3 \mathrm{~m}$ point quadrat ( 49 point intersections) placed centrally within each plot and converted to population dry weight using a calibration of the average population dry weight per unit $\%$ cover estimated across five control plots during the disturbance experiment. See appendix A1 for the details of the calibration multiplier values. Biomass could not be measured directly as this would have involved removing plants from experimental plots, all of which were being monitored for compensation dynamics over time.

### 2.3.5 Estimating Primary Productivity

Gross Community Productivity (GCP) was estimated as $\mathrm{CO}_{2}$ flux recorded using an LI-840 $\mathrm{CO}_{2} / \mathrm{H}_{2} 0$ gas analyzer (LI-COR Biosciences, USA) connected to a clear plexiglass chamber $\left(0.09 \mathrm{~m}^{2}\right.$ internal base area, 0.19 m high, internal volume $=17.1$ litres $)$ seated firmly on the marsh surface (see Figure 2.3.3). GCP was estimated using the rate of $\mathrm{CO}_{2}$ flux recorded during consecutive light and dark measurements representing net community productivity (NCP, $\mathrm{CO}_{2}$ utilization by photosynthesis plus $\mathrm{CO}_{2}$ production by respiration) and Community Respiration (CR, $\mathrm{CO}_{2}$ production during respiration) respectively. GCP was then estimated as $G C P=N C P-C R$ and expressed at the community level as $\mathrm{mmol} \mathrm{CO}_{2} \mathrm{~m}^{-2} \mathrm{~h}^{-1} . \mathrm{CO}_{2}$ flux


Figure 2.3.3 $\mathrm{CO}_{2}$ flux apparatus used to quantify gross community productivity (GCP) in salt marsh plant assemblages. Left. The plexiglass flux chamber used to enclose plant communities allowing estimates of $\mathrm{CO}_{2}$ flux to be made. Right. The analytical equipment consisted of a LI- $840 \mathrm{CO}_{2} / \mathrm{H}_{2} 0$ analyzer linked via air tubing to the flux chamber. A Brailford 2D-NA pump was used to maintain a constant air flow of $1.001 \mathrm{~min}^{-1}$. Data was $\mathrm{CO}_{2}$ concentration was recorded every 5 seconds using an LI-1400 data logger measurements were recorded in a stratified random order (where treatments are sampled randomly within four blocks of replicates) between 10:00hrs and 14:00hrs BST during a neap tidal cycle on days with low cloud cover in order to minimise the effect of variation in light level and other abiotic factors on photosynthetic rates. GCP measurements were recorded only where light levels exceeded $700 \mu \mathrm{~mol}$ PPFD $\mathrm{m}^{-2} \mathrm{~s}^{-1}$, a previously defined threshold above which variation in ambient light levels has minimal impacts on primary production in this salt marsh community (Appendix A2). Variation in light levels during each recording of GCP through time are presented in Appendix A3.

### 2.3.6 Data analysis

In order to establish whether resistant species in species poor plots compensated functionally and numerically for the loss of species, the difference between the average control value of GCP or BM and the average value of each species richness treatment was calculated at each time point ( $\Delta \mathrm{GCP}$ or $\Delta \mathrm{BM}$ ). Where the value of $\Delta \mathrm{GCP}$ or $\Delta \mathrm{BM}$ for a particular treatment reduces over time, this is an indication of an increase community biomass or GCP relative to the controls and hence compensation. It was anticipated that species poor plots would display reductions in $\triangle \mathrm{GCP}$ or $\triangle \mathrm{BM}$ due to competitive release while the higher levels of
competition in species rich plots would inhibit compensatory responses and hence $\triangle \mathrm{GCP} / \mathrm{BM}$ would remain relatively static over time. Evidence of this compensatory effect was tested using an Analysis of Co-Variance (ANCOVA) performed separately for community biomass and GCP in each season (2009 and 2010) where species richness was treated as a fixed factor and time as a covariate with $\triangle \mathrm{GCP}$ or $\triangle \mathrm{BM}$ being the response variable. Where the rate of decline in $\triangle \mathrm{GCP} / \mathrm{BM}$ over time increases with decreasing species richness (i.e. a significant interaction between time and species richness treatment), species poor plots are increasing in biomass of primary production compared to species rich plots, hence compensatory responses are occurring. No significant interaction between species richness and time indicates that the ecosystem has not responded to species loss either by increases in the abundance of extinction resistant species or by increases in the productivity of these species.

### 2.4 Results

### 2.4.1 Disturbance Phase

The application of netting to procedural control plots had no effect on the $\%$ cover of species used in the analysis compared with true control plots (ANOVA; Plantago, $F_{1,8}=0.19, p=$ 0.676; Triglochin, $F_{1,8}=0.03, p=0.873 ;$ Aster, $F_{1,8}=0.59, p=0.465 ;$ Salicornia, $F_{1,8}=0.09$, $p=0.772 ;$ Armeria, $F_{l, 8}=0.15, p=0.712 ;$ Limonium, $F_{l, 8}=0.74, p=0.415 ;$ Puccinellia, $F_{l, 8}$ $=3.02, p=0.120$ ). The $\%$ cover of all species decreased significantly in response to the algal mat treatment with the exception of Triglochin and Aster which were not significantly affected by algal mat deposition (Figure 2.4.1, Table 2.4.1). Salicornia was the most extinction susceptible species followed by Puccinellia, Armeria, Limonium and Plantago(Table 2.4.1). The relative \% cover of Triglochin increased at intermediate


Figure 2.4.1 The relationship between algal treatment and relative \% cover for each salt marsh plant species. Extinction susceptibility was estimated as the slope of the regression model when forced through 0 . Points above zero represent an increase in \% cover above that in control plots (fertiliser affects) while those below 0 are indicative of biomass loss in response to treatment by algae. Individual points are the mean values $\pm 95 \% \mathrm{CI}(\mathrm{n}=5)$ for responses at each treatment level. Open points were omitted from the analysis to prevent them influencing regression estimates. Dashed lines represent significant relationships between the volume of algae applied and relative \% cover.
disturbance levels while Aster displayed a negative but not significant response (Figure
2.3.1). Given this and the difference in the regression slope estimates of these two species, it
was assumed that Triglochin was the least extinction susceptible species with Aster being the second least extinction susceptible. The disturbance treatment therefore provided an
extinction order (Table 2.4.1) which could be used to generate a gradient of species richness in the community disassembly and predictive phases.

Table 2.4.1 The rank extinction order of salt marsh plants in response to deposition of fucoid algal mats. Ranks are determined by the order of the slope coefficients ( $\pm 95 \% \mathrm{CI}$ ) derived from 0 origin regression models relating relative \% cover against the application of Fucus serratus at 5 different treatment volumes. Values of $p$ $>0.05$ were considered non significant.

| Species | Slope $\pm \mathbf{9 5 \%} \mathbf{C I}$ | $\boldsymbol{F}$ | $\boldsymbol{p}$ | $\mathbf{R}^{\mathbf{2}}$ | Rank ES |
| :--- | :--- | :---: | :---: | :---: | :---: |
| Salicornia ramossissima | $-0.189 \pm 0.016$ | ${ }_{(1,2)} 25.75$ | 0.037 | 0.93 | 1 |
| Puccinnellia maritima | $-0.071 \pm 0.030$ | ${ }_{(1,4)} 43.83$ | 0.003 | 0.92 | 2 |
| Armeria maritima | $-0.060 \pm 0.020$ | ${ }_{(1,4)} 62.58$ | 0.001 | 0.94 | 4 |
| Limonium humile | $-0.056 \pm 0.014$ | ${ }_{(1,4)} 32.04$ | 0.005 | 0.89 | 5 |
| Plantago maritima | $-0.040 \pm 0.022$ | ${ }_{(1,4)} 33.82$ | 0.004 | 0.89 | 6 |
| Aster tripolium | $-0.016 \pm 0.038$ | ${ }_{(1,4)} 1.155$ | 0.343 | 0.22 | 7 |
| Triglochin maritima | $0.027 \pm 0.076$ | ${ }_{(1,4)} 2.223$ | 0.210 | 0.36 | 8 |

### 2.4.2 Community manipulation and ecosystem function

Initially values of $\triangle \mathrm{GCP}$ and $\triangle \mathrm{BM}$ increased with decreasing species richness in both years (Figures 2.4.2 and 2.4.3 B and D ) as the removal of species equates to a removal of biomass and hence productivity. Visual inspection of the raw changes in GCP over the 2009 growing season indicated that GCP in high species richness (SR) treatments ( $\mathrm{SR}=7$ to 3 ) varied synchronously with the control plots, while low species richness treatments (SR=0 to 2 ) marginally increased in GCP independently of the control plots in September of 2009 in treatments where species richness was equal to 0,1 and 2 respectively (Figure 2.4.2A). Hence $\Delta \mathrm{GCP}$ reduced over the 2009 growing season where species richness was between 0 and 2 , reduced marginally where species richness $=3$ and remained relatively static between


Figure 2.4.2 Compensation of gross community productivity (GCP) in a salt marsh plant assemblage undergoing species loss in response to algal mat deposition. A and C : The response of GCP over time ( $\mathrm{SR}=$ species richness) in the 2009 (A) and 2010 (C) growing seasons, legend of A applies to all. B and D: The interaction between the effect of species richness treatment (SR, legend of B applies to D) and time on $\triangle G C P$ (the difference in GCP between the mean of each treatment and the mean of the controls) in the 2009 (B) and 2010 (D) growing seasons. In B $\triangle$ GCP declines more rapidly at low species richness than at high species richness indicating an increase in GCP relative to the controls, and hence compensation in low species richness plots.
species richness treatments 4 to 7 (Figure 2.4.2 B). ANCOVA confirmed a negative interaction between species richness and time ( $F_{15,7}=11.81, p=0.001$ ), indicating that functional compensation of GCP was occurring at low levels of species richness during the 2009 growing season but not at high levels of species richness. However this functional


Figure 2.4.3 Compensation of community biomass in a salt marsh plant assemblage undergoing species loss in response to algal mat deposition. A and C : The response of community biomass over time ( $\mathrm{SR}=$ species richness) in the 2009 (A) and 2010 (B) growing seasons, legend of A applies to all. B and D: The interaction between the affects species richness treatment (SR, legend of $B$ applies to $D$ ) and time on $\triangle B M$ (the difference in biomass between the mean of each treatment and the mean of the controls) in the 2009 (B) and 2010 (D) growing seasons. $\Delta B M$ increased on average over both the 2009 and 2010 growing seasons hence there was little indication of numerical compensation. This trend was not significantly different between species richness treatments. Error bars are 95\% confidence intervals of the mean in each case.
recovery was not repeated during the 2010 growing season (ANCOVA species
richness*month interaction, $F_{15,7}=0.18, p=0.982$ ) (Figure 2.4.2 C and D). Closer inspection of the raw data suggested that the apparent recovery of GCP in 2009 was mostly due to the synchronous decline of GCP in species richness treatments 3 to 7 and controls, as opposed to


Figure 2.4.4 Increases in the \% cover of the green mat forming algae Rhizoclonium sp. In low species richness plots over the 2009 growing season. In species richness plots where $\mathrm{SR}=0$ (open points, solid line), $\mathrm{SR}=1$ (grey points, dashed line), and $\mathrm{SR}=2$ (black points, dotted line) . Rhizoclonium mats increased significantly in \% cover in all of these treatments suggesting that this species may have been responsible for the observed compensation of Gross Community Productivity in low species richness plots. Reliable tests of whether Rhizoclonium increased in high species richness plots could not performed as the analysis was conducted using photographic images in which the presence of the dominant plant species, Plantago in plots where species richness was higher than 2 , blocked a large proportion of the view of the soil surface.
the marginal increase in GCP in species richness treatments 0 to 3 (Figure 2.4.2 A). It is also important to note that the marginal increases in GCP observed between June and September 2009 where no species were present $(\mathrm{SR}=0)$ was similar $\left(3.3 \mathrm{mmol} \mathrm{CO}_{2} \mathrm{~m}^{-2} \mathrm{hr}^{-1}\right)$ to where only Triglochin was present $\left(\mathrm{SR}=1: 3.8 \mathrm{mmol} \mathrm{CO} \mathrm{m}^{-2} \mathrm{hr}^{-1}\right)$, and Triglochin and Aster were present ( $\mathrm{SR}=2: 2 \mathrm{mmol} \mathrm{CO} \mathrm{m}^{-2} \mathrm{hr}^{-1}$ ) indicating that neither Triglochin or Aster were responsible for the observed recovery in GCP. Biomass also varied synchronously over the 2009 growing season across all species richness treatments and hence the rate of decline in $\Delta \mathrm{BM}$ did not vary significantly across species richness treatments (ANCOVA species richness*month interaction, $F_{15,7}=0.23, p=0.964$ ) (Figure 2.4.3A and B). A series of OLS regressions revealed that the \% cover of Triglochin in species richness treatments 1 and 2 and Aster in species richness treatment 1 did not increase significantly over the 2009 growing
season (Triglochin: $F_{1,7}=0.13, p=0.733$; and $F_{1,7}=7.31, p=0.346$ where $\mathrm{SR}=2$ and 1 respectively) (Aster: $F_{1,7}=1.58, p=0.249$ where $\mathrm{SR}=2$ ). Hence there was no supporting evidence of compensation through growth of biomass by extinction resistant species which could have explained the apparent compensation of GCP. Collectively these results suggested that the compensation of primary productivity in 2009 was not due to increases in the biomass of extinction resistant plant species, and cast doubt as to whether they were due to increases in the photosynthetic rate of extinction resistant plant species. Referral to photographs (taken at the same time as GCP and biomass measurements) using a digitally overlaid 49 point quadrat in image-J revealed that the $\%$ cover of the mat forming green algae Rhizoclonium increased significantly in all three species richness treatments 0,1 and $2\left(F_{1,7}=\right.$ 6.76, $p=0.036 ; F_{1,7}=21.88, p=0.002 ;$ and $F_{1,7}=10.64, p=0.014$ where $\mathrm{SR}=0,1$ and 2 respectively) (Figure 2.4.4). This provided a good indication that Rhizoclonium mats could be responsible for the functional compensation effect observed over the 2009 growing season.

### 2.5 Discussion

The aim of this study was to establish whether extinction resistant species compensated for loss of ecosystem functioning associated with the removal of their more extinction prone competitors during a realistic extinction event. The results suggest that while some compensation of primary productivity was observed during the three months following species removal in 2009, this was likely due to the proliferation of Rhizoclonium algal mats as opposed to increases in the primary production or biomass of the vascular plants within the assemblage. No evidence was found that primary production recovered in low species richness plots over the 2010 growing season, and community biomass varied synchronously between species richness treatments in both the 2009 and 2010 growing seasons. It was
concluded that the vascular plants within this salt marsh assemblage therefore did not compensate either numerically in terms of biomass or functionally in terms of primary production for species loss during the simulated extinction event over the two growing seasons studied here. It should be noted, however, that the biomass estimates used in this study were derived from \% cover data which could be less sensitive to small variations in plant biomass than direct biomass estimates. Nonetheless if a small degree of biomass compensation had occurred but not been detected in species poor plots, there was little evidence to suggest this translated into compensation of primary production.

It was hypothesised that extinction resistant species would compensate for the loss of more extinction prone species by increasing their productivity and/or biomass in species poor treatments. Both intuition and previous research suggest that disturbance resistant species will compensate for the loss of their competitors (Fischer et al. 2001, Cross and Harte 2007, Peters et al. 2009) It was a surprise then that little evidence was found of density compensation in this salt marsh ecosystem. It is difficult to conclude whether compensation was completely absent in the salt marsh plant assemblage studied here because it may be the case that such processes occur over a longer time scale than was available to sample in this study. Because the plant growth in northern temperate Europe is mostly limited to the spring and summer growing seasons compensation was effectively monitored over a two year period in this study. In a study which experimentally removed shallow rooted forb species from a subalpine meadow, Cross and Harte (2007) found that tap rooted forbs fully compensated for biomass after a three year removal period, but displayed little evidence of compensation after two years. Contrastingly Munson and Lauenroth (2009) found that two subdominant perennial grass species Sporobolus cryptandrus and Agropyron smithii significantly compensated for the removal of the dominant perennial grass in a shortgrass steppe within two years along with increases in the abundance of perennial forbs, dwarf shrubs and annual
forbs. However not all plant species in this assemblage displayed significant compensatory responses (Munson and Lauenroth 2009). The time scales over which compensatory responses occur in natural communities of plants therefore appear to be variable and are likely to be context dependent on a number of factors, for example the resources available to stimulate rapid compensatory growth (Zhang and Zhang 2006, Cross and Harte 2007), annual precipitation (Munson and Lauenroth 2009), and the identity of the species remaining in the ecosystem after species loss (Walker et al. 1999, Munson and Lauenroth 2009).

It is feasible that compensatory growth of extinction resistant species was suppressed by low resource availability. For example compensation of above ground biomass was faster where nitrogen was added to plots than compared to when compensation was allowed to continue under ambient nitrogen concentrations during Cross and Harte's experimental removal of shallow rooted forbs (Cross and Harte 2007). The vegetation within the ecosystem studied here was short despite the absence of grazing (pers obs) indicating that this marsh could be developing under nutrient limited conditions. The positive relationship between nutrient availability and speed of recovery has, however, not been consistently observed across ecosystems in general, and indeed some studies have found the inverse to be the case (Zhang and Zhang 2006). These authors found that when exposing microalgal communities to cold perturbations in mesocosms, compensatory responses were observed only under nutrient poor conditions, while community biomass decreased under nutrient rich conditions. Nonetheless it seems intuitive to suggest that low nutrient input may be a factor which regulated the scale of temporal responses among extinction resistant species in this experiment. If this is the case across autotrophic ecosystems in general, then the productivity of nutrient poor systems is likely to be more susceptible to the impacts of species loss comparative to nutrient rich systems, due to slower or limited compensation dynamics.

It is important to note that results from several studies suggest that compensation is not a common property of all natural ecosystems (Klug et al. 2000, Fischer et al. 2001, Houlahan et al. 2007, Winfree et al. 2007, Winfree and Kremen 2009). For example Winfree and Kremen (2009) found no evidence of negative co-variances between different native bee species pollinating water melon plants in California and New Jersey suggesting that density compensation cannot be assumed to be a stabilizing mechanism for pollination services. It is therefore also feasible that compensation was not occurring among the vascular plants within the salt marsh plant assemblage studied here. One reason for this might be that this plant assemblage was species poor (species richness $=8$ ) relative to other natural assemblages and there is therefore less scope for species displaying large overlaps in their fundamental niche characteristics. While Fischer (2001) found evidence of compensation in acidified lake zooplankton communities this compensation was dependent on species which are functionally similar displaying different responses to environmental perturbations (Klug et al. 2000, Fischer et al. 2001). The presence of this 'functional redundancy' (Walker 1992, Walker et al. 1999) is a necessary feature of ecosystems displaying compensation in nature. However functional redundancy can be affected by a number of community properties including the number of functional groups and the number and evenness of species within an ecosystem (Lawton et al. 1998, Fonseca and Ganade 2001, Petchey and Gaston 2002). As the number of functional groups increases across a fixed species pool, the level of redundancy decreases, however as the number of species increases across a fixed number of functional groups the level of functional redundancy and hence the potential for density compensation increases (Fonseca and Ganade 2001). This raises the question of whether there was a sufficient number of species relative to the number of functional groups for compensatory responses to be possible in the salt marsh plant assemblage studied here.

The extinction scenario simulated here consisted of one type of disturbance, algal mat deposition, however a variety of disturbances threaten salt marsh ecosystems globally (Gedan et al. 2009). For example, at three sites in New England, simulated climate warming of $<4^{\circ} \mathrm{C}$ resulted in declines in overall marsh diversity due to the takeover of Spartina patens in otherwise more diverse salt pannes (Gedan and Bertness 2009). Whether or not common response traits have sufficient influence on organism survivorship to confer similar extinction patterns under different disturbance scenarios is largely unknown. In chapter 5 of this thesis I demonstrate how the extinction order with respect to species contributions to ecosystem functioning determines how rapidly ecosystem function declines with species loss. However this also has important consequences for the scope for compensation within an assemblage. During a simulation of macroinvertebrate extinction in a soft sediment ecosystem Solan (2004) found that when species extinction susceptibilities were ranked according to their body size or rarity, compensation by extinction resistant species did not ameliorate the impact of biodiversity loss on bioturbation. This was because small species had a low contribution to bioturbation and hence increases in their abundance could not offset the functional consequences of loosing larger species, and because where dominant species are among the most extinction resistant, increases in the abundance of rarer species can only ameliorate small declines in bioturbation (Solan et al. 2004). In plots where above ground biomass had been removed following the disturbance experiment in 2008, Salicornia ramosissima and Puccinellia maritima rapidly colonised the bare soil surface in the salt marsh plant assemblage here because unlike the community manipulation and compensation experiment described, these species were not removed every month (per obs). By contrast the two extinction resistant species Triglochin maritima and Aster tripolium did not rapidly compensate for extinction in the community manipulation experiment presented here. This contrast likely reflects differences in the life history traits of these species. The extinction
order therefore determines not only the short term consequences of biodiversity loss for ecosystem functioning but also the scope for compensation, and the extinction order itself is dependent on the context of the disturbance and how it filters for particular functional traits within the ecosystem.

The results of this study suggest that compensation in this salt marsh plant assemblage was either not possible or slow relative to some other studies. This study therefore highlights that rapid compensatory dynamics are not necessarily a general feature of ecosystems, and are likely to be dependent both on the structure of the ecosystem undergoing species loss and on environmental context. This is fundamentally important as conventional approaches to testing theoretical biodiversity - ecosystem functioning relationships require that initial densities are standardised across species richness treatments (Hector et al. 1999, Tilman 1999a, Marquard et al. 2009). Hence these experiments make an a priori assumption that density compensation will reduce the impact of species loss over the long term at least to some degree in natural communities. While such approaches are useful in that they allow us to test the mechanisms which may underpin biodiversity effects on ecosystem functioning, they shed little light on the processes which govern the loss of ecosystem functioning during species extinction in nature.

In order to move towards achieving a basis for predicting the long term consequences of biodiversity loss for ecosystem functioning, researchers need to conduct species removal experiments which allow us to establish the context under which compensation may ameliorate the impact of species loss on ecosystem functioning. In the absence of understanding this context, researchers could seek alternative approaches to quantifying biodiversity-ecosystem function relationships so that conservation priorities can be set for ecosystems undergoing disturbances which are likely to impact heavily on important ecosystem processes. One such approach is firstly to seek an understanding of the
community properties which determine the short term consequences of species removal for ecosystem functioning so that 'worst case scenarios" of biodiversity-ecosystem function relationships can be predicted, and secondly by developing approaches which simulate how compensation can ameliorate the impact of species extinction on ecosystem functioning under 'best case scenarios' of density compensation.

## Chapter 3. Multiple ecosystem processes are

 controlled by dominant species during realistic extinction events in a macroalgae assemblage.

# Chapter 3. Multiple ecosystem processes are controlled by dominant species during realistic extinction events in a macroalgae assemblage. 

### 3.1 Abstract

Research into the impact of species extinctions on ecosystem functioning has to date been mostly limited to singular ecosystem functions. However ecosystems often perform a range of different functions of conservation importance, and if different ecosystem functions are controlled by different species, then overall ecosystem functioning (ecosystem multifunctionality) is expected to collapse more rapidly with species loss than when functions are considered independently. Few investigations have tested this hypothesis in natural assemblages using realistic extinction scenarios. The aim of this investigation was to conduct a realistic in situ biodiversity manipulation to establish whether more species are required to maintain multiple ecosystem functions than when functions are considered independently. An assemblage of intertidal macroalgae was manipulated to simulate an empirically derived extinction order in response to elevated wave exposure, and changes in multiple ecosystem processes (uptake of nutrients and primary productivity) were quantified across the resulting gradient of species richness. The manipulation used an additive design in which community biomass was allowed to vary with species loss, and hence was representative of a 'worst case' extinction scenario in the absence of density compensation. Species contributions to individual ecosystem processes were equally proportional to their contributions to community biomass. Hence, the minimum number of species required to maintain overall ecosystem functioning did not increase with the number of processes considered. These results suggest that establishing the position of dominant species along biodiversity-extinction curves could be crucial as their loss can result in a sudden collapses of multiple ecosystem services.

### 3.2 Introduction

The number of publications concerned with understanding the relationship between biodiversity loss and ecosystem functioning has been rising exponentially over the last decade (Solan et al. 2009). Yet while there is now a general consensus that biodiversity is important for the provision of ecosystem services (Schmid et al. 2009), little is known of how biodiversity loss will affect ecosystem services in the real world. Hence the ability to predict the impact of biodiversity loss on ecosystem functioning under real world scenarios is lacking. This paradox stems from the fact that despite extensive research very few investigations have sought to manipulate biodiversity to simulate realistic extinction scenarios in situ. The staple of biodiversity-ecosystem functioning (BEF) research has instead been to generate gradients of species richness using randomly selected species from a larger species pool (Symstad et al. 1998, Hector et al. 1999, Emmerson et al. 2001, Hector et al. 2001, Tilman et al. 2006, Marquard et al. 2009). In order to test species richness effects, initial species densities are usually standardised using a replacement series design which assumes that extinction resistant species can compensate for loss of function associated with extinction in nature. In addition BEF relationships are typically quantified only for singular ecosystem functions. Translating the results of such investigations into real world scenarios is difficult because often species go extinct in a deterministic order contingent on the presence or absence of particular functional response traits (Diaz and Cabido 2001), species are present in unequal densities (Whittaker 1975), the compensatory dynamics of ecosystems undergoing biodiversity loss are little understood (Gonzalez and Loreau 2009), and ecosystems provide multiple services which may not respond similarly to specific patterns of biodiversity loss (Kremen and Ostfeld 2005, Bennett et al. 2009, Reiss et al. 2009).

Recent BEF research has highlighted how ecosystem functioning can be more sensitive to realistic patterns of biodiversity loss compared to the results of traditional random assembly design experiments (Ostfeld and LoGiudice 2003, Solan et al. 2004, Zavaleta and Hulvey 2004, Larsen et al. 2005, Bracken et al. 2008). For example Bracken et al.., (2008) found that natural increases in the diversity of a macroalgal assemblage resulted in enhanced rates of nitrogen uptake while random increases in diversity had no affect on nitrogen uptake. These experiments represent a step towards a real world understanding of the consequences of biodiversity loss for ecosystem services. However few investigations have quantified realistic species extinction sequences using empirically derived data from in situ disturbance experiments. Such an approach is necessary if ecologists are to establish whether common rules can be applied to predict patterns of biodiversity loss across different disturbance scenarios.

In order to accurately predict the consequences of biodiversity loss for ecosystem functioning ecologists must gain an understanding of how different functions respond to realistic species extinctions. Where different species are responsible for performing different functions then it is expected that overall ecosystem functioning will be more sensitive to species loss because more species are required to maintain all ecosystem functions (Gamfeldt et al. 2008). For example studies of terrestrial plants indicate that more species are required to maintain ecosystem multifunctionality as more ecosystem processes are considered to be important for overall ecosystem functioning (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010). These studies use a replacement series design where initial species densities are fixed across species richness treatments, hence they assume that extinction resistant species compensate for the loss of their more extinction prone competitors in the real world. Current consensus suggests however, that extinction resistant species do not always compensate for the loss of extinction
prone species in natural ecosystems (Gonzalez and Loreau 2009), and to date few investigations have attempted to understand the mechanisms underpinning density compensation in the real world (but see Fischer et al. 2001, Cross and Harte 2007, Peters et al. 2009, Winfree and Kremen 2009). Hence predicting the long term consequences of biodiversity loss for ecosystem functioning in natural ecosystems is difficult.

Previously Solan et al.., (2004) and McIntyre et al.., (2007) estimated worst case scenario (in the absence density compensation) predictions of the decline in ecosystem functioning with species extinction. Given that our current understanding of compensatory dynamics is limited, such worst case scenario predictions can be used as useful guidelines for ecosystem function conservation. mass-ratio theory (Grime 1998) may help predict worst case scenarios of biodiversity-ecosystem function relationships, because it stipulates that ecosystem processes can be expected to be dominated by the most dominant species in natural ecosystems. Hence the contribution of species to ecosystem processes is proportional to and can therefore be predicted from their contributions to community biomass. Understanding the wider application of this theory across multiple ecosystem processes is crucial as it suggests that dominant species could consistently dominate a variety of ecosystem processes in nature, and hence their extinction could result in a sudden collapse of ecosystem multifunctionality if extinction resistant species fail to compensate for the loss of their competitors.

The aim of the current study was to conduct a realistic biodiversity - ecosystem function manipulation in an assemblage of intertidal macroalgae by manipulating natural assemblages to simulate species extinction in response to a realistic disturbance. Multiple ecosystem processes were then quantified across the resulting gradient of species richness. In contrast to previous multifunctionality research (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010),
this study tested the hypothesis that the short term consequences of biodiversity loss are driven by biomass for all ecosystem processes, as opposed to explicitly testing for the mechanisms underpinning species richness effects in the longer term. Hence it was hypothesised that the number of species required to maintain overall ecosystem functioning is the same regardless of the number of functions being performed by an assemblage.

### 3.3 Methods

### 3.3.1 Overview

An assemblage of macroalgae was manipulated to simulate community disassembly in response to wave exposure, a key structuring disturbance of rocky shore communities (Dayton 1971) which is predicted to increase in frequency and severity in the North East Atlantic (Ulbrich and Christoph 1999, Holland and Webster 2007). A species extinction sequence was obtained by mimicking elevated wave exposure on a sheltered natural macroalgal assemblage. Previously undisturbed plots were then manipulated in an additive design to simulate the pattern of community disassembly observed during the disturbance so that biomass was allowed to vary naturally as each species was removed. Changes in primary production and the uptake of key nutrients ammonium $\left(\mathrm{NH}_{4}{ }^{+}\right)$, and nitrate $\left(\mathrm{NO}_{3}{ }^{-}\right)$were then quantified across the resulting gradient of species richness. Macroalgal species have been demonstrated to display preferences for the uptake of different forms of Nitrogen leading to resource use complementarity in intertidal rock pools (Bracken and Stachowicz 2006), hence each of these nutrient fluxes were considered independent ecosystem processes. Species contributions to each ecosystem process could then be quantified and related to their contributions to community biomass. The relationship between species richness and ecosystem multifunctionality was then quantified to
establish whether overall ecosystem functioning was more sensitive to species loss than when considering individual ecosystem processes.

### 3.2.2 Experimental Field Site

The experimental field site was located in a boulder field located on the sublittoral fringe of a sheltered soft sedimentary shore near Penmon Point, Anglesey, UK ( $53^{\circ} 17^{\prime} 59.79^{\prime}$ 'N, $4^{\circ} 03^{\prime} 04.96^{\prime} \mathrm{W}$ ). This site was selected for the homogenous distributions of the most dominant macroalgae species (i.e. low patchiness) which it was envisaged would facilitate accurate estimates of extinction susceptibility and contributions to ecosystem function. The communities contained a diverse array of species representing all three macroalgae phyla (Chlorophyta, Heterokontophyta, and Rhodophyta).

### 3.2.3 Quantifying Extinction susceptibility

In order to quantify a realistic extinction order of algae species to wave exposure a high pressure hose was used to mimic a series of high impact wave events and the \% cover of each species quantified through time. Ten $0.3 \times 0.3 \mathrm{~m}$ plots were allocated to 8 medium to large sized ( 2 m largest diameter) boulders on the 27/02/10. \% cover of all macroalgal species was recorded in all plots on 28/02/10 prior to disturbance. Five randomly selected plots were disturbed using a high pressure hose. The hose consisted of a Honda WX10 petrol powered water pump with a 1.27 cm nozzle fixed to the end of the outlet pipe to increase water velocity (Figure 3.3.1). This provided a variable water velocity between 9.53 and $11.44 \mathrm{~m} \mathrm{~s}^{-1}$ which is within the upper range of maximum breaking wave velocities recorded at other locations (Bell and Denny 1994, Gaylord 1999). Plots were disturbed by holding the nozzle perpendicular to the rock surface at a distance of $\sim 5 \mathrm{~cm}$ and spraying randomly within the plot area for a period of 2 minutes. This


Figure 3.3.1 High impact wave events were simulated by disturbing macroalgae communities with a high pressure hose for 2 minutes.
disturbance was repeated once every low spring tide period for 60 days (4 disturbances in total). The remaining 5 plots were left undisturbed as a control treatment to monitor natural changes in species abundance over the duration of the disturbance treatment. \% cover was recorded for all species on the spring tide following each disturbance to allow time for recovery (i.e. the day prior to the following disturbance event). The extinction susceptibility of each of the 8 most dominant species was then estimated as the slope value obtained from 0 intercept standardised OLS regression of relative \% cover against time [Relative \% cover = (\% cover/mean initial \% cover)-1]. In this instance the slope of this relationship represents a realistic comparative measure of susceptibility to disturbance which can be used as a surrogate of extinction susceptibility because it incorporates both resistance to loss of biomass resulting from the physical action of wave exposure, and recovery of biomass between each disturbance treatment. This was performed independently for each species using averaged treatment responses in the disturbed plots and the same process repeated for the control plots as a comparison. The extinction order of species in response to wave disturbance was established by ranking species in
order of the slope values obtained from the regression estimates. Rarer species were omitted from the analysis as changes in their \% cover could not be reliably distinguished from variability due to patchiness.

### 3.2.4 Community Disassembly

On the 13/06/2010 Fourteen experimental plots were allocated randomly to boulders which had not been used during the disturbance phase. Plots were demarcated by screwing a clear Plexiglass frame ( $20 \times 20 \mathrm{~cm}$ internal dimentions) to the rock surface (Figure 3.3.2.). Because measurements of ecosystem function were initially intended to be conducted in situ, the frames were fitted with a compressible neoprene gasket to facilitate a water tight seal with the rock surface. A 15 cm tall plexiglass cube could then be fitted inside the frame and sealed using CT1 underwater sealant. This provided an in situ mesocosm similar to that described by Tait \& Schiel (2010) in which immersed Primary Productivity could be quantified (Figure 3.2.2). Initial trials of the mesocosm setup conducted on 16/06/10 were successful in providing in situ estimates of primary productivity without any leaks.

Macroalgal assemblages were manipulated on the 12/07/10. Only fourteen mesocosms were available to conduct the experiment and the number of available boulders was limited, hence community disassembly was simulated only for the top five species contributing to Total Community Biomass. Two replicate plots for each of seven treatments were manipulated to simulate the extinction order observed from the disturbance phase by carefully picking algae to ensure whole individuals were removed. This provided a gradient of species richness over which ecosystem function could be quantified. For example where species richness (SR) was equal to 0


Figure 3.3.2 Mesocosms designed for in situ measurements of immersed Gross Community Productivity. Left: A trial mesocosm consisting of a plexiglass chamber sealed inside a plexiglass frame using CT1 underwater sealant. The frame is fixed in place using screws and sealed using a compressible neoprene rubber material which moulds to fit irregularities in the rock surface. Right: A trial measurement of immersed Gross Community Productivity using a HACH LD40 probe.
all algae species were removed, where $\mathrm{SR}=1$ only the most extinction resistant species was present, $\mathrm{SR}=2$ plots contained the two most extinction resistant species etc. Remaining rarer species were removed from all but two experimental plots in order to quantify their collective contribution to community ecosystem processes. All removed biomass was kept in order to later quantify the population dry weight of each species.

### 3.3.5 Measuring Ecosystem Processes

Plexiglass mesocosms were deployed on $13 / 07 / 2010$. Despite numerous attempts to seal the cubes and the frames, leaks in all mesocosms persisted. Observations in the field revealed this was likely due to the presence of the tube building polychaete Sabellaria encrusting the rock surface. The initial tight seal of the frames caused individuals of this species to die and decay leaving a network of tube casts which acted as capillaries channelling water out from underneath the neoprene seal. In situ quantification of ecosystem function was therefore abandoned on 14/07/2010 in favour of an alternative outdoor mesocosm setup. All macroalgae was removed


Figure 3.3.3 Estimating Gross Community Productivity on Menai Bridge Pier. Macroalgae communities were placed in large plastic tubs and stirred frequently. Picture is a dark measurement which quantified $\mathrm{O}_{2}$ uptake through respiration of the macroalgae community.
from plots and immediately transported back to Menai Bridge Pier. Each plots algal community was placed in a $25 \times 25 \mathrm{~cm}$ mesocosm containing $5200 \mathrm{~cm}^{3}$ of fresh seawater from the Menai Strait for estimation of nutrient fluxes and primary productivity (Figure 3.3.3.). Nutrient concentration was sampled in duplicate 10,50 and 90 minutes following the addition of algae with water being stirred prior to each measurement. For each sample 20 ml of seawater was filtered through a 0.45 um GF Whatman filter into acid rinsed bottles and stored at $\sim 10^{\circ} \mathrm{C}$ in dark. On completion all samples were immediately transported back to the laboratory and stored at $-20^{\circ} \mathrm{C}$ for later analysis. Seawater in seven randomly selected mesocosms was then replaced and $\mathrm{O}_{2}$ concentration immediately quantified in duplicate using two calibrated HACH LD40 probes. Gross Community Productivity was estimated following the method outlined by Noel et al.., (2010). $\mathrm{O}_{2}$ utilization during Community Respiration was first quantified by immediately covering mesocosms in blacking out fabric removing $100 \%$ of available light. $\mathrm{O}_{2}$ concentration was measured $\sim 30$ and 50 minutes later. Following dark measurements the blacking out fabric was removed and Net Community Productivity estimated by sampling $\mathrm{O}_{2}$ concentration a further

70 and 100 minutes later. Gross Primary Productivity was then estimated by subtracting the rate of $\mathrm{O}_{2}$ utilization during community respiration from the rate of $\mathrm{O}_{2}$ production through Net Community Productivity and expressed as $\mathrm{mg} \mathrm{O}_{2} \mathrm{~min}^{-1}$. Seawater was then replaced in the remaining seven mesocosms and Gross Community Productivity quantified in the same fashion. To ensure that productivity estimates were not affected by changes in ambient light levels between the two sets of replicates, light levels were recorded every 30 seconds during light measurements using a LI190SA Quantum Sensor (LICOR BIOSCIENCES). Following nutrient flux and productivity measurements, algae biomass was transported back to the laboratory and frozen at $-20^{\circ} \mathrm{C}$ in order to later estimate population dry weight. Nutrient samples were analysed in the laboratory to quantify fluxes of Ammonium $\left(\mathrm{NH}^{+}\right)$and Nitrate $\left(\mathrm{NO}_{3}{ }^{-}\right)$. Nitrate concentrations were determined using an A5X-500 Series XYZ Auto Sampler (Zellweger analytics). Ammonium concentrations were determined fluorometrically using an F-2000 Fluorescence Spectrophotometer (Hitachi). The rate of nutrient flux was determined as the slope of the relationship between concentration and time for each of the nutrients analysed and expressed in $\mu \mathrm{mol} \mathrm{hr}^{-1}$. Concentrations of Nitrate were low ( $<1 \mu \mathrm{~mol}$ ) and the apparatus used gave negative values in some instances, however sufficient data (i.e. at least 1 replicate from the duplicate samples taken at each time interval) was obtained to perform the analysis.

### 3.3.5 Data analysis

In order to quantify the relationship between species loss (richness) and ecosystem process rates a range of linear and nonlinear models were fitted to each of the datasets in the statistics platform $R$ (see Table 3.3.2) for the full range of linear and non linear models fitted). Non linear models were fitted using the CRAN package nlrwr (see Ritz and Streibig 2008 for detailed description). The most parsimonious model fit was then selected using Akaike's Information Criterion (AIC)
which optimises model selection by penalising goodness of fit for the addition of model parameters. The model with the lowest AIC values was deemed to be the most appropriate fit to the data. ANOVA was then performed on all models to confirm whether the selected model was a reliable and significant fit to the data. Ecosystem processes for which no significant model fits could be found were presumed to not be affected by species loss and therefore omitted from the remainder of the analysis. The contribution of each species to each ecosystem process (the functional contribution) was then estimated as the difference in the fitted model values between the two species richness values over which that species was lost. For example the contribution of the most extinction resistant species was estimated as the difference in the fitted model values between $\mathrm{SR}=1$ and $\mathrm{SR}=0$.

To establish whether the relationship between relative contribution to an ecosystem process and relative contribution to community biomass was different for different ecosystem processes, Population Dry Wt was estimated for each species by taking the average of population dry wt (the sum of the dry mass of material removed during the manipulations and that remaining after measurements of ecosystem processes had been made) of each species across all fourteen plots used during the manipulation and ecosystem function measurements. In order to compare whether species functional contributions were consistently driven by their contributions to total community biomass and hence whether dominant species were primarily responsible for all ecosystem processes, both functional contribution values and population dry wt values were first standardised to relative values by converting to percentages of their respective totals (i.e. the sum of their respective values). Analysis of Covariance (ANCOVA) was then performed on the resulting relationships to ascertain whether the relationship between relative contribution to an

Ecosystem Process and relative contribution to Community Biomass was different for different Ecosystem Processes.

It was anticipated that species contributions to all ecosystem processes would be proportional to their contributions to community biomass. Hence we hypothesised that the number of species required to maintain overall ecosystem functioning would not be significantly different from that required to maintain individual ecosystem processes. To test this overall ecosystem functioning was estimated following a similar technique to that outlined by Gamfeldt et al.. (2008) as the minimum value of richness necessary to maintain all ecosystem functions. Ecosystem processes were first transformed to percentages of their respective maximum values. The two minimum percentage values recorded for all ecosystem processes in each treatment were then selected as they represented the minimum value of richness necessary to maintain all ecosystem functions. This provided a distribution of the minimum percentage data values recorded across species richness treatments with the same replication as for individual ecosystem processes. ANCOVA was then used to test whether the relationship between species richness and overall ecosystem functioning was significantly different from each of the individual ecosystem processes measured. For non linear data, ANCOVA was performed using the method outlined by in which Analysis of Variance is used to compare two non linear regression models, one which fits a single set of model parameters to both datasets (overall ecosystem functioning and an individual ecosystem process), and one which fits separate model parameters for each of the data sets being compared.

### 3.4 Results

### 3.4.1 Quantifying Extinction susceptibility



Figure 3.4.1 Macroalgae species responses to wave disturbance mimicked using high pressure hosing. The decline in relative $\%$ cover $\left(\left(\%\right.\right.$ cover/mean $\%$ cover at time $\left.\left.{ }_{0}\right)-1\right)$ of each macroalgal species over time in response to fortnightly wave disturbance events simulated using a high pressure hose (filled points). Open points represent changes in the relative $\%$ cover of species in control (undisturbed) plots. Points represent the average relative $\%$ cover of each species measured over five $0.3 \times 0.3 \mathrm{~m}$ plots prior to each simulated disturbance event (error bars are $95 \%$ confidence intervals). Dashed and dotted lines represent a significant change in macroalgal abundance over time in disturbed and control plots respectively. Note that y axis values vary.

Of the eight species examined during the disturbance experiment, Chondrus, Ectocarpus, Fucus, Ceramium and Membranoptera displayed no significant change in relative $\%$ cover over time in the five control plots $\left(F_{l, 4}=3.547, p=0.1365 ; F_{l, 4}=3.224, p=0.147 ; F_{l, 4}=0.022, p=0.888\right.$;
$F_{l, 4}=0.786, p=0.425 ; F_{l, 4}=0.884, p=0.400$ respectively) while Ulva, Gracilaria and Cladophora displayed significant increases in relative $\%$ cover $\left(F_{1,4}=24.56, p=0.008, r^{2}=\right.$ $0.83 ; F_{1,4}=12.21, p=0.025, r^{2}=0.69 ; F_{1,4}=15.29, p=0.017, r^{2}=0.74$ respectively) (Figure 3.4.1..). Hence any decrease in relative $\%$ cover in the disturbed plots was attributed to the artificial wave disturbance treatment. All species responded differently (albeit marginally in some cases) to the artificial wave disturbance treatment (Figure 3.4.1., Table 3.4.1). Ectocarpus spp., Ulva spp., Membranoptera and Fucus all responded negatively to artificially elevated wave disturbance (Figure 3.4.1, Table 3.4.1). Gracilaria, Chondrus and Ceramium displayed non significant responses while Cladophora increased in abundance (Figure 3.4.1). The large increase in the relative \% cover displayed by Cladophora in the control treatment was due to low abundance $(0.4 \%$ cover $)$ at the start of the disturbance experiment and rapid growth of this species over the duration of the spring to $6.53 \%$ cover by the end of the disturbance period 58 days later. The significant growth of Cladophora and Graciliaria in the control plots suggested that their resilience to the disturbance may in part be due to rapid rates of recovery. Contrastingly the significant growth of Ulva in the control plots was insufficient to prevent loss of $\%$ cover in the disturbed plots (Figure 3.4.1). By ranking species in order of the slope estimate of the relationship between \% cover and time, an extinction scenario was established which followed the order Ectocarpus $>$ Ulva $>$ Membranoptera $>$ Fucus $>$ Gracilaria $>$ Ceramium $>$ Chondrus crispus and Cladophora with Ectocarpus being the most and Cladophora the least susceptible to becoming extinct as a result of wave disturbance.

### 3.4.2 Community disassembly and ecosystem function

A total of sixteen species representing Rhodophyta, Heterokontophyta and Chlorophyta were identified across all the plots included in the community disassembly manipulation (Figure

Table 3.4.1. The ranked extirpation susceptibility of macroalgal species in response to wave disturbance events mimicked using a high pressure hose. Species are ranked according to the slope of the relationship between relative $\%$ cover and time during which high intensity wave impact events were simulated ( $\pm$ the $95 \%$ confidence intervals of the relationships). Extirpation susceptibility decreases with increasing rank value.

| Species | Slope | $\pm$ | $95 \% \mathrm{CI}$ | $F_{(l, 4)}$ | $p$ value | $\mathrm{R}^{2}$ | Rank |
| :--- | ---: | :--- | :--- | :--- | :--- | :--- | :--- |
|  |  |  |  |  |  |  |  |
| Ectocarpus sp. | -0.011 | $\pm$ | 0.007 | 18.91 | 0.012 | 0.78 | 1 |
| Ulva sp. | -0.010 | $\pm$ | 0.005 | 34.91 | 0.004 | 0.87 | 2 |
| Membranoptera alata | -0.009 | $\pm$ | 0.007 | 10.97 | 0.030 | 0.67 | 3 |
| Fucus serratus | -0.008 | $\pm$ | 0.007 | 11.52 | 0.024 | 0.68 | 4 |
| Gracillaria | -0.005 | $\pm$ | 0.006 | 4.94 | 0.090 | 0.44 | 5 |
| Ceramium rubrum | -0.004 | $\pm$ | 0.008 | 1.39 | 0.304 | 0.07 | 6 |
| Chondrus crispus | 0.001 | $\pm$ | 0.002 | 1.52 | 0.286 | 0.09 | 7 |
| Cladophora sp. | 0.039 | $\pm$ | 0.037 | 8.19 | 0.046 | 0.59 | 8 |

3.4.2). The five most dominant species selected for estimating contributions to ecosystem function were Chondrus crispus $>$ Gracilaria verrucosa $>$ Ceramium $\mathrm{sp} .>$ Ectocarpus sp. $>$ Ulva sp. (from most to least dominant) (Figure 3.4.2). These species represented $94 \%$ of the Total Community Biomass, hence we were confident that ecosystem processes rates would be controlled mostly by these species. Average light levels were not significantly different between the two sets of replicate productivity measurements (Kruskal-Wallis $\chi^{2}=0.0143, p=0.905$ ). The AIC model selection procedure indicated that both Gross Community Productivity and Ammonium $\left(\mathrm{NH}_{4}{ }^{+}\right)$uptake displayed saturating relationships with increasing species richness following a Michaelis-Menten relationship (Table 3.4.2, Figure 3.4.3). No significant model fit was identified for Nitrate $\left(\mathrm{NO}_{3}{ }^{-}\right)$(Table 3.4.2). Hence species contributions to ecosystem processes were estimated only for Ammonium flux and Gross Community Productivity using the Michaelis-Menten curves fitted.


Figure 3.4.2 The distribution of biomass across species within the macroalgae turf assemblage used during the manipulation and ecosystem function experiment at Penmon Point, Anglesey (A). B. represents the distribution of biomass on a logarithmic y axis to display occurrences of rarer species. Error bars represent average values ( $\pm 95 \%$ confidence intervals) of all 14 experimental plots. Species to the left of the dashed red line were included in the estimation of contribution to ecosystem function while species to the right were removed from all two experimental plots to standardise species richness values for each treatment stage of community disassembly. The upper limit on the number of species to be included was defined by constraints on replication.

Gross Community Productivity and Ammonium Flux were both dominated by the most dominant and extinction resistant species, Chondrus. In addition the rank order of species contributions to ecosystem processes was the same for both Gross Community Productivity and

Ammonium flux (Chondrus $51 \%$ > Ceramium 23\% > Gracilaria 14\% > Ulva sp. 9\% >
Ectocarpus sp. $6 \%$ and Chondrus $61 \%>$ Ceramium $20 \%>$ Gracilaria $10 \%>$ Ulva sp. $6 \%>$
Ectocarpus sp. $4 \%$ respectively). 'Other' species contributed $26 \%$ and $16 \%$ to Total Gross


Figure 3.4.3 The relationship between species loss (Species Richness) and 4 Ecosystem processes; Gross Community Productivity, Ammonium (NH4+) flux, and Nitrate (NO3-) flux in a macroalgae assemblage. Black points represent the simulated extinction scenario in response to wave exposure of the 5 most dominant species and hence were used for the model fitting and selection procedure. Grey points represent controls in which rarer 'other' species were included as a reference but were not used in the model fitting and selection procedure. Dashed lines represent a significant relationship between species loss (Species Richness) and an Ecosystem Process.

Community Productivity and Total Community Ammonium flux respectively although these
values were not included when data for the most dominant species was standardised for this

Table 3.4.2 The range of linear and non linear model types fitted to extinction - ecosystem process relationships in a macroalgae assemblage. AIC values provide an indication of the most parsimonious or optimum model fit to the data. The lower the AIC value, the better the fit. $p$ values represent the significance of individual model parameters, $\mathrm{NF}=\mathrm{No}$ Fit (i.e. the model could not be fitted to the data).

| Model Type | Model | Parameters | GCP |  | $\mathrm{NH}_{4}^{+}$flux |  | $\mathrm{NO}_{3}{ }^{-}$flux |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | AIC | $p$ | AIC | $p$ | AIC | $p$ |
| Linear | $y=S R^{*} b+c$ | $\dddot{b}$ | 4.665 | $\begin{aligned} & 0.002 \\ & 0.148 \end{aligned}$ | -8.423 | $\begin{aligned} & 0.013 \\ & 0.031 \end{aligned}$ | -12.70 | 0.159 0.803 |
| Linear(exponen tial) | $y=b^{*} \exp (S R)+c$ | $b$ | 11.640 | $\begin{aligned} & 0.002 \\ & 0.037 \end{aligned}$ | -2.823 | $\begin{aligned} & 0.192 \\ & <0.001 \end{aligned}$ | -10.41 | $\begin{aligned} & 0.691 \\ & 0.112 \end{aligned}$ |
| MichaelisMenten | $y=V m * S R /(K+S R)$ | $\begin{gathered} V m \\ K \end{gathered}$ | 1.583 | $\begin{aligned} & 0.007 \\ & 0.238 \end{aligned}$ | -11.74 | $\begin{aligned} & 0.002 \\ & 0.275 \end{aligned}$ | NF | NF |
| Asymptotic | $\begin{aligned} & y=A s y m+(R 0-A s y m) * \exp (- \\ & \exp (l r c) S R) \end{aligned}$ | Asym <br> RO <br> lrc | 4.040 | $\begin{aligned} & 0.001 \\ & 0.927 \\ & 0.483 \end{aligned}$ | -10.43 | $\begin{aligned} & <0.001 \\ & 0.592 \\ & 0.713 \end{aligned}$ | NF | NF |
| Logistic | $\begin{aligned} & y=A+(B-A) /(1+\exp ((\text { xmid }- \\ & S R) / \text { scal })) \end{aligned}$ | $\begin{gathered} A \\ B \\ \text { xmid } \\ \text { scal } \end{gathered}$ | NF | NF | -9.378 | $\begin{aligned} & 0.652 \\ & <0.001 \\ & 0.068 \\ & 0.477 \end{aligned}$ | NF | NF |



Figure 3.4.4 Mass-ratio relationships are similar for contrasting ecosystem processes in a macroalgae assemblage. The relationship between species contributions to Gross Community Productivity and Ammonium flux for the 5 most dominant species in a macroalgal assemblage. The relationship was not significantly different for each of the processes being considered.
analysis. Species relative contributions to Community Biomass explained $88 \%$ of the variability in relative contributions to Ecosystem Processes $\left(F_{1,8}=64.941, p=4.14 \times 10^{-5}\right)$ (Figure 3.4.4), and this relationship was not significantly different between Gross Community Productivity and Ammonium Flux (ANCOVA, $F_{1,6}=1.25, p=0.306$ ). Hence the contribution of species to ecosystem processes was similarly proportional to their contributions to community biomass for both Gross Community Productivity and Ammonium Flux.

Biomass determined species contributions to both Gross Community Productivity and Ammonium uptake, hence each species displayed similar contributions to both ecosystem processes. The relationship between overall ecosystem functioning (the minimum number of species required to maintain all ecosystem processes) and species loss was therefore not significantly different from each of the individual ecosystem processes measured (ANCOVA; $\mathrm{F}_{2,20}=1.90, \mathrm{p}=0.176$ for Ammonium uptake; and $\mathrm{F}_{2,20}=1.77, \mathrm{p}=0.195$ for gross community productivity). Hence the same number of species were required to maintain multiple ecosystem processes as were required to maintain each ecosystem process independently

### 3.5 Discussion

The number of species required to maintain all ecosystem processes affected by species loss (gross community productivity and nitrate uptake) was not different from that required to maintain each individual process. This was because species contributions to both of these ecosystem processes were similarly proportional to their contributions to community biomass. These results provide a new perspective of how ecosystem functioning is affected by species loss in two ways. Firstly many of those investigations which generate random patterns of species loss using replacement series designs test explicitly for positive species richness effects (Hector et al. 1999, Hector et al. 2001, Loreau and Hector 2001, Hector and Bagchi 2007, Marquard et al. 2009, Zavaleta et al. 2010), while the strength of the link between biomass and ecosystem processes demonstrated in the current study suggests that positive species interactions such as resource use partitioning are negligible in the short term compared to loss of biomass. Secondly, where these studies consider multiple ecosystem functions (Hector and Bagchi 2007, Zavaleta et al. 2010) they find that the number species required to maintain ecosystem multifunctionality
increases with the number of processes being performed by an ecosystem. The results of this study are not necessarily conflicting with these findings. This is firstly because one of the ecosystem processes (nitrate uptake) was not affected by species loss, hence only two ecosystem processes were used to estimate overall ecosystem multifunctionality, while several would have been more robust and comparative to previous studies (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010). Secondly the experimental design allowed biomass to vary as each species became extinct from the ecosystem, while initial densities are fixed across species richness gradients in previous BEF experiments which evaluate both singular and multiple ecosystem functions (Hector et al. 1999, Hector et al. 2001, Loreau and Hector 2001, Hector and Bagchi 2007, Marquard et al. 2009, Zavaleta et al. 2010). Essentially a 'worst case scenario' of species loss was assumed where density compensation does not occur, while replacement series experiments assume that density compensation is commonplace in nature.

The link between biomass and ecosystem functioning could provide a central basis from which real world short term BEF relationships can be predicted. Yet the wider application of Massratio theory to ecosystems in general has been largely unexplored. Initially it was considered only applicable to autotrophic systems (Grime 1998), however in silico simulations have highlighted its potential importance in driving BEF relationships in detritivorous macrofaunal assemblages (Solan et al. 2004) where $83 \%$ of the population level bioturbation of species was explained by abundance, and two multitrophic fish assemblages (McIntyre et al. 2007) where biomass explained $99 \%$ and $83 \%$ of variation in nitrogen cycling rates. Empirical evidence for mass-ratio theory has to date been restricted to terrestrial plant assemblages (Smith and Knapp 2003, Garnier et al. 2004, Gilbert et al. 2009). Here we have demonstrated the importance of considering biomass for determining species contributions to ecosystem processes in a
macroalgae assemblage and hence reinforced the wider application of mass-ratio theory to autotrophic systems in general. Understanding the importance of mass-ratio theory to ecosystems in general however requires further empirical based research in a wider diversity of ecosystems. Also our analysis was restricted to ecosystem processes which may be expected intuitively to be strongly dependent on biomass. When considering biological functions such as crop pollination and secondary productivity mass-ratio theory may well not apply due to the increased complexity of biological interactions taking place (although see Gilbert et al. 2009).

It has previously been suggested that standing plant biomass is a poor indicator of primary productivity in aquatic algal ecosystems (Bruno et al. 2005) because high herbivory rates reduce resource limitation which maximises productivity (Carpenter 1986). However the strong link between biomass and Gross Community Productivity demonstrated in the current study indicates that the loss of standing plant biomass can still be a very good proxy for declining primary production. In addition where replacement series designs have been used to analyze species richness - productivity relationships in macroalgal assemblages, they often find that Primary Productivity of fixed density assemblages is dependent on species identity (Bruno et al. 2005, Bruno et al. 2006). This occurs because ephemeral species such as Ulva spp. display higher growth rates and therefore per capita productivity. The range of species used in this study is comparable to those of Bruno et al.., $(2005,2006)$ in that it incorporates representatives of all three major macroalgae phyla and includes genera such as Ulva, Gracilaria and Ceramium. Similar to the results of Bruno et al.., $(2005,2006)$, estimated rates of productivity per capita biomass were in general higher for ephemeral vs slower growing less transient species
(Ceramium $=0.441>$ Ulva $=0.444>$ Ectocarpus $=0.219>$ Chondrus $=0.173>$ Gracilaria $=$ $0.155 \mathrm{mg} \mathrm{O}_{2} \mathrm{hr}^{-1} \mathrm{~g}^{-1}$ Dry Wt, estimated from the fitted model data presented in Figure 3, Table
2). However because the design used here allowed biomass to vary with species loss as opposed to fixing total biomass across species richness treatments, differences in per capita productivity between species were rendered negligable by their large differences in population biomass. Where extinction resistant species compensate for the loss of their extinction prone competitors, such differences in per capita contributions to function are important in determining long term declines in ecosystem functioning during extinction. However in this study those species which are most resistant to increases in the frequency and severity of wave impact events are often the least productive (for example Chondrus and Gracilaria). Hence it was anticipated that in the long term, increases in the frequency and severity of storm events in the North West Atlantic will lead to a greater dominance of slower growing low productivity species.

Macroalgae are known to use both the ammonium and nitrate components of the nitrogen pool, and different species display preferences for each of these nutrients based on life history strategy (Pedersen and Borum 1997, Bracken and Stachowicz 2006). Hence the lack of a significant relationship between nitrate uptake and species loss in the current study was surprising. Using a replacement series design Bracken and Stachowicz (2006) demonstrate how the dominant species Cladophora columbiana and Prionitis lanceolata partition the nitrogen pool by predominantly utilizing ammonium and nitrate respectively, leading to positive species diversity affects through resource use complementarity. Contrastingly, the results presented here suggest that all species in the macroalgal assemblage primarily utilize ammonium over nitrate as only ammonium displayed significant reductions in uptake rates as species were lost. However it should be noted that our nutrient uptake rates were estimated in natural seawater from the Menai Strait during July when nutrient concentrations would have been at their lowest (Ewins and Spencer 1967). Previous authors have demonstrated that macroalgal species rapidly take up
ammonium comparative to nitrate when their tissues are in a nutrient deprived state (Fujita 1985, Pedersen and Borum 1997), and uptake rates in the current study were generally higher for ammonium compared with nitrate (range $=0.064$ to $0.669 \mu \mathrm{~mol} \mathrm{hr}^{-1}$ and -0.060 to $0.402 \mu \mathrm{~mol} \mathrm{hr}$ ${ }^{1}$ respectively). This suggests that the lack of a significant trend in uptake of nitrate with species loss may have resulted from surge uptake of ammonium in nutrient limited conditions and the time duration of nutrient sampling ( 80 min ) may have been insufficient to reliably quantify the relatively slower assimilation of nitrate.

This study highlights how the mechanisms underpinning biodiversity-ecosystem function relationships can differ depending on whether experiments are conducted on the short term in the real world or using artificial assemblages which study longer term positive biodiversity affects. The link between biomass and function highlights how dominant species could be primarily responsible for a variety of ecosystem processes in natural systems, hence their extinction could lead to rapid collapses of ecosystem multifunctionality in the absence of density compensation. More accurate long term forecasts of the deterioration in ecosystem functioning however requires that researchers unravel the mechanisms underpinning density compensation in natural systems. Nonetheless these results indicate that biomass can be used as a surrogate for predicting the decline in different ecosystem processes with species loss in the short term, a tool which is potentially useful for ecosystem function conservation.

Chapter 4. Mass-Ratio theory describes extinctionecosystem process relationships in fouling invertebrate communities.


# Chapter 4 Mass-Ratio theory describes extinction-ecosystem process 

 relationships in fouling invertebrate communities.
### 4.1 Abstract

Numerous investigations have sought to understand the impact of biodiversity on the functioning of ecosystems. Yet few have directly addressed how extinction affects ecosystem functioning in nature. Conventional replacement series designs seek to establish the validity of positive biodiversity affects on ecosystem functioning in the long term where extinction resistant species compensate numerically for the loss of their competitors. However mass-ratio theory stipulates that dominant species perform the majority of ecosystem processes in the short term because they are numerically dominant in terms of biomass. Mass-ratio theory therefore has the potential to predict the short term consequences of extinction for ecosystem functioning in natural communities because ecosystem functioning will be dependent on the resilience of dominant species to extinction. The application of mass-ratio theory to communities outside of autotrophic assemblages has, however, so far not been tested. In this investigation two assemblages of sessile suspension feeding invertebrates which were contrasting in their species composition were manipulated to simulate empirically derived extinction orders in response to a hypoxic disturbance event. Ecosystem functioning in the form of the rate of clearance of microalgae from the water column was then quantified across the resulting gradient of species richness, and species contributions to this ecosystem process related their contributions to community biomass. Community biomass explained $93 \%$ of the variability in the rate of community clearance of microalgae across both assemblages in a positive linear relationship. This relationship was not significantly different for each of the assemblages considered. This result suggests that massratio theory is applicable to assemblages of sessile suspension feeding invertebrates, supporting its wider application to assemblages other than those which are autotrophic. Further testing of the validity of mass-ratio theory in contrasting ecosystems could yield a common property of natural assemblages which can be applied to predict the short term consequences of species loss for ecosystem functioning using community biomass data.

### 4.2 Introduction

Much of the biodiversity-ecosystem function research to date has focused on long term biodiversity effects on productivity, processes and stability in artificial communities (Hooper et al. 2005, Emmett Duffy et al. 2009). In doing so, studies have primarily focused on establishing whether species richness was important for a variety of ecosystem functions by generating experimental gradients of species richness using randomly selected subsets of species from a larger species pool in a replacement series design (Symstad et al. 1998, Hector et al. 1999, Tilman 1999a, Hector et al. 2001, Marquard et al. 2009). This experimental design has proved to be a robust approach to testing the theoretical mechanisms underpinning biodiversity effects. Niche complementarity, for example, predicts that species rich assemblages will be more productive than species poor assemblages because resources become more effectively partitioned where competitive constraints are dominated by interspecific as opposed to intraspecific interactions (Hooper et al. 2005). However the lack of realism inherent in these experiments inhibits the application of their findings in real world contexts. For example there is now a substantial body of evidence which suggests that in nature species extinction or extirpation is a non random process (Pimm et al. 1988, Gaston and Blackburn 1995, Davies et al. 2000, Dulvy et al. 2003, Reynolds et al. 2005, Olden et al. 2007), and that ecosystem function responds differently to non random vs. random species loss scenarios (Solan et al. 2004, Bracken et al. 2008).

Recently BEF research has began investigating biodiversity affects under real world scenarios using both computer simulation and empirical experimentation (Solan et al. 2004, Zavaleta and Hulvey 2004, McIntyre et al. 2007, Zavaleta and Hulvey 2007, Bracken et al. 2008). These experiments attempt to observe the impact of biodiversity loss on ecosystem function during
realistic extinction events with the aim of understanding how the findings of more tightly controlled BEF experiments transfer into the natural realm. Natural communities are often numerically dominated by a small proportion of their constituent species, it seems likely that dominant species will also control the majority of ecosystem processes (Grime 1998, Schwartz et al. 2000). This 'mass - ratio theory' (Grime 1998) implies that ecosystem processes will be dominated by the most dominant species. Hence the rate of decline in an ecosystem process will depend on and can be predicted from the position of dominant species within the extinction order and the ability of extinction resistant species to compensate for the loss of their competitors. It is important to note that this does not imply that all species are contributing the same to ecosystem processes on a per capita (unit biomass) basis, rather it suggests that the population biomass of species constituent within an assemblage will be the largest determinant of their contributions to ecosystem processes, and differences in per capita contributions will be comparatively negligable. The maximum rate of an ecosystem process will therefore be dependent on the functional trait characteristics of the most dominant species. Nor does mass-ratio theory imply that positive species interactions are not important for ecosystem functioning. Positive species interactions on short time scales (i.e. in the absence of density compensation) may be rendered negligible by large differences in community biomass between species (Smith and Knapp 2003), but may become more important with time as density compensation occurs.

There is now a growing body of evidence in support of mass-ratio theory in autotrophic ecosystems (Smith and Knapp 2003, Gilbert et al. 2009). While some evidence suggests it may be applied in animal communities (Solan et al. 2004, McIntyre et al. 2007), this evidence is limited to modelled simulations, and empirical evidence is lacking. Establishing whether this theory is applicable to a wider array of ecosystem types could provide a simple rule for
predicting the consequences of species loss for ecosystem processes. Sub-tidal fouling assemblages provide an ideal model ecosystem in which to test the hypothesis that species contributions to ecosystem processes are proportional to their contributions to community biomass. These communities consist of sessile epibenthic suspension feeding invertebrates which can colonise and grow on hard substrates in the aquatic environment and filter particulate organic matter and micro algae from the water column. Clearance of microalgae and associated particulate organic matter is a process performed by all benthic suspension feeding invertebrates which is important for the benthic -pelagic cycling of carbon and key nutrients such as nitrogen and silica in coastal ecosystems (Cloern 1982, Officer et al. 1982, Smaal et al. 1986, Chauvand et al. 2000, Grall and Chauvaud 2000) (see Grall and Chauvaud 2000 for review). Such communities are typically phylogenetically and functionally diverse in that they contain a wide variety of organisms including molluscs, barnacles, solitary and colonial ascidians, hrydrozoans, anthazoans, sponges and bryozoans. The constituent sessile species share a common food resource (micro algal cells and particulate organic matter in suspension) and consequently there exists a rich diversity of morphological adaptations to feeding (Labarbera 1984, Riisgard and Larsen 2000). This results in species being morphologically specialised to feeding on specific fractions of the particle sizes available to them (Randlov and Riisgard 1979, Jorgensen et al. 1984, Riisgard 1988, Turon et al. 1997). For example the bivalve molluscs most efficiently retain particles 4-5 um in diameter (Riisgard 1988) while ascidians retain particles efficiently down to 1-2 um in diameter (Randlov and Riisgard 1979, Jorgensen et al. 1984). Consequently it might be expected that the rate of microalgae uptake (clearance rate) provided by these communities is strongly dependent on the presence of a variety of species and hence functional morphologies to more effectively utilise the various size fractions of the microalgal resource
pool. Contrastingly large differences in population biomass between species may render any niche complementarity through morphological specialization negligible, because subordinate species have a population biomass that is too low to contribute to a large proportion of microalgae uptake.

The aim of this investigation was to test whether mass-ratio theory can be used to describe how microalgae clearance rates decline with species loss in response to a realistic disturbance in intertidal fouling communities. It was hypothesised that two communities of sessile invertebrates which are contrasting in their composition would display similar relationships between the proportional contributions of species to community biomass and proportional contributions to clearance rates of microalgae. It was expected that the community clearance rate would be primarily controlled by the functional characteristics of the most dominant species, and the short term biodiversity-ecosystem processes relationship would depend on the position of dominant species within the extinction order.

### 4.3 Methods

### 4.3.1 Overview

Fouling communities (sessile suspension feeding invertebrates which foul man made structures) were obtained by deploying PVC tiles in the Menai Strait and allowing them to colonise naturally over two separate years, April 2008 to February 2009 (the 2009 assemblage), and April 2009 to February $2010^{1}$ (the 2010 assemblage). In each year the resulting communities were contrasting in terms of their species composition allowing for the uniformity of the mass-ratio

[^0]hypothesis across different fouling assemblages to be tested. In order to obtain a realistic order of extinction for each community, tiles were exposed to a hypoxic disturbance as oxygen depletion has become an environmental issue of increasing concern in coastal and deep sea environments (Diaz and Rosenberg 1995, Diaz and Rosenberg 2008). Undisturbed communities were then manipulated to simulate the extinction order observed in response to hypoxic disturbance in an additive fashion where biomass was allowed to vary with each species removed. Changes in clearance rates of microalgae were then quantified across the resulting extinction gradient. This allowed individual species contributions to community clearance rate to be quantified and related to their respective contributions to community biomass for both assemblages. The resulting relationships for each assemblage could then be compared for consistency.

### 4.3.2 Settlement

In both years roughened grey PVC tiles ( $120 \mathrm{~mm} \times 110 \mathrm{~mm}$ in 2009 and $100 \times 110 \mathrm{~mm}$ in 2010) were deployed face down on wire mesh racks on a pontoon in the Menai Strait (Figure 4.3.1) $\left(53^{\circ} 13^{\prime} 46.74^{\prime \prime} \mathrm{N}, 4^{\circ} 09^{\prime} 10.44^{\prime \prime} \mathrm{W}\right)$. The resulting communities contained a wide diversity of functional morphologies in both years, which was different between years (Figure 4.3.2). In 2009 the assemblage was dominated by the barnacle Balanus crenatus, and consisted of a number of other common species including the mussel Mytilus edulis, the solitary ascidian Ascidiella aspersa, and two sponges Scypha compressa and Sycon ciliatum. In 2010 the assemblage was dominated by Mytilus while Balanus was rare, and the colonial ascidian Diplosoma listeraneum was common. Ascidiella, Scypha, and Sycon were among the dominant species in both years. These dominant species represented the top $90 \%$ of the dry tissue biomass of the community in both years. Experimentation focused on these species so that estimates of
extinction susceptibility and functional contribution could be reliably quantified. Rarer species displayed heterogenous or patchy distributions meaning that their natural abundance could not be


Figure 4.3.1 Colonisation of Fouling communities. Left. The School of Ocean Science settlement pontoon where grey PVC tiles were left to colonise naturally in 2008 and 2009. Right. The wire mesh rack on which tiles were deployed. Tiles were deployed face down on wire mesh racks, however were reorientated upwards when experimentation commenced.


Figure 4.3.2 The community structure of two contrasting assemblages of fouling sessile invertebrates, one colonised in the year prior to 2009 and one colonised in the year prior to 2010. Bars represent average values with error bars representing $95 \%$ confidence intervals. Population dry weight (Dry Wt) values are shown for the most dominant taxa whose cumulative biomass was $>90 \%$ of community biomass. 'Other' represents the remaining rarer species in the community.
reliably quantified and hence reliable estimates of extinction susceptibility or functional contribution could not be made.

### 4.3.3 Quantifying Extinction Susceptibility

In order to quantify a realistic pattern of species extinction, the susceptibility of each species to hypoxia was quantified. In both years fouling communities were exposed to hypoxia for different time durations. Hypoxia was generated by removing colonised tiles and sealing them inside polyethylene bags encapsulating seawater Bags were then placed in tanks with free flowing seawater from the Menai Strait under laboratory conditions (Figure 4.3.3).

Temperatures in the tanks were not significantly different from those in the Menai Strait over the duration of the hypoxic disturbance in either year (2009: tank temperature $=7.7 \pm 0.5 \mathrm{SE}{ }^{\circ} \mathrm{C}$, Menai Strait temperature $\left.=7.1 \pm 0.2 \mathrm{SE}{ }^{\circ} \mathrm{C}, F_{(1,8)}=1.51, p=0.254\right)(2010:$ tank temperature $=$ $5.1 \pm 0.38 \mathrm{SE}{ }^{\circ} \mathrm{C}$, Menai Strait temperature $\left.=4.7 \pm 0.4 \mathrm{SE}^{\circ} \mathrm{C}, F_{(l, 12)}=0.657, p=0.433\right)$, and the light regime was natural. Because the encapsulated water was sealed from external oxygen sources, oxygen levels depleted as the communities continued to respire leading to the onset of hypoxic conditions. Communities were exposed to hypoxic conditions for $0,1,3,4$ and 7 days in $2009(\mathrm{n}=4$ per treatment) and $0,1,3,7$ and 9 days in $2010(\mathrm{n}=5$ per treatment except 0 days where $\mathrm{n}=8$ ). $\mathrm{O}_{2}$ concentrations in the bags dropped exponentially to $22,7,5$ and $2 \%$ of natural seawater $\mathrm{O}_{2}$ concentration in the Menai Strait on the 1st, 3rd, 4th and 7th days of disturbance respectively in 2009 , and $47,35,15,15$, and $14 \%$ of natural seawater $\mathrm{O}_{2}$ concentration in the Menai Strait on the 1st, 3rd, 7th, and 9th days of disturbance in 2010. Following hypoxic
treatments, tiles were removed from bags and placed back in the Menai Strait to allow deceased individuals to decay for one week allowing them to be reliably differentiated from living individuals. The population wet tissue weight of each species was then quantified across all tiles in the laboratory. For both years population wet tissue weights were converted to relative wet tissue weight for each species by dividing by the average of the control treatment (where no hypoxia was simulated) and subtracting 1. By forcing the relationship between average wet weight per treatment and duration of hypoxia (in days) through 0 , the slope of the regression estimate becomes a comparable measure of extinction susceptibility between species. In cases where complete loss of a species was observed during disturbance treatments lower than the maximum duration of hypoxia applied, responses from higher disturbance treatments were excluded from the analysis to prevent further 0 abundance measurements underestimating the regression slope estimate and hence extinction susceptibility. Residual normality was checked using the Shapiro-Francia test. One data point for Ascidiella aspersa, day 2 of hypoxia in 2009, was omitted from the analysis following verification of incorrect identification of deceased individuals by reference to previously archived photographs of tiles taken following disturbance.

### 4.3.4 Simulating Extinction

Undisturbed communities were manipulated to simulate the extinction order observed in response to hypoxic disturbance so that the rate of decline in community clearance of micro algae during a realistic extinction event could be quantified. Tiles were collected from the settlement pontoon and transferred immediately into fresh UV irradiated 0.1 um filtered seawater at $9^{\circ} \mathrm{C}$. The natural communities on the tiles were then manipulated to simulate the order of extinction observed from the hypoxic disturbance experiments ( $\mathrm{n}=3$ per treatment in 2009, and $\mathrm{n}=4$ per treatment in 2010) by removing species. Species were removed in a subtractive fashion
so that each tile represented a progressive stage of community disassembly as a result of hypoxia in the absence of density compensation. Because realistically we could only quantify the contribution of homogenously distributed species to community clearance rates, those species cumulatively contributing to $>90 \%$ of the biomass of each assemblage were included in the extinction simulation. Rare species were removed from all the treatments except a control reference treatment in which no species were removed. These control references were not included in the statistical analysis. All biological material removed during manipulations was stored and later quantified along with the remaining biological material following measurements of clearance rate to make estimates of species population dry weight. Population dry weight was estimated from wet weight data using calibration curves for Ascidiella aspersa, Mytilus edulis and Balanus crenatus (see appendix C1). Following manipulation, tiles were immediately transferred to circular 21 tanks containing $0.1 \mu \mathrm{~m}$ filtered aerated seawater at $9^{\circ} \mathrm{C}$ ambient room temperature and fasted for 24 hrs prior to clearance rate measurements (Fig 4.3.3.).

### 4.3.5 Quantifying Clearance Rates

Clearance Rates of microalgae were estimated under laboratory conditions. Mixed microalgal cultures comprising of five different species (Nannochloropsis sp., Isochrysis sp., Pavlova sp., Tetraselmis sp., and Thalassiosira weissflogii, Varicon Aqua) ranging in size from 1 to $20 \mu \mathrm{~m}$ cell diameter were added to give initial cell concentrations of $158,761 \pm 38,898 \mathrm{SE}_{\mathrm{Se}}$ cells ml ${ }^{-1} \mathrm{~g}^{-1}$ community dry tissue weight in 2009 and $73,326 \pm 32,001 \mathrm{SE}$ cells $\mathrm{ml}^{-1} \mathrm{~g}^{-1}$ community dry tissue weight in 2010. The range of microalgal cell sizes provided a resource that the communities were expected to partition. The 0 species treatment consisted of a bare PVC tile from which the sessile community had been completely removed. 30 ml seawater samples were taken at regular time intervals of $5,10,15,20,30$ and 45 minutes in 2009 and $5,10,15,30,35$ and 45 minutes in

2010 and preserved in $2 \%$ lugol's iodine pending analysis of cell concentration using a Coulter Multisizer II. Tank water was stirred continuously at 60 revolutions per minute throughout the clearance rate assays using mechanical stirrers to prevent microalgae settlement. Community


Figure 4.3.3. Hypoxic disturbance of fouling invertebrate communities. Tiles were sealed inside plastic bags encapsulating seawater and left in free flowing water from the Menai Strait for different time periods. Tiles can be seen here in treatment bags clipped to the sides of tanks used to maintain ambient environmental conditions. clearance rate $C R_{\text {tot }}$ was estimated using the equation of (Fox et al. 1937) $\left[C R_{t o t}=V(a-b)\right]$ where $a$ is the rate of decline in log transformed particle concentration in each test suspension and $b$ is the average rate of decline in log transformed particle concentration recorded from the three replicate 0 species treatments. $b$ is subtracted from all values of $a$ to account for any gravitational settlement of cells. $V$ is the volume of water in each tank.

### 4.3.6 Data Analysis

The relationship between species richness and microalgae clearance rate was initially quantified in each year by fitting a variety of linear (linear, log linear and exponential linear) and non-linear (Michaelis-Menten, asymptotic and logistic) regression models to the data described by Ritz and Streibig (2008) (see Table 3.4 .4 in chapter 3 for model descriptions). Akaike's Information Criterion was then minimised to select the model which most parsimoniously described the relationship. Non linear models were fitted using the CRAN package nlrwr in the statistics
platform R. The fitted values of the selected relationship were then used to estimate the contribution of each species to community clearance rate (the Functional Contribution, FC) by


Figure 4.3.3 Quantifying clearance of microalgae. Left. The clearance rate assay set up consisted of two lines of 521 circular mesocosms continually stirred with mechanical stirrers. Right. Close up of a tile during a clearance rate measurement.
subtracting each fitted value at species richness $i$ from that at species richness $i+1$. For example to estimate the contribution of the most extinction susceptible species, the value of clearance rate at species richness $=0$ was subtracted from the value at species richness $=1$. Per capita (i.e. per unit biomass) contributions to clearance rate were estimated by dividing values of FC by the population dry tissue weight of each species. Per capita functional contributions were later used to assess whether differences in total community clearance rate between years were due to changes in the identity of the dominant species. In order to test the hypothesis that species contributions to community clearance rate were proportional to their contributions to community dry weight (the mass-ratio relationship), all individual species values were converted to percentages of community values. The \% contribution of species to total community clearance rate could then be related to the $\%$ contribution of species to total community dry tissue weight using OLS regression. The consistency of the relationship between \% functional contribution
and \% biomass contribution between the two contrasting fouling assemblages in different years was assessed using Analysis of Covariance (ANCOVA).

### 4.4 Results

### 4.4.1 Extinction Susceptibility

All species representing the top $90 \%$ of community dry tissue weight responded negatively to hypoxic disturbance in both years (Fig 4.4.1). The resulting relationships between relative population dry tissue weight and time were significant at the $95 \%$ confidence level in all cases except for Mytilus edulis in 2010 which was significant at the $90 \%$ confidence level (Table 4.4.1). In general the communities displayed similar extinction orders in both years with the sponges Scypha and Sycon being the most susceptible species to hypoxia, the ascidians Diplosoma and Ascidiella being of intermediate susceptibility and species with external shell structures such as Mytilus and Balanus being least susceptible to hypoxia (Table 4.4.1). An

Table 4.4.1 The rank order of extinction of fouling invertebrates in response to hypoxic disturbance. Species are ranked according to the rate of decline in relative population wet wt through time (days) estimated using OLS regression.

| Ecosystem | Species | Slope $\pm 95 \%$ CI |  |  | $F$ | $p$ | $\mathrm{R}^{2}$ | Rank ES |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Fouling <br> Invertebrates <br> 2009 | Scypha compressa | -0.294 | $\pm$ | 0.129 | (1,3) 207.6 | 0.002 | 0.96 | 1 |
|  | Sycon ciliatum | -0.243 | $\pm$ | 0.056 | (1,3) 147.6 | 0.000 | 0.97 | 2 |
|  | Ascidiella aspersa | -0.222 | $\pm$ | 0.068 | (1,3) 196 | 0.001 | 0.98 | 3 |
|  | Mytilus edulis | -0.085 | $\pm$ | 0.062 | (1,4) 12.87 | 0.013 | 0.69 | 4 |
|  | Balanus crenatus | -0.055 | $\pm$ | 0.026 | (1.4) 113.3 | 0.002 | 0.85 | 5 |
| Fouling Invertebrates 2010 | Sycon ciliatum | -0.117 | $\pm$ | 0.082 | (1,4) 15.56 | 0.017 | 0.74 | 1 |
|  | Scypha compressa | -0.114 | $\pm$ | 0.102 | (1.4) 9.674 | 0.036 | 0.63 | 2 |
|  | Diplosoma listeraneum | -0.102 | $\pm$ | 0.101 | (1,4) 7.753 | 0.050 | 0.58 | 3 |
|  | Ascidiella aspersa | -0.094 | $\pm$ | 0.082 | (1,4) 10.17 | 0.033 | 0.65 | 4 |
|  | Mytilus edulis | -0.058 | $\pm$ | 0.061 | ${ }_{(1,4)} 6.802$ | 0.060 | 0.54 | 5 |



Figure 4.4.1 The extinction susceptibilities of sessile fouling invertebrate species in response to an acute hypoxic disturbance event. Extinction susceptibility was measured as the rate of decline in relative population dry weight (dashed regression line). Left column contains species representing $>90 \%$ cumulative community dry weight from the 2009 invertebrate assemblage. Right column contains species representing $>90 \%$ cumulative community dry weight from the 2020 invertebrate assemblage. Filled points were excluded from the regression fit to prevent 0 value entries underestimating extinction susceptibility. Complete removal of species occurs when relative population dry weight is equal to -1
extinction order in response to hypoxic disturbance which could be used to manipulate undisturbed tiles was therefore obtained for the two contrasting assemblages of each year.

Community clearance rate did not decline rapidly with species loss in both the 2009 and 2010 assemblages, with the most extinction resistant species contributing to the majority of clearance rate in both years (Fig 4.4.2). Akaike's information criterion selected different but


Figure 4.4.2 The decline in community clearance rate (CCRtot) with species loss (represented as increasing species richness) in two assemblages of fouling invertebrates in 2009 and 2010. Points represent the average treatment response with error bars representing the $95 \%$ confidence intervals of the average treatment response

Table 4.4.2 Species contributions to community clearance rates. Population $\left(1 \mathrm{~m}^{2} \mathrm{hr}^{-1}\right)$ and per capita $\left(1 \mathrm{~g}^{-1}\right.$ Dry Wt ) contributions of species to community clearance rates of microalgae in two contrasting fouling communities colonised during the year prior to 2009 and 2010. $\mathrm{NP}=$ not present.

| Species | Clearance rate (CR) |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  | 2009 |  | 2010 |  |
|  | Population CR | Per capita CR | $\underset{\mathrm{CR}}{\text { Population }}$ | Per capita CR |
|  | $\left(1 \mathrm{~m}^{-2} \mathrm{hr}^{-1}\right)$ | $\left(1^{-1} \mathrm{~g}^{-1}\right.$ Dry Wt) | $\left(1 \mathrm{~m}^{-2} \mathrm{hr}^{-1}\right)$ | $\left(1^{-1} \mathrm{~g}^{-1}\right.$ Dry Wt) |
| Balanus crenatus | 46.64 | 0.36 | NP | NP |
| Mytilus edulis | 4.48 | 0.26 | 179.408 | 2.84 |
| Ascidiella aspersa | 0.31 | 0.021 | 36.32 | 5.18 |
| Diplosoma listeraneum | NP | NP | 14.46 | 11.57 |
| Scypha compressa | 0.0015 | 0.021 | 7.77 | 0.44 |
| Sycon ciliatum | 0.022 | 0.0036 | 4.85 | 2.52 |

similarly shaped relationships between species richness and community clearance rate for each year (Figure 4.4.2). In 2009 an asymptotic curve most parsimoniously described the
relationship(AIC: Asymptotic $=36.20<$ Michaelis - Menten $=45.23<\log$ linear $=47.20<$ linear $=55.29<$ exponential linear $=57.88<\log$ linear NO FIT), while in 2010 a Michelis Menten curve most parsimoniously described the relationship (AIC: Michelis Menten = $71.83<\log$ linear $=73.79<$ linear $=78.84<$ exponential linear $=80.31<\log$ linear and
asymptotic NO FIT) (Figure 4.4.2). In 2009 the maximum observed clearance rate was markedly lower ( $56 \pm 10$


Figure 4.4.3 The mass ratio relationship in sub-tidal fouling communities. Left: the forth root transformed relationship between \% contribution to community clearance rate (functional contribution, FC) and \% contribution to community dry weight (Dry Wt contribution) in two contrasting assemblages of fouling invertebrates colonised in the year prior to 2009 (filled points) and 2010 (open points). Right: The untransformed relationship between \% Dry Wt contribution and \% Functional Contribution. Solid lines represent significant relationship, dashed lines represent the $95 \%$ confidence intervals of this relationship. $\left.95 \% \mathrm{CI} \mathrm{m}^{-2} \mathrm{hr}^{-1}\right)$ than that of $2010\left(360 \pm 117.795 \% \mathrm{CI} \mathrm{m}^{-2} \mathrm{hr}^{-1}\right)$. Initially it was considered that this difference could be due to a change in the identity of the dominant species from Balanus crenatus in 2009 to Mytilus edulis in 2010, with the latter having a higher per capita clearance rate. The average population biomass of Mytilus was $\sim 4$ times greater in $2010\left(66.9 \pm 7.5795 \%\right.$ CI g dry tissue weight $\left.\mathrm{m}^{-2}\right)$ than in $2009(17.07 \pm 6.61$ $95 \% \mathrm{CI} \mathrm{g}$ dry tissue weight $\mathrm{m}^{-2}$ ). However the per capita functional contribution of Mytilus was also markedly different between years (Table 4.4.2), suggesting that the identity of the dominant species alone does not adequately explain the difference in maximum observed clearance rates between years. Nonetheless \% contributions to community dry tissue weight explained $93 \%$ of the variability in \% functional contribution when the data for each year was not treated independently $\left(F_{1,8}=123.2, p<0.0001\right)$ (Figure 4.4.3). When data was fourth root transformed to remove the leverage effect of dominant species, contributions to community
dry tissue weight still explained $50 \%$ of the variability in $\%$ functional contribution in a $1: 1$ ratio across both years $\left(F_{1,8}=9.982, p=0.013\right)$ (Figure 4.4.3), and this relationship was not significantly different between years (ANCOVA, $F_{l, 6}=3.207, p=0.124$ ). The proportional contribution of species to community clearance rate can therefore be estimated from species contributions to community biomass within both of these fouling invertebrate assemblages

### 4.5 Discussion

The results of this study demonstrate that, consistent with mass-ratio theory, the contribution of invertebrate suspension feeding species to community clearance of microalgae is proportional to their population biomass. Hence the rate of decline in community clearance rate was saturating in each of two fouling assemblages, because in both assemblages the dominant and therefore largest contributing species to community clearance rate was the most resistant to extinction during acute exposure to hypoxic conditions.

Previously evidence for the application of a mass-ratio theory to faunal communities was limited to modelled simulations of extinction scenarios (Solan et al. 2004, McIntyre et al. 2007). This result is novel in that it demonstrates that mass-ratio theory can be applied to a broader array of ecosystem types including fauna, where previously it was considered only applicable to autotrophic assemblages (Grime 1998). The strength of the link between biomass and functional contribution means that rapid and simple assessments of the dominance structure of natural communities can be used to estimate the proportional contributions of species to ecosystem processes. Hence the short term consequences of species removal for ecosystem functioning can be predicted providing worst case scenarios of the rate of decline in ecosystem processes with species loss in the absence of density compensation. Predicting the longer term consequences of species loss requires a sound knowledge of how extinction resistant species respond to the removal of their competitors
(Houlahan et al. 2007, Gonzalez and Loreau 2009). For example Peters et al. (2009) found that in two species of raid-swarming army ant, Dorylus molestus compensated for the decline in abundance and raiding rates of Dorylus wilverthi driven by the clearance and fragmentation of tropical rainforest in Kenya. Whether such compensatory responses are common place in nature, and the extent to which functional trait overlap between species influences the potential for such responses is however poorly understood (Houlahan et al. 2007, Gonzalez and Loreau 2009). Biodiversity experiments which use a replacement series approach (Hector et al. 1999, Tilman 1999a, Marquard et al. 2009) standardise initial species densities across species richness treatments, and hence assume to some extent that compensatory interactions are commonplace in nature. Hence the results of these investigations differ from the current study in that they often find that species or functional richness has a positive influence on ecosystem functioning in the long term (Hector et al. 1999, Tilman 1999a, Marquard et al. 2009). For example Stachowicz et al.. (1999) found that resistance to invasion by an alien species was significantly reduced at low species richness in a fouling assemblage consisting of mussels, colonial and solitary ascidians and bryozoans. Such results are commonplace in experimentally assembled communities, however observational studies have suggested that positive biodiversity affects are context dependent on resource availability and heterogeneity (Stachowicz and Byrnes 2006, Tylianakis et al. 2008). Because biomass was allowed to vary with species removal in the current study, positive biodiversity effects may have been masked by the comparatively larger impact of removing species biomass. It is important to highlight however that in both of the fouling communities studied here, little decline in community clearance rate was observed among rare species, even when all but the most dominant species were removed, implying that neither loss of biomass nor positive species interactions among rarer species made significant contributions to community clearance rates in the short term.

The rate of overall community clearance rate was six fold higher where the bivalve Mytlius edulis dominated the assemblage than compared to when the barnacle Balanus crenatus dominated the assemblage suggesting that changes in the identity of the dominant species can have a major impact on maximum rates of clearance in these communities. This result is consistent with that of a previous study which demonstrated that the filtration rate of two fouling assemblages, one from Helgoland and one from Plymouth were strongly dependent on functional identity with mussels displaying the highest clearance rate per unit biomass (Valdivia et al. 2009). Although the population biomass of Mytilus in the current study was approximately four times greater in the 2010 assemblage compared to the 2009 assemblage, the contribution of Mytilus on a per unit biomass basis was also higher suggesting that this species was feeding at a much higher rate during the clearance rate assays performed on the 2010 assemblage. Filtration rates in bivalve molluses and Mytilus in particular are well documented to be dependent on the concentration of particles in the water column, with increases in cell concentration causing a reduction in filtration rate (Winter 1973, Widdows et al. 1979, Bricelj and Malouf 1984, Sprung and Rose 1988). Although a target initial cell concentration of 70,000 cells $\mathrm{ml}^{-1} \mathrm{~g}^{-1}$ dry tissue weight was set in both years, in 2009 the actual observed initial cell concentration was 158,761 cells $\mathrm{ml}^{-1} \mathrm{~g}^{-1}$ dry tissue weight. It is likely then that the large difference in maximum community clearance rate between the two assemblages was due to a change in the identity of the dominant species from Balanus to Mytilus, with Mytilus displaying a higher population biomass in 2010, and an increase in the filtration rate of Mytilus individuals caused by the markedly lower cell concentration used during the 2010 clearance rate assay.

This study has demonstrated that mass-ratio theory can be applied to describe how the performance of an ecosystem process, community clearance of microalgae, is distributed across two contrasting assemblages of sub-tidal fouling invertebrates. Chapter 3 of this thesis
described results which indicated that mass-ratio theory described the relationship between macroalgae diversity and two different ecosystem processes, gross community productivity and uptake of ammonium. This provides a good basis for extending the application of this theory across unitrophic assemblages in general to help predict the short term consequences of biodiversity loss for ecosystem processes in natural communities. In Chapter 5 of this thesis, the results of chapters 3 and 4 are combined with data collected during the salt marsh experiment described in chapter 2 to test whether the mass-ratio relationship is the same for all ecosystems and ecosystem processes.

## Chapter 5. Predicting the consequences of

extinction for ecosystem processes in coastal marine
ecosystems.


## Chapter 5. Predicting the consequences of extinction for ecosystem processes in coastal marine ecosystems.

### 5.1 Abstract

Over a decade of research shows that the services ecosystems provide to humanity can be affected by biodiversity loss. Yet the ability to predict the consequences of species loss on ecosystem functioning has proved elusive. We conducted a series of empirically informed realistic biodiversity manipulations in three contrasting unitrophic marine communities. Our aim was to test whether species contributions to community biomass can be used as surrogate measures of their contribution to ecosystem processes (functional contribution), as this could be used to predict the short term ('worst case scenario') consequences of species loss for ecosystem processes. The functional contribution of species was directly proportional to their contribution to community biomass in a $1: 1$ ratio. This relationship was consistent across three contrasting marine ecosystems and three ecosystem processes. Hence population biomass estimates can be used to predict worst case scenarios of the decline in ecosystem processes with species loss. We also modelled a best case scenario which accounts for density compensation by the highest per capita contributing extant species to ecosystem processes. When combined, the best and worst case scenarios provide an estimate of the maximum and minimum number of species required to maintain different levels of ecosystem processes.

### 5.2 Introduction

Future scenarios consistently predict that biodiversity will continue to decline in the $21^{\text {st }}$ century in terrestrial, marine and freshwater ecosystems (Pereira et al. 2010). Yet the capacity to predict the consequences of biodiversity loss for ecosystem functioning remains a major challenge, despite almost two decades of explicitly focused research and the generation of three meta-analyses which collectively demonstrate that species and functional diversity can have a positive effect on a variety of ecosystem processes (Balvanera et al. 2006, Cardinale et al. 2006, Schmid et al. 2009). The major focus in biodiversity - ecosystem functioning research has been the use of replacement series designs, in which extinction patterns are generally simulated randomly and initial densities are fixed across species richness treatments (Hector et al. 1999, Tilman 1999a, Emmerson et al. 2001, Marquard et al. 2009). Translating the effects of species richness on ecosystem functioning derived from such investigations into the effect of species loss on ecosystem functioning in the real world is however difficult. This is because species extinction is often deterministic (Pimm et al. 1988, Roberts and Hawkins 1999), community biomass is often dominated by few species (Whittaker 1975), and the potential for extinction resistant species to compensate for biodiversity loss is poorly understood (Houlahan et al. 2007, Winfree and Kremen 2009). Therefore only generalized conclusions and insight into the mechanism of biodiversity effects, as opposed to real world predictions can be made about the impact of biodiversity loss on ecosystem functioning. A limited number of investigations have highlighted that ecosystems undergoing non-random extinction can display more rapid declines in ecosystem functioning compared to random species loss scenarios (Ives and Cardinale 2004, Solan et al. 2004, Zavaleta and Hulvey 2004, Bunker et al. 2005, McIntyre et al. 2007, Bracken et al. 2008). For example manipulations of intertidal macroalgae assemblages which simulated extinctions driven by accelerated wave exposure had a greater impact on nitrogen uptake than
random extinctions (Bracken et al. 2008). Hence in order to understand exactly how ecosystem functioning will respond to species loss in the context of natural communities there is a need to quantify biodiversity ecosystem function relationships under realistic extinction scenarios and in natural ecosystems.

In order to predict the impact of species extinction on ecosystem functioning, firstly we need to understand what response traits make species vulnerable to extinction (Pimm et al. 1988, Roberts and Hawkins 1999) so that accurate extinction forecasts can be made. Secondly there is a need to establish those effect traits which, in the absence of density compensation, drive static state contributions of species to ecosystem functioning. The correlation between functional response and effect traits can then be used to predict the impact of extinctions on ecosystem functioning (Diaz and Cabido 2001, Larsen et al. 2005) in the absence of compensation by extinction resistant species, or put another way 'worst case scenarios' of biodiversity - ecosystem functioning relationships (Solan et al. 2004, Larsen et al. 2005). Thirdly there is a need to understand to what degree functional trait overlap allows extinction resistant species to compensate for the extinction of their competitors (Gonzalez and Loreau 2009), and the time frame over which such compensation takes place, so that more realistic predictions about the long term affect of extinction on ecosystem functioning can be made. Moving towards predicting the ecosystem level consequences of species extinction requires that researchers conduct in situ manipulations of biodiversity simulating realistic disturbances and impacts on natural communities.

The principle focus of this investigation was to establish whether a simple community property, mass-ratio theory (Grime 1998), exists that can be used to better enable the prediction of the affect of biodiversity loss on ecosystem processes. Specifically this study explored whether biomass determines the contribution of species to ecosystem processes (Functional Contribution, FC) across multiple marine ecosystems, and hence whether
community biomass data alone can be used to make worst case scenario predictions of the impact of extinction on ecosystem processes. This theory is a kin to The Metabolic Theory of Ecology which predicts that the turnover of energy by a population will be proportional to the biomass of that population because species metabolic rates scale positively with individual biomass in the same ratio as population density scales negatively with individual biomass (Ernest et al. 2003, Brown et al. 2004). It was envisaged that for ecosystems with communities displaying strong patterns of dominance, where a small fraction of species are responsible for the majority of community biomass, the rate of decline in ecosystem functioning would predominantly depend on the position of dominant species within the extinction order. However in communities displaying more even distributions of biomass, positive species complementarity may play a more important role in determining the rate of decline in ecosystem functioning with species loss (Smith and Knapp 2003) because large differences in population biomass do not render positive biodiversity effects negligible. By contrasting realistic extinction scenarios in marine communities which differ both in terms of species composition and dominance structure, the usefulness of biomass for predicting worst case scenario declines in ecosystem functioning with species loss was explored.

While species contributions to community biomass might predict the functional consequences of species loss in the short term, achieving longer term predictions requires that models account for compensation by extinction resistant species (Zavaleta et al. 2009). Although a limited number of studies have modeled density compensation during extinction (Gross and Cardinale 2005), little empirical evidence is currently available to enable compensatory dynamics to be included in real world predictions of biodiversity loss (Houlahan et al. 2007). A technique is described which can be used to quantify a best case scenario of how extinction impacts on ecosystem functioning which accounts for functional compensation by extinction resistant species. Collectively the best and worst case scenarios represent the boundaries of
the envelope of possible biodiversity - ecosystem process relationships in an ecosystem undergoing long term species loss. Hence they can be used to estimate the minimum and maximum number of species required to maintain various levels of ecosystem functioning.

### 5.3 Methods

### 5.3.1 Overview

Three contrasting marine communities (salt marsh plants, two assemblages an assemblage of sessile suspension feeding invertebrates, and a macroalgal turf) were manipulated to simulate realistic extinction scenarios and changes in multiple ecosystem processes measured across the resulting gradients of species richness. A range of processes important for the functioning of marine coastal ecosystems were measured including gross community productivity (salt marsh plants and macroalgal turfs), uptake of key nutrients ammonium and nitrate (macroalgal turfs) and clearance rates of micro-algae (sessile invertebrate assemblage). In contrast to previous realistic extinction scenario investigations which use either species traits (Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007) or observational approaches (Solan et al. 2004, Zavaleta and Hulvey 2004, Bracken et al. 2008) to determine realistic species extinction sequences, an in situ disturbance experiment was conducted in each of our previously undisturbed ecosystems to empirically quantify extinction patterns. In the salt marsh an increase in the quantity of algal mat deposited was simulated while in the macroalgal turfs an increase in wave exposure was simulated. Both of these disturbances are likely to impact these communities more with predicted increases in the frequency and severity of storms in the North East Atlantic (Ulbrich and Christoph 1999) and have been shown to significantly alter the structure of those communities where they are prevalent (Dayton 1971, van Hulzen et al. 2006). The sessile invertebrate assemblage was exposed to an acute hypoxic event simulating the kind of oxygen depletion which has become
an environmental issue of increasing concern in coastal and deep sea environments (Diaz and Rosenberg 1995, Diaz and Rosenberg 2008). Using this approach (see methods) extinction susceptibilities were estimated for those species which were sufficiently abundant, and homogenous in their distribution, for accurate extinction estimates to be made.

Natural communities were manipulated by removing species sequentially in a subtractive fashion to simulate the derived extinction orders. Changes in ecosystem processes were then quantified across the resulting gradient of species richness. Because biomass was allowed to vary with each species removed, and compensation in these ecosystems occurs at time scales that are impractical to measure (months to years), the derived relationships represented worse case scenarios of the rate of depletion in ecosystem processes with species loss. Individual species contributions to individual ecosystem processes were then estimated as the change in the resulting fitted values of each ecosystem process as each species was lost from the ecosystem, and then related to species contributions to community biomass.

In contrast to the worst case scenario predictions which do not account for functional compensation by extinction resistant species, in the best case scenario the extant species with the highest per capita (unit biomass) contribution to ecosystem functioning were assumed to fully compensate for the loss of biomass associated with each extinction. The worst and best case scenarios of density compensation could then be used to define the maximum and minimum number of species required to sustain various fractions of an ecosystem process. The methods described here are a summary description of the methods outlined in the previous three chapters with the exception of modeling density compensation.

### 5.3.2 Experimental Communities

All experimental communities were located on or around the Isle of Anglesey, UK. The salt marsh plant assemblage was a previously undisturbed naturally formed marsh located in the

Cefni Estuary ( $53^{\circ} 10^{\prime} 12^{\prime \prime} \mathrm{N}: 4^{\circ} 23^{\prime} 39^{\prime \prime} \mathrm{W}$ ). The fouling communities were left to colonise on roughened grey PVC tiles in the Menai Straits ( $53^{\circ} 13^{\prime} 46^{\prime \prime} \mathrm{N}: 4^{\circ} 09^{\prime} 10.44^{\prime \prime} \mathrm{W}$ ) from April 2008 to January 2009. The macroalgal turf community was located at the subtidal fringe of an intertidal boulder field located on a sheltered shore near Penmon Point ( $53^{\circ} 17^{\prime}$ $\left.59^{\prime \prime} \mathrm{N}: 4^{\circ} 03^{\prime} 04^{\prime \prime} \mathrm{W}\right)$.

### 5.3.3 Quantifying Extinction Order

Communities were exposed to increasing severity, frequency or duration of disturbance. Salt marsh plants were exposed to five different quantities (severity) of fucoid algal mat netted onto $1 \mathrm{~m}^{2}$ plots for 60 days. Treatments consisted of $0,3,6,9,131 \mathrm{~m}^{-2} \mathrm{wk}^{-1}$, with five replicates in each treatment except 0 which contained ten replicates. Following disturbance $\%$ cover of each species was quantified using a $0.25 \mathrm{~m}^{2} 49$ point quadrat placed centrally within each plot.

The sessile invertebrate community was exposed to hypoxia for different time periods (duration). Hypoxia was generated by removing colonised tiles and sealing them inside polyethylene bags encapsulating seawater. Bags were then placed in free flowing seawater from the Menai Strait under laboratory conditions. Communities were exposed to hypoxic conditions for $0,1,3,4$ and 7 days ( $\mathrm{n}=4$ per treatment). $\mathrm{O}_{2}$ concentrations in the bags dropped exponentially to $22,7,5$ and $2 \%$ of natural seawater $\mathrm{O}_{2}$ concentration in the Menai straits on the 1st, 3rd, 4th and 7th days of disturbance respectively. Following hypoxic treatments tiles were placed back in the Menai Straits to allow deceased individuals to decay for 7 days allowing them to be reliably differentiated from living individuals. The population wet tissue weight of each species was then quantified across all tiles in the laboratory.

Macroalgae communities were disturbed for 2 minutes using a high pressure hose to mimic an increase in wave impact velocity (intensity). This disturbance was repeated on the lowest
spring tide of each month from 27/02/2010 to 26/04/2010 (4 disturbances total) to simulate an increase in the frequency of wave impact events at this intensity. Five $0.09 \mathrm{~m}^{2}$ plots were disturbed while five control plots were left undisturbed. \% cover of each species was recorded in all plots prior to each disturbance event using a 16 point intercept quadrat. Hence $\%$ cover was recorded following $0,1,2,3$ and 4 disturbances.

Abundance measures were converted to relative abundance in the case of all ecosystems by dividing by the average of the control treatment (where no disturbance was simulated) and subtracting 1. In forcing the relationship between average abundance per treatment and disturbance through 0 , the slope of the regression estimate becomes a comparable measure of extinction susceptibility between species. Regressions were performed between relative \% cover and quantity of algae deposited in the salt marsh, relative wet tissue weight and time in the fouling invertebrate community, and relative $\%$ cover and time in the macroalgae communities. In cases where complete loss of a species was observed during disturbance treatments lower than the maximum applied (Salicornia for Saltmarsh plants, Scypha compressa and Sycon ciliatum for fouling invertebrates), responses from higher disturbance treatments were excluded from the analysis to prevent further 0 abundance measurements underestimating the regression slope estimate and hence extinction susceptibility. Residual normality was checked using the Shapiro-Francia test. One data point for Ascidiella aspersa, day 2 of hypoxia in 2009, was omitted from the analysis following verification of incorrect identification of deceased individuals by reference to previously archived photographs of tiles taken following disturbance.

### 5.3.4 Simulating extinction

Natural communities were manipulated to simulate the order of extinction observed from the disturbance experiments ( $\mathrm{n}=4$ per treatment for salt marsh plants, $\mathrm{n}=3$ for Fouling
communities 2009, $\mathrm{n}=2$ per treatment for macroalgae turfs). Species were removed in a subtractive fashion so that each experimental unit represented a progressive stage of community disassembly in the absence of density compensation. Because realistically we could only quantify the functional contribution of homogenously distributed species, the most abundant species which cumulatively contributed to $>90 \%$ of the biomass of each assemblage were included in our experimental simulation of extinction. Rare species were removed from all the treatments used to test species richness - ecosystem function relationships. However, control plots in which no species were removed were included in each manipulation as a reference. All biological material removed during manipulations was stored and later quantified along with the remaining biological material following measurements of ecosystem function to make estimates of species population dry weight. In the case of salt marsh plants it was our intention to continue running the manipulation to monitor compensatory responses over time. Estimates of population Dry Weight were therefore made using a conversion multiplier estimated for \% cover data (average Dry Weight values per unit \% cover estimated over 5 plots).

### 5.3.5 Measuring Ecosystem Processes

Gross community productivity was measured in saltmarsh plants using a LICOR LI840 $\mathrm{CO}_{2} / \mathrm{H}_{2} \mathrm{O}$ gas analyzer linked to a $30 \times 30 \mathrm{~cm}$ clear plexiglass incubation chamber. $\mathrm{CO}_{2}$ uptake during photosynthesis and output through respiration were first measured during a light measurement (Net Community Productivity, NCP). $\mathrm{CO}_{2}$ output from respiration was then measured independently during a dark measurement (Community Respiration, CR). Gross community productivity (GCP) was then estimated as GCP=NCP-CR.

Clearance Rates of microalgae were estimated for sessile invertebrates under laboratory conditions. Tiles were placed in circular 21 tanks containing 0.1 um filtered seawater at
constant temperature and fasted for 24 hrs . Mixed microalgae cultures comprising of 5 different species (Nannochloropsis sp., Isochrysis sp., Pavlova sp., Tetraselmis sp., and Thalassiosira weissflogii, Varicon Aqua) ranging in size from 1 to 20um cell diameter were added to give initial cell concentrations of $1.6 \times 10^{-5} \pm 0.4 \times 10^{-5} \mathrm{SE}^{\mathrm{S}}$ cells $\mathrm{ml}^{-1} \mathrm{~g}^{-1}$ community dry tissue weight in. The range of microalgae cell sizes provided a resource that the communities were expected to partition as different groups of sessile invertebrates are well demonstrated in having contrasting optimum cell size ranges which they feed on (Randlov and Riisgard 1979, Jorgensen et al. 1984, Riisgard 1988, Turon et al. 1997). The 0 species treatment consisted of a bare PVC tile. 30 ml seawater samples were taken at regular time intervals of $5,10,15,20,30$ and 45 minutes and preserved in $2 \%$ Lugol's iodine pending analysis. Tanks were stirred continuously at 60 revolutions per minute throughout the clearance rate assays using mechanical stirrers to prevent microalgae settlement. Total cell concentrations were later estimated using a Coulter Multisizer II. Community clearance rate was estimated using the equation of (Fox et al. 1937) $\left[C R_{\text {tot }}=V(a-b)\right]$ where $a$ is the rate of decline in each test suspension and $b$ is the average rate of decline in log transformed particle concentration recorded from the 3 replicate 0 species treatments. $b$ is subtracted from all values of $a$ to account for any gravitational settlement of cells. $V$ is the volume of the test suspension.

Gross community productivity and nutrient uptake of macroalgal assemblages were quantified using a $25 \times 25 \mathrm{~cm}$ mesocosms on Menai Bridge Pier. Each mesocosm was filled with 5.21 of fresh seawater from the Menai Strait prior to the estimation of both nutrient fluxes and gross community productivity. 20 ml nutrient samples (filtered through a 0.45 um GF Whatman filter into acid rinsed bottles) were taken in duplicate 10,50 and 90 minutes following the addition of algae with water being stirred prior to each measurement. On completion all samples were immediately transported back to the laboratory and stored at -
$20^{\circ} \mathrm{C}$ for later analysis. Nutrient samples were later analysed in the laboratory to quantify fluxes of Ammonium $\left(\mathrm{NH}_{4}^{+}\right)$and Nitrate $\left(\mathrm{NO}_{3}{ }^{-}\right)$. Nitrate concentrations were determined using an A5X-500 Series XYZ Auto Sampler (Zellweger analytics). Ammonium concentrations were determined fluorometrically using an F-2000 Fluorescence Spectrophotometer (Hitachi). The rate of nutrient flux was determined as the slope of the relationship between concentration and time for each of the nutrients analysed and expressed in $\mu \mathrm{mol} \mathrm{hr}{ }^{-1}$. Gross Community Productivity was estimated as $\mathrm{O}_{2}$ flux in $\mathrm{mg} \mathrm{O}_{2} \mathrm{~min}^{-1}$ using two calibrated HACH LD40 probes following the method outlined by Noel et al.., (2010). $\mathrm{O}_{2}$ utilization during Community Respiration (CR) was first quantified by immediately covering mesocosms in blacking out fabric removing $100 \%$ of available light. $\mathrm{O}_{2}$ concentration was measured $\sim 30$ and 50 minutes later. Following dark measurements the blacking out fabric was removed and Net Community Productivity (NCP) estimated by sampling $\mathrm{O}_{2}$ concentration a further 70 and 100 minutes later. Gross Primary Productivity (GCP) was then estimated as $\mathrm{GCP}=\mathrm{NCP}-\mathrm{CR}$.

### 5.3.6 Statistical Analysis

The rate of decline in each measured ecosystem process was estimated by fitting a variety of linear and non linear models to each relationship and selecting the optimum significant model fit using Akike's Information Criterion. Non linear models were fitted using the CRAN package nlrwr in the statistics platform R (Ritz and Streibig 2008). Functional contributions of species were estimated as the difference in the fitted values of the selected model between the two treatments where that species was lost, and standardized to a $\%$ of their summed value. Biomass contributions were estimated from the average population biomasses of species across all experimental units used to derive the species richness-ecosystem functioning relationship and expressed as a $\%$ of their community biomass (the sum of the population biomass values in each ecosystem). The relationship between $\%$ functional
contribution and \% biomass contribution was then analysed using OLS regression. Because dominant species had an overly large leverage affect on the data, data were $4^{\text {th }}$ root transformed prior to analysis. To establish whether the relationship between \% functional contribution and \% biomass contribution was significantly different between ecosystems or ecosystem processes, a separate Analysis of Covariance was performed in each case. Residual normality was checked using Anderson-Darling tests and homogeneity of variance checked using Levene's test.

### 5.3.7 Modelling Density Compensation

The best case scenario of compensation by extinction resistant species was modelled using the functional contributions derived from the fitted model values of the relationship between species richness and ecosystem functioning for all ecosystems and ecosystem processes. Functional contributions were divided by the population dry weight of each species to provide per capita (unit biomass) contributions. Compensation was modelled by first sequentially removing species population biomass values from the community in sequence of extinction, the biomass of the extant species at each stage of community disassembly with the highest per capita contribution to ecosystem function was then artificially increased so that overall community biomass remained constant across all levels of species richness. The resulting population biomass values were then multiplied by the pre calculated per capita functional contributions of each species and totalled to provide an estimate of ecosystem functioning at each stage of community disassembly where the species with the highest per capita contribution always fully compensates for biomass loss associated with extinction, a best case scenario. Ecosystem functioning was expressed as a percentage of the maximum fitted value of an ecosystem process (i.e. the value at the highest level of species richness) derived from the original relationship between species richness and $\%$ ecosystem function in the absence of density compensation (the worst case scenario). The resulting relationship
was compared with the worst case species richness ecosystem functioning relationship by estimating the number of species required to maintain each level of ecosystem functioning from 0 to $100 \%$.

### 5.4 Results

The resulting extinction orders (previously presented independently for each ecosystem in tables 2.4.1, 3.4.1 and 4.4.1) are presented in Table 5.4.1. The biodiversity ecosystem process relationships quantified under each of these extinction scenarios are presented in Figure 5.4.1. All but one of the ecosystem processes measured (nitrate uptake in macroalgal turfs) were significantly affected by species loss (Figure 5.4.1). Gross community productivity declined in a sigmoidal fashion with species loss in salt marsh plants (AIC: log logistic $=213.32<$ Michelis - Menton $=244.84<$ asymptotic $=245.39<$ linear $=250.68<$ exponential linear $=288.80)($ Figure 5.4 .1 A$)$. Community clearance rates of micro algae declined in a saturating fashion the sessile invertebrate assemblage with the relationship being most optimally described by an asymptotic curve (Figure 5.4.1B) (AIC: asymptotic $=$ $153.75<$ Michelis-Menton $=159.27<$ linear $=165.96<$ exponential linear $=170.32<\log$ logistic $=$ NO FIT). Both gross community productivity and ammonium uptake declined in a saturating fashion with species loss, optimally described by a Michelis-Menton curve (Figure 5.4.1C) (AIC: Michelis-Menton $=1.58<$ asymptotic $=4.04<$ linear $=4.66<$ exponential linear $=11.64<\log$ logistic $=$ NO FIT for gross community productivity; and MichelisMenton $=-11.74<$ asymptotic $=-10.43<\log$ logistic $=-9.38<$ linear $=-8.42<$ exponential linear $=-2.82$ ). Where species did influence an ecosystem process the proportional affect of each species was directly related to the proportion of the biomass that species represents in a community in a 1:1 ratio ( $F_{1,20}=27.97, p<0.0001$ performed on $4^{\text {th }} \mathrm{rt}$ transformed data to remove leverage

Table 5.4.1 The rank order of species extinction in response to different disturbances in natural undisturbed marine coastal ecosystems. A species extinction order was obtained in the case of each ecosystem by ranking the value of the slope of the 0 standardised relationship between relative abundance and disturbance intensity in the case of salt marsh plants and duration in the remaining communities. Salt marsh plants were treated with elevated quantities of fucoid algal mats, fouling invertebrate communities were exposed to hypoxia, and elevated wave exposure was simulated on macroalgal turfs. Numbers in parenthesis represent the degrees of freedom of each regression estimate. Where complete species extinction was observed during the disturbance, further 0 abundance responses were removed from the analysis to prevent them underestimating the slope and hence the extinction susceptibility of a species.

| Ecosystem | Species | Slope $\pm 95 \%$ CI |  |  | F | $p$ | $\mathbf{R}^{2}$ | $\begin{gathered} \text { Rank } \\ \text { ES } \\ \hline \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Salicornia ramossissima | -0.189 |  | 0.016 | (1,2) 25.75 | 0.037 | 0.93 | 1 |
|  | Puccinnellia maritima | -0.071 |  | 0.030 | (1,4) 43.83 | 0.003 | 0.92 | 2 |
| Saltmarsh | Armeria maritima | -0.060 | $\pm$ | 0.020 | ${ }_{(1,4)} 62.58$ | 0.001 | 0.94 | 4 |
| Plants | Limonium humile | -0.056 | $\pm$ | 0.014 | (1,4) 32.04 | 0.005 | 0.89 | 5 |
|  | Plantago maritima | -0.040 | $\pm$ | 0.022 | (1,4) 33.82 | 0.004 | 0.89 | 6 |
|  | Aster tripolium | -0.016 | $\pm$ | 0.038 | (1.4) 1.155 | 0.343 | 0.22 | 7 |
|  | Triglochin maritima | 0.027 | $\pm$ | 0.076 | (1,4) 2.223 | 0.210 | 0.36 | 8 |
|  | Scypha compressa | -0.294 | $\pm$ | 0.129 | (1,3) 207.6 | 0.002 | 0.96 | 1 |
| Fouling | Sycon ciliatum | -0.243 | $\pm$ | 0.056 | ${ }_{(1,3)} 147.6$ | 0.000 | 0.97 | 2 |
| Invertebrates 2009 | Ascidiella aspersa | -0.222 | $\pm$ | 0.068 | (1,3) 196 | 0.001 | 0.98 | 3 |
|  | Mytilus edulis | -0.085 | $\pm$ | 0.062 | (1,4) 12.87 | 0.013 | 0.69 | 4 |
|  | Balanus crenatus | -0.055 |  | 0.026 | ${ }_{(1,4)} 113.3$ | 0.002 | 0.85 | 5 |
|  | Sycon ciliatum | -0.117 | $\pm$ | 0.082 | (1.4) 15.56 | 0.017 | 0.74 | 1 |
|  | Scypha compressa | -0.114 | $\pm$ | 0.102 | ${ }_{(1,4)} 9.674$ | 0.036 | 0.63 | 2 |
| Invertebrates 2010 | Diplosoma listeraneum | -0.102 | $\pm$ | 0.101 | ${ }_{(1,4)} 7.753$ | 0.050 | 0.58 | 3 |
|  | Ascidiella aspersa | -0.094 |  | 0.082 | (1,4) 10.17 | 0.033 | 0.65 | 4 |
|  | Mytilus edulis | -0.058 | $\pm$ | 0.061 | $(1.4) 6.802$ | 0.060 | 0.54 | 5 |
|  | Ectocarpus sp. | -0.011 | $\pm$ | 0.007 | (1.4) 18.91 | 0.012 | 0.78 | 1 |
|  | Ulva sp. | -0.010 | $\pm$ | 0.005 | (1.4) 34.91 | 0.004 | 0.87 | 2 |
|  | Membranoptera alata | -0.009 | $\pm$ | 0.007 | (1.4) 10.97 | 0.030 | 0.67 | 3 |
| Macroalgae | Fucus serratus | -0.008 | $\pm$ | 0.007 | (1.4) 11.52 | 0.024 | 0.68 | 4 |
| turfs | Gracillaria verrucosa | -0.005 | $\pm$ | 0.006 | (1.4) 4.938 | 0.090 | 0.44 | 5 |
|  | Ceramium rubrum | -0.004 |  | 0.008 | (1.4) 1.391 | 0.304 | 0.07 | 6 |
|  | Chondrus crispus | 0.001 | $\pm$ | 0.002 | (1.4) 1.516 | 0.286 | 0.09 | 7 |
|  | Cladaphora sp. | 0.039 | $\pm$ | 0.037 | (1,4) 8.189 | 0.046 | 0.59 | 8 |



Figure 5.4.1 Short term biodiversity ecosystem function relationships can be described from the order of species extinct with respect to their population biomass. Bar charts represent the average population dry weight ( $95 \%$ confidence intervals) of constituent species in order of their extinction position correspondent to each of the biodiversity ecosystem function relationships below. Gross Community Productivity (GCP) in salt marsh plants $(\odot)$ declined in a sigmoidal fashion with species loss because the dominant species was not the most or least resistant to extinction. Community Clearance Rates (CCR) of microalgae in a sessile invertebrate assemblage ( $\mathbf{\Delta}$ ), and Gross Community Productivity (GCP) ( $\boxed{)}$ ) and ammonium uptake ( $\mathbf{\square}$ ) in intertidal macroalgae declined in a saturating fashion because the dominant species was the most resistant to extinction. The influence of dominance structure and extinction order on the resulting biodiversity ecosystem function relationships is explained by the $1: 1$ ratio between biomass contribution and functional contribution described by figure 5.4.2.
of dominant species) (Figure 5.4.2). This relationship was not significantly different between
the tested ecosystems (ANCOVA $F_{2,16}=1.70, p=0.215$ ) or ecosystem processes (ANCOVA


Figure 5.4.2 The Mass-Ratio relationship in multiple marine communities. A, Species contributions to community biomass (\% Dry Wt contribution) describe $89 \%$ of the variability in their contributions to different ecosystem processes (Functional Contribution, FC) across contrasting ecosystems. B. This relationship was independent of the ecosystem or ecosystem process being studied when data were fourth root transformed to reduce the leverage of dominant species. Solid lines represent significant regression fits with dotted lines representing their $95 \%$ confidence intervals. Symbol and colour assignment is the same as Figure 5.4.1.
$F_{2,16}=1.12, p=0.350$ ). The link between biomass and functional contribution translates into the resulting BEF relationships in two ways. Firstly the dominance structure of the ecosystem (Figure 5.4 .1 A ) determines the severity of response of an ecosystem process to species loss. More even assemblages such as the macroalgal turfs display less saturating and more linear species richness - ecosystem functioning relationships (Figure 5.4.1B). Secondly the order of extinction with respect to the population biomass of species determines whether ecosystem processes will decline in a saturating (Figure 5.4.1, fouling communities and macroalgae), sigmoidal (Figure 5.4.1, salt marsh plants) or exponential fashion (not observed) depending on the position of dominant species within the extinction order. In Figure 5.4.3 the number of species required to sustain ecosystem functioning from 0 to $100 \%$ is presented for all three of the ecosystems studied and all three of the individual processes affected by species loss. For example between two and seven species are required to sustain $100 \%$ gross community productivity in the salt marsh plant assemblage, while between one and five species are required to sustain $100 \%$ clearance rate of microalgae in the sessile invertebrate assemblage.


Figure 5.4.3. Worst and best case scenarios of the impacts of extinction on ecosystem functioning in contrasting marine communities. Worst case scenarios (solid lines) represent the maximum number of species required to maintain different levels of ecosystem processes, while best case scenarios (broken lines) represent the minimum number of species required to maintain different levels of ecosystem processes. Results are predicted for a salt marsh plant assemblage exposed to climate driven elevated algal mat deposition, two fouling invertebrate assemblages exposed to acute hypoxia and an assemblage of intertidal macroalgae exposed to climate driven impacts from wave exposure.

In order to maintain $50 \%$ ecosystem functioning between two and three species are required for salt marsh plants, one species for the fouling invertebrate assemblage, between one and two species for gross community productivity in macroalgae, and one species for ammonium uptake in macroalgae. The scope for compensation is reduced, however, where species which strongly dominate ecosystem processes are most resistant to extinction. For example in the fouling invertebrate assemblage, one species sustained $>90 \%$ of community clearancerate in the absence of density compensation, while in the macroalgae assemblage, compensation by the most extinction resistant species sustained $>90 \%$ of ammonium uptake, whereas four species were required to maintain this level of functioning in the absence of
density compensation (Figure 5.4.3). With the salt marsh plants, the two most extinction resistant species can maintain full ( $100 \%$ ) gross community productivity where this would require four species in the absence of density compensation (Figure 5.4.3).

### 5.5 Discussion

This investigation tested whether species contributions to community biomass approximate their contributions to different ecosystem processes across multiple coastal marine ecosystems. The results indicate that there is a $1: 1$ ratio between contributions to community biomass and contributions to ecosystem processes across all processes and ecosystems measured. Hence ecosystem processes measured in the short term were relatively insensitive to species loss for the majority of the ecosystems investigated because the biomass of most ecosystems was strongly dominated by one species, and that species was consistently among the most resistant to extinction. This mass-ratio relationship allows for the short term or 'worst case scenario' consequences of species loss for ecosystem processes to be predicted provided a reliable order of species extinction can be predicted. In order to predict the boundaries of possible biodiversity - ecosystem function relationships in the long term, the worst case scenario results were combined with best case scenario predictions in which the highest per capita (unit biomass) contributing species to ecosystem functioning in the extant community was assumed to fully compensate for biomass loss. Under the best case scenario, compensation reduced the number of species required to maintain ecosystem functioning in the majority of ecosystems, however the impact of density compensation was dependent on the position of the dominant species within the extinction order.

Collectively the best and worst case scenario curves presented in Figure 5.4.3 represent the minimum and maximum number of species required to sustain ecosystem functioning during specific extinction events likely to occur in nature. It is important to note these predictions
are specific to the structure of each community and the extinction order with respect to population biomass. Obtaining similar predictions for alternative ecosystems requires that the distribution of biomass in the assemblage is known, the per capita functional contribution of each species is known, and the extinction order is known.

This study demonstrates how the mass-ratio relationship can move conservation a step closer to making useful predictions of biodiversity-ecosystem function relationships in nature. The link between biomass and productivity has been previously demonstrated in terrestrial plants (Wardle et al. 1997, Smith and Knapp 2003). Its wider application to alternative ecosystems and ecosystem processes, and the potential usefulness it has for the prediction of biodiversity - ecosystem function relationships has, however, not previously been explored. Computer simulations of nutrient fluxes in multi-trophic fish assemblages (McIntyre et al. 2007), bioturbation in sub-tidal macro-invertebrates (Solan et al. 2004), and resilience in rocky intertidal communities (Wootton 2004, Wootton 2010) suggest that the mass-ratio link may be important for driving the short term responses of ecosystem processes to species loss in widely contrasting systems and ecosystems. This study finds strong evidence for the application of mass-ratio theory in both floral and faunal unitrophic assemblages. Whether this can be applied to alternative ecosystem functions such crop pollination, secondary productivity and habitat provision is however uncertain. While a link between biomass and biochemical ecosystem processes seems intuitive, the strength of the relationship when considering the added complexity of animal behavior is uncertain. It is also important to highlight that whilst the mass-ratio relationship stipulates that the rate of decline in ecosystem processes will be highly dependent on the extinction susceptibility of dominant species in the short term, the loss of functional diversity associated with the extinction of rarer species may render communities and hence ecosystem processes more unstable in the face of fluctuating environmental stressors at longer time scales (community stability). Yet while results from
artificially assembled communities suggest that species diversity provides greater temporal stability in community biomass (Tilman et al. 2006), recent investigations which experimentally remove species from natural ecosystems suggest that community stability is highly dependent on the resilience of dominant species to environmental fluctuations (Grman et al. 2010, Sasaki and Lauenroth 2011). For example Grman et al. (2010) found that stability was maintained in grassland communities where multiple species were removed due to increased dominance by particularly stable dominant species under nitrogen rich conditions. Similarly Sasaki and Lauenroth et al. (2011) found that as the number and relative abundance of rare species increased, the temporal stability of plant assemblages decreased, while stability increased with increases in the relative abundance of the dominant grass species Bouteloua gracilis. These results suggest that at least in some unitrophic communities dominant species control temporal stability, a notion consistent with mass-ratio theory. It is also important to note that while dominant species may control the temporal stability of unitrophic assemblages, in many multitrophic assembales the removal of certain 'keystone' species with proportionally small biomass can have disproportionate impacts on ecosystem structure and function through top down or bottom up effects (Power et al. 1996, Estes et al. 1998, Jackson et al. 2001). Further research is required therefore to establish the relevance of the mass-ratio link to multitrophic assemblages.

The worst and best case scenarios presented here represent the boundary of possibilities of the true long term biodiversity - ecosystem process relationship. Positive biodiversity effects in the long term such as niche complementarity can be expected to increase the number of species required to maintain an ecosystem process above that predicted by the best case scenario while remaining below that predicted by the worst case scenario. This is because the best case scenario assumes that increases in intraspecific competition associated with decreasing biodiversity do not affect the maximum standing biomass of an ecosystem, where
in reality such increases in competitive interactions have been shown to decrease the maximum standing biomass of plant assemblages in many large scale biodiversity-ecosystem functioning investigations (Hector et al. 1999, Hooper et al. 2005). Predicting the true number of species required to maintain ecosystem functioning in the long term requires a better understanding of how extinction resistant species compensate for the loss of their competitors in nature, and the processes on which such interactions can be dependent. This study demonstrates evidence of a clear link between biomass and ecosystem processes which provides conservation managers with real opportunities to predict the short term consequences of species loss for ecosystem processes in nature. Further research is required to establish the wider relevance of this link to alternative types of ecosystem functioning and in particular biological response measures such as crop pollination. While achieving accurate predictions of biodiversity-ecosystem functioning relationships which can account for density compensation is currently difficult, the worst and best case scenarios presented here demonstrate how readily obtainable information on the per capita functional contribution of species can be combined with biomass data to define the boundaries of future rates of depletion in ecosystem services with species extinction. Future research which focuses on understanding compensatory interactions between extinction resistant and susceptible species in the real world could provide useful insights for predicting more realistically the consequences of extinction in natural communities for ecosystem functioning.

## Chapter 6. General Discussion

## Chapter 6. General Discussion

The aim of this thesis was to establish whether a mass-ratio theory (Grime 1998) can be used to predict the short term consequences of species extinction for ecosystem functioning. Realistic biodiversity manipulations were conducted in four contrasting communities, representing three ecosystem types. In chapter 2, an assemblage of salt marsh plants was manipulated to simulate extinction in response to climate driven increases in the volume of algal mat deposited on the plant community. In chapter 3, a macroalgae assemblage was manipulated to simulate extinction in response to climate driven increases in the frequency and intensity of wave impact events. In chapter 4, two contrasting assemblages of fouling invertebrates were manipulated to simulate extinction in response to an acute hypoxic disturbance event. Four contrasting ecosystem processes were measured across the resulting simulated extinction gradients, primary productivity in salt marsh plants and macroalgae turfs, clearance rates of microalgae in fouling invertebrate communities, and ammonium uptake and nitrate uptake in macroalgae turfs. In Chapter 5 three of the ecosystems were compared to test the validity of applying the mass-ratio relationship to multiple marine communities. The results of this study indicate that in these natural assemblages, the contribution species make to ecosystem processes is proportional to the contribution they make to community biomass. Hence the proportional role which species play in maintaining ecosystem processes can be estimated from community biomass data alone, and where accurate species extinction forecasts can be applied, the short term consequences of species loss for ecosystem functioning in the absence of density compensation can be predicted. Making long term predictions of the biodiversity-ecosystem function relationship requires in depth knowledge of the processes which govern whether and at what rate extinction resistant species can compensate for the loss of their more extinction prone competitors.

This thesis has demonstrated the importance of mass ratio in describing the contributions which species make to ecosystem processes in natural ecosystems. However all the ecosystems studied were unitrophic, and the impact of species loss on ecosystem processes was only measured in the short term except in the case of salt marsh plants. The role of mass ratio theory in predicting the long term consequences of species loss for ecosystem functioning is less certain, primarily due to the increased complexity of biological interactions taking place. For example extinction resistant species can increase in abundance when their more extinction prone competitors are removed from natural assemblages (Cross and Harte 2007), and prey species can increase in abundance when predators are removed (Estes et al. 1998). This is especially true when considering whole food webs as opposed to unitrophic assemblages as often in nature the removal of one species can result in cascading effects on whole ecosystem structure, despite this species being relatively rare (Paine 1966, Power et al. 1996, Estes et al. 1998, Jackson et al. 2001). The presence of such 'keystone' species (Paine 1966, 1969, Power et al. 1996) can make predicting the ecosystem level consequences of species removal a more complex process. However whether keystone species are generally found in the majority of ecosystems is yet to be established (Power et al. 1996). While recent research has highlighted how dominant species can control temporal stability of community biomass in unitrophic plant assemblages (Grman et al. 2010, Sasaki and Lauenroth 2011), investigations conducted on more complex food webs have highlighted how decreasing food web complexity has a negative impact on the temporal stability of ecosystems (Dunne et al. 2002, Steiner et al. 2005, Otto et al. 2008). It is seems likely that while mass-ratio theory may describe the temporal stability of ecosystem processes in unitrophic assemblages, it will be much less powerful at describing temporal variability of such processes in multitrophic assemblages.

In order to understand the wider application of mass-ratio theory, researchers need to conduct experiments on natural ecosystems of increasing complexity (Reiss et al. 2009), and measure a variety of ecosystem functions additional to ecosystem processes. While in situ experiments allow us to test the relevance of mass ratio theory in natural communities (Diaz et al. 2003), testing its relevance in more complex ecosystems may demand more tightly controlled experimentation using mesocosm based approaches, because they allow for the generation of simplified multitrophic communities. By generating assemblages of plants, grazers and competitors which reflect densities in the natural environment, researchers can test the impact of removing individual species and/or whole trophic guilds on ecosystem processes such as nitrate uptake and primary productivity. This would allow researchers to establish whether the role of species in performing these processes is proportional to their population biomass, despite the increased number of biological links through which a species may influence an individual ecosystem process. Suitable model systems for testing such hypothesis are wide ranging. Tidal pool communities consisting of macroalgae, gastropod grazers and common predators such as the decapod custacean Carcinus maenus may provide one suitable system to use, because the species are generally easy to maintain in laboratory conditions, trophic structure can be readily manipulated, and while the food webs generated are more complex than working with unitrophic assemblages alone, they are simple enough to allow for reliable interpretation of results. Alternatively communities of salt marsh plants and insects can be assembled with similar ease and potential for generating good results, along with other relatively simple terrestrial ecosystems.

Chapter 2 of this thesis established that density compensation cannot be generally assumed to rapidly stabilize for the deterioration in ecosystem functioning associated with species loss nature. Over two consecutive growing seasons in 2009 and 2010, the two extinction resistant salt marsh plant species, Triglochin maritima and Aster tripolium did not compensate for loss
of biomass and primary productivity. While a number of studies have found evidence that compensation by both plants and animals during species loss can occur (Peres and Dolman 2000, Cross and Harte 2007, Peters et al. 2009), other studies suggest that this is not a common feature of ecosystems (Houlahan et al. 2007). The inconsistency of compensatory responses in nature could in part be due differences in ambient environmental conditions between different ecosystems. Some investigations which selectively remove species from natural assemblages have found that the time scales over which such compensatory interactions occur can be context dependent on factors such as nutrient availability (Cross and Harte 2007) and precipitation (Munson and Lauenroth 2009). In order to better understand how compensation by extinction resistant species can ameliorate the impact of biodiversity loss on ecosystem functioning, researchers can conduct in situ manipulations of natural assemblages to reflect realistic extinction patterns. Alternatively artificial communities with high rates of reproductive turnover, such as microalgal communities, can be assembled to simulate multiple extinction orders (Wittebolle et al. 2009), and the compensation potential between individual species quantified to provide an overall indication of the compensation potential of an ecosystem. Such an approach would however be costly in that it demands the use of advanced flow cytometry techniques to isolate individual phytoplankton species and generate artificial assemblages.

Achieving a thorough understanding of the scope for compensation of ecosystem function when species are lost in nature should be a major focus of ecological research today. Yet the number of studies seeking to understand the factors which govern density compensation are few. Hence chapter five of this thesis introduces a technique which can be used to predict the envelope of all possible biodiversity ecosystem function relationships over time. In the 'worst case' scenario, loss of biomass associated with extinction is not compensated for by resistant species. Hence the mass-ratio hypothesis predicts that ecosystem processes will
decline according to the order of species extinction with respect to their population biomass. The proportional decline in ecosystem processes can therefore be assumed to be equal to the proportional decline in community biomass with species loss. Positive biodiversity effects could theoretically accelerate the decline in ecosystem processes with species loss, however the results presented in this thesis suggest that this is not the case because the contribution species made to ecosystem processes was directly proportional to the contribution they made to community biomass in a one to one ratio. The best case scenario assumes that over time the extant species with the highest per capita contribution to an ecosystem process fully compensates for loss of community biomass associated with extinction. Here positive biodiversity effects can result in more rapid deterioration in ecosystem processes with species loss than predicted by the best case scenario. This is because as species are lost from the ecosystem, the theory of niche complementarity asserts that the ecosystem will become occupied by functionally similar species which intensifies competition for resources, and results in lower overall community biomass. However positive species interactions do not result in greater loss of functioning than predicted by the worst case scenarios because the mass-ratio relationship described in this thesis stipulates that in the short term, species contributions to ecosystem processes are dependent on their biomass, and independent of one another. Where the presence of species facilitates the presence of others, the rate of decline in ecosystem functioning through time may be more rapid due to cascading extinction sequences, however this does not change the form of the relationship between an ecosystem process and species richness. It should be noted that the best and worst case scenarios provide the envelope of all possible negative relationships between biodiversity and ecosystem functioning only, however it is possible that species removal could result in an increase for example, in standing biomass and productivity.

Adopting approaches capable of predicting worst and best case scenarios such as those presented in chapter 5 could provide a useful tool for conservation managers to identify future biodiversity targets for maintaining ecosystem services. In addition the maximum and minimum numbers of species required to maintain certain ecosystem processes during extinction events in nature can be predicted.. For example, increasing $\mathrm{CO}_{2}$ uptake by the oceans is resulting in rising ocean acidity (Caldeira and Wickett 2005), which can have deleterious effects of many calcifying marine organisms (Feely et al. 2004, Ravens et al. 2005b, Feely et al. 2008) which are crucial in performing a wide variety of biogeochemical processes including nutrient uptake, clearance of particulate organic matter, bioturbation and nutrient recycling, and primary production. Dissolution rates for many of the major carbonate forming taxa are already available in the literature (Ravens et al. 2005a) and provide a good basis for predicting an extinction order in response to ocean acidification. Species can be placed into groups according to the processes to which they contribute. Estimates of species population biomass in coastal shelf seas can then be used as a proxy of their contribution to these ecosystem processes and the short term (worst case scenario) decline in key biogeochemical processes performed by coastal shelf seas modelled with species loss resulting from ocean acidification. Estimates of contributions to ecosystem processes on a per capita basis can be made using laboratory based mesocosm experiments and/or in situ measurements of ecosystem processes where possible. This data can then be used to model the long term decline in ecosystem processes with species loss under a best case scenario where the extant species which displays the highest per capita contribution to an ecosystem process fully compensates for biomass loss associated with extinction. Combined together the worst and best case scenarios represent a forecast of what can be expected to happen to the biogeochemical cycling of oxygen, carbon and nutrients in the
ocean as a result of acidification. Such predictions however require a certain degree of ground truthing before they can be applied reliably in the natural environment.

While previous theoretical based research has shed much light how higher biodiversity can have positive effects for ecosystem functioning (Schmid et al. 2009), it has provided little insight into how ecosystem functioning will respond to species loss in nature. This thesis presents an alternative approach to the biodiversity-ecosystem function question. Instead of asking whether biodiversity has a positive effect on ecosystem function, this thesis has tackled the question of how to predict the consequences of species extinctions for biodiversity loss in nature. In doing so this research has identified an elegant property of ecosystems, mass ratio theory, which can bring researchers a step closer to achieving the capacity to make such predictions. Adopting similar approaches is crucial if humanity is to strike a truly sustainable balance between the exploitation of earth's natural ecosystems and the preservation of goods and services on which we depend.

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## Appendices

## APPENDIX A: Appendices to chapter 2.

A1. Light curve. The relationship between Gross Community Productivity (GCP) and Light Intensity was quantified over a days' light cycle on a single patch of natural marsh vegetation. The dashed red line represents the defined threshold above which all experimental GCP measurements were recorded ( $700 \mu \mathrm{~mol}$
Photosynthetic Photon Flux Density (PPFD) $\mathrm{m}^{-2} \mathrm{~s}^{-1}$. This was set to minimize variability in GCP attributable to variation in ambient light levels.


A2. Mean light intensity during experimental recordings of Net Community Productivity (NCP). Each point represents the average light intensity over the duration of the light (NCP) measurements recorded across plots of varying species richness (SR). Points are colour coded according to SR (see legend). The dashed red line represents the defined threshold above which all experimental recordings of NCP should be taken to minimize variation in NCP associated with variability in ambient light levels.


A3. \% cover to population dry weight calibration for salt marsh plants. Bars represent mean population dry weight per unit $\%$ cover estimated over 5 control plots at the end of the disturbance experiment in September 2008. Error bars represent the $95 \%$ confidence intervals of the means.


A4. Calibration multiplier values of salt marsh plant population dry per unit \% cover.

| Species | Mean population dry <br> weight $\left(\mathrm{g} \mathrm{m}^{-2}\right) / \%$ <br> cover | $95 \% \mathrm{CI}$ |
| :--- | :---: | :---: |
| Plantago maritima | 3.33 | 0.856172 |
| Limonium humile | 1.18 | 0.281057 |
| Armeria maritima | 1.30 | 0.483826 |
| Puccinellia maritima | 0.51 | 0.206227 |
| Aster tripolium | 0.62 | 0.359929 |
| Triglochin maritima | 1.38 | 1.300992 |
| Salicornia ramosissima | 0.25 | 0.06836 |
| Atriplex portulacoides | 1.45 | 1.005034 |
| Spergularia media | 1.00 | 0.766877 |

A5. R2 values of Net Community Productivity and Community Respiration estimates. Points are colour coded according to each species richness (SR) treatment (see inset legend). Each point represents an individual plot


A6. Algal mat disturbance raw \% cover measurements.

| $\begin{aligned} & \text { Algal volume (I } \\ & \left.\mathrm{m}^{-2} \text { week }^{-1}\right) \end{aligned}$ | Plantago | Limonium | Aster | Armeria | Atriplex | Salicornia | Triglochin | Puccinellia | Spergularia | Spartina | Sueda |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 13 | 17 | 5 | 2 | 1 | 1 | 0 | 5 | 0 | 0 | 1 | 0 |
| 0 | 49 | 25 | 2 | 18 | 4 | 10 | 2 | 11 | 2 | 0 | 0 |
| 0 | 38 | 7 | 9 | 11 | 1 | 25 | 9 | 6 | 2 | 0 | 0 |
| 0 | 36 | 17 | 4 | 3 | 7 | 18 | 6 | 8 | 0 | 0 | 0 |
| 13 | 13 | 10 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| 3 | 40 | 6 | 3 | 12 | 5 | 1 | 3 | 17 | 4 | 0 | 0 |
| 6 | 43 | 7 | 5 | 8 | 0 | 0 | 9 | 1 | 0 | 0 | 0 |
| 6 | 35 | 7 | 0 | 4 | 5 | 2 | 11 | 1 | 0 | 0 | 0 |
| 0 | 41 | 23 | 5 | 18 | 11 | 20 | 6 | 13 | 3 | 0 | 0 |
| 3 | 49 | 12 | 3 | 14 | 0 | 0 | 3 | 2 | 1 | 0 | 0 |
| 0 | 43 | 25 | 2 | 16 | 13 | 10 | 1 | 4 | 1 | 0 | 2 |
| 0 | 45 | 18 | 3 | 14 | 7 | 25 | 4 | 14 | 0 | 0 | 0 |
| 13 | 11 | 6 | 3 | 1 | 6 | 0 | 3 | 0 | 0 | 0 | 0 |
| 0 | 47 | 13 | 3 | 26 | 6 | 17 | 3 | 5 | 2 | 3 | 0 |
| 0 | 44 | 12 | 8 | 24 | 2 | 12 | 3 | 13 | 0 | 0 | 0 |
| 3 | 45 | 11 | 20 | 39 | 2 | 3 | 10 | 12 | 1 | 0 | 0 |
| 0 | 46 | 16 | 3 | 14 | 0 | 8 | 1 | 13 | 0 | 0 | 0 |
| 10 | 34 | 7 | 5 | 15 | 0 | 0 | 0 | 3 | 0 | 1 | 0 |
| 13 | 19 | 6 | 4 | 5 | 0 | 0 | 6 | 1 | 0 | 0 | 0 |
| 6 | 42 | 10 | 2 | 16 | 1 | 0 | 3 | 4 | 0 | 0 | 0 |
| 10 | 26 | 4 | 3 | 4 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| 10 | 40 | 4 | 6 | 15 | 10 | 0 | 9 | 4 | 1 | 0 | 0 |
| 10 | 21 | 3 | 2 | 1 | 2 | 0 | 3 | 0 | 2 | 0 | 0 |
| 3 | 39 | 26 | 1 | 1 | 3 | 1 | 10 | 15 | 1 | 0 | 0 |
| 10 | 25 | 12 | 6 | 8 | 4 | 0 | 11 | 10 | 2 | 0 | 0 |
| 6 | 39 | 10 | 4 | 8 | 0 | 0 | 3 | 6 | 0 | 0 | 0 |
| 0 | 49 | 14 | 3 | 19 | 6 | 6 | 3 | 8 | 2 | 0 | 0 |
| 6 | 38 | 4 | 3 | 14 | 0 | 0 | 3 | 2 | 1 | 0 | 0 |
| 13 | 13 | 14 | 3 | 1 | 0 | 0 | 4 | 3 | 1 | 0 | 0 |
| 3 | 46 | 3 | 1 | 17 | 2 | 4 | 3 | 3 | 1 | 0 | 0 |

A7. Manipulation and recovery 2009/2010. Raw \% cover data from continued monitoring of plot recovery.

June 2009

| SR | Plot | Armeria | Aster | Puccinellia | Atriplex | Limonium | Plantago | Salicornia | Triglochin | Spergularia |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 83 | 27 | 2 | 10 | 0 | 27 | 98 | 4 | 8 | 2 |
| 8 | 22 | 24 | 6 | 12 | 2 | 47 | 86 | 6 | 14 | 0 |
| 8 | 56 | 20 | 4 | 41 | 0 | 33 | 92 | 31 | 12 | 6 |
| 8 | 19 | 20 | 16 | 57 | 0 | 27 | 80 | 20 | 41 | 4 |
| 7 | 26 | 29 | 12 | 27 | 0 | 22 | 94 | 20 | 6 | 0 |
| 7 | 14 | 2 | 16 | 59 | 0 | 59 | 53 | 24 | 4 | 0 |
| 7 | 75 | 12 | 2 | 6 | 0 | 24 | 96 | 8 | 6 | 0 |
| 7 | 24 | 16 | 2 | 39 | 0 | 39 | 90 | 47 | 12 | 0 |
| 6 | 84 | 4 | 2 | 10 | 0 | 20 | 98 | 0 | 20 | 0 |
| 6 | 43 | 4 | 4 | 37 | 0 | 47 | 76 | 0 | 20 | 0 |
| 6 | 88 | 8 | 6 | 65 | 0 | 49 | 96 | 0 | 2 | 0 |
| 6 | 16 | 20 | 14 | 53 | 0 | 20 | 67 | 0 | 10 | 0 |
| 5 | 41 | 45 | 4 | 0 | 0 | 65 | 82 | 0 | 18 | 0 |
| 5 | 32 | 6 | 6 | 0 | 0 | 31 | 96 | 0 | 22 | 0 |
| 5 | 52 | 20 | 6 | 0 | 0 | 47 | 96 | 0 | 8 | 0 |
| 5 | 11 | 24 | 12 | 0 | 0 | 31 | 92 | 0 | 14 | 0 |
| 4 | 89 | 0 | 8 | 0 | 0 | 18 | 98 | 0 | 14 | 0 |
| 4 | 4 | 0 | 4 | 0 | 0 | 61 | 86 | 0 | 10 | 0 |
| 4 | 34 | 0 | 20 | 0 | 0 | 71 | 88 | 0 | 45 | 0 |
| 4 | 46 | 0 | 6 | 0 | 0 | 10 | 98 | 0 | 24 | 0 |
| 3 | 40 | 0 | 10 | 0 | 0 | 0 | 96 | 0 | 29 | 0 |
| 3 | 45 | 0 | 4 | 0 | 0 | 0 | 96 | 0 | 16 | 0 |
| 3 | 51 | 0 | 4 | 0 | 0 | 0 | 73 | 0 | 10 | 0 |
| 3 | 58 | 0 | 10 | 0 | 0 | 0 | 90 | 0 | 8 | 0 |
| 2 | 18 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 45 | 0 |
| 2 | 82 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 39 | 0 |
| 2 | 63 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 22 | 0 |
| 2 | 76 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 39 | 0 |
| 1 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 |
| 1 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 37 | 0 |
| 1 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 |
| 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 0 |
| 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |  |  |

July 2009

| SR | Plot | Armeria | Aster | Puccinellia | Atriplex | Limonium | Plantago | Salicornia | Triglochin | Spergularia |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 83 | 33 | 6 | 8 | 0 | 16 | 100 | 6 | 4 | 0 |
| 8 | 22 | 29 | 6 | 6 | 2 | 59 | 100 | 8 | 12 | 2 |
| 8 | 56 | 20 | 6 | 45 | 0 | 67 | 96 | 22 | 20 | 4 |
| 8 | 19 | 39 | 20 | 69 | 0 | 31 | 88 | 35 | 33 | 4 |
| 7 | 26 | 33 | 8 | 37 | 0 | 27 | 98 | 27 | 18 | 0 |
| 7 | 14 | 4 | 18 | 78 | 0 | 65 | 61 | 35 | 4 | 0 |
| 7 | 75 | 16 | 4 | 2 | 0 | 35 | 98 | 12 | 14 | 0 |
| 7 | 24 | 4 | 4 | 27 | 0 | 33 | 86 | 39 | 18 | 0 |
| 6 | 84 | 6 | 4 | 8 | 0 | 24 | 98 | 0 | 20 | 0 |
| 6 | 43 | 6 | 4 | 37 | 0 | 61 | 82 | 0 | 24 | 0 |
| 6 | 88 | 4 | 4 | 61 | 0 | 65 | 94 | 0 | 4 | 0 |
| 6 | 16 | 27 | 8 | 55 | 0 | 27 | 73 | 0 | 27 | 0 |
| 5 | 41 | 41 | 4 | 0 | 0 | 69 | 76 | 0 | 18 | 0 |
| 5 | 32 | 8 | 2 | 0 | 0 | 33 | 100 | 0 | 35 | 0 |
| 5 | 52 | 33 | 4 | 0 | 0 | 31 | 94 | 0 | 14 | 0 |
| 5 | 11 | 45 | 12 | 0 | 0 | 35 | 88 | 0 | 29 | 0 |
| 4 | 89 | 0 | 6 | 0 | 0 | 24 | 98 | 0 | 16 | 0 |
| 4 | 4 | 0 | 4 | 0 | 0 | 53 | 94 | 0 | 47 | 0 |
| 4 | 34 | 0 | 8 | 0 | 0 | 65 | 86 | 0 | 33 | 0 |
| 4 | 46 | 0 | 4 | 0 | 0 | 4 | 100 | 0 | 37 | 0 |
| 3 | 40 | 0 | 12 | 0 | 0 | 0 | 100 | 0 | 37 | 0 |
| 3 | 45 | 0 | 4 | 0 | 0 | 0 | 98 | 0 | 16 | 0 |
| 3 | 51 | 0 | 2 | 0 | 0 | 0 | 78 | 0 | 8 | 0 |
| 3 | 58 | 0 | 6 | 0 | 0 | 0 | 88 | 0 | 8 | 10 |
| 2 | 18 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 51 | 0 |
| 2 | 82 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 31 | 0 |
| 2 | 63 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 16 | 0 |
| 2 | 76 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 31 | 0 |
| 1 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 |
| 1 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 |
| 1 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 0 |
| 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 |
| 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

August 2009

| SR | Plot | Armeria | Aster | Puccinellia | Atriplex | Limonium | Plantago | Salicornia | Triglochin | Spergularia |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 83 | 45 | 6 | 8 | 0 | 14 | 98 | 4 | 16 | 0 |
| 8 | 22 | 33 | 6 | 4 | 0 | 43 | 96 | 10 | 14 | 2 |
| 8 | 56 | 31 | 10 | 41 | 0 | 16 | 96 | 24 | 24 | 6 |
| 8 | 19 | 45 | 24 | 65 | 0 | 24 | 88 | 43 | 43 | 6 |
| 7 | 26 | 59 | 10 | 41 | 0 | 14 | 96 | 24 | 18 | 0 |
| 7 | 14 | 8 | 24 | 80 | 0 | 61 | 59 | 37 | 20 | 0 |
| 7 | 75 | 24 | 4 | 4 | 0 | 24 | 98 | 12 | 12 | 0 |
| 7 | 24 | 20 | 2 | 24 | 0 | 37 | 84 | 47 | 39 | 0 |
| 6 | 84 | 14 | 10 | 10 | 0 | 22 | 92 | 0 | 49 | 0 |
| 6 | 43 | 14 | 4 | 53 | 0 | 33 | 80 | 0 | 18 | 0 |
| 6 | 88 | 10 | 6 | 84 | 0 | 47 | 90 | 0 | 14 | 0 |
| 6 | 16 | 37 | 12 | 71 | 0 | 24 | 76 | 0 | 18 | 0 |
| 5 | 41 | 57 | 14 | 0 | 0 | 59 | 78 | 0 | 24 | 0 |
| 5 | 32 | 8 | 6 | 0 | 0 | 33 | 100 | 0 | 31 | 0 |
| 5 | 52 | 41 | 8 | 0 | 0 | 33 | 92 | 0 | 20 | 0 |
| 5 | 11 | 49 | 12 | 0 | 0 | 24 | 94 | 0 | 31 | 0 |
| 4 | 89 | 0 | 14 | 0 | 0 | 24 | 96 | 0 | 20 | 0 |
| 4 | 4 | 0 | 8 | 0 | 0 | 51 | 96 | 0 | 29 | 0 |
| 4 | 34 | 0 | 8 | 0 | 0 | 37 | 86 | 0 | 31 | 0 |
| 4 | 46 | 0 | 8 | 0 | 0 | 8 | 100 | 0 | 41 | 0 |
| 3 | 40 | 0 | 18 | 0 | 0 | 0 | 92 | 0 | 59 | 0 |
| 3 | 45 | 0 | 4 | 0 | 0 | 0 | 94 | 0 | 20 | 0 |
| 3 | 51 | 0 | 8 | 0 | 0 | 0 | 71 | 0 | 10 | 0 |
| 3 | 58 | 0 | 8 | 0 | 0 | 0 | 88 | 0 | 14 | 0 |
| 2 | 18 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 55 | 0 |
| 2 | 82 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 31 | 0 |
| 2 | 63 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 18 | 0 |
| 2 | 76 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 39 | 0 |
| 1 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 65 | 0 |
| 1 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 |
| 1 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 0 |
| 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 33 | 0 |
| 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 44 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

May 2010

| SR | Plot | Armeria | Aster | Puccinellia | Atriplex | Limonium | Plantago | Salicornia | Triglochin | Spergularia |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 83 | 33 | 2 | 14 | 0 | 27 | 98 | 12 | 12 | 2 |
| 8 | 22 | 18 | 2 | 8 | 0 | 27 | 98 | 10 | 2 | 2 |
| 8 | 56 | 24 | 8 | 27 | 0 | 29 | 90 | 53 | 20 | 4 |
| 8 | 19 | 37 | 18 | 65 | 0 | 24 | 80 | 67 | 39 | 8 |
| 7 | 26 | 31 | 12 | 37 | 0 | 20 | 84 | 39 | 24 | 0 |
| 7 | 14 | 4 | 16 | 76 | 0 | 55 | 55 | 45 | 4 | 0 |
| 7 | 75 | 10 | 4 | 10 | 0 | 14 | 96 | 18 | 20 | 0 |
| 7 | 24 | 6 | 4 | 37 | 0 | 33 | 78 | 63 | 35 | 0 |
| 6 | 84 | 12 | 4 | 16 | 0 | 18 | 98 | 0 | 43 | 0 |
| 6 | 43 | 4 | 2 | 43 | 0 | 41 | 73 | 0 | 37 | 0 |
| 6 | 88 | 8 | 4 | 73 | 0 | 53 | 90 | 0 | 6 | 0 |
| 6 | 16 | 29 | 10 | 69 | 0 | 14 | 63 | 0 | 20 | 0 |
| 5 | 41 | 53 | 12 | 0 | 0 | 51 | 69 | 0 | 27 | 0 |
| 5 | 32 | 4 | 6 | 0 | 0 | 18 | 96 | 0 | 35 | 0 |
| 5 | 52 | 31 | 8 | 0 | 0 | 39 | 88 | 0 | 22 | 0 |
| 5 | 11 | 29 | 6 | 0 | 0 | 29 | 88 | 0 | 31 | 0 |
| 4 | 89 | 0 | 2 | 0 | 0 | 20 | 94 | 0 | 18 | 0 |
| 4 | 4 | 0 | 6 | 0 | 0 | 47 | 90 | 0 | 27 | 0 |
| 4 | 34 | 0 | 14 | 0 | 0 | 47 | 76 | 0 | 31 | 0 |
| 4 | 46 | 0 | 4 | 0 | 0 | 12 | 98 | 0 | 35 | 0 |
| 3 | 40 | 0 | 12 | 0 | 0 | 0 | 78 | 0 | 59 | 0 |
| 3 | 45 | 0 | 4 | 0 | 0 | 0 | 82 | 0 | 27 | 0 |
| 3 | 51 | 0 | 2 | 0 | 0 | 0 | 65 | 0 | 12 | 0 |
| 3 | 58 | 0 | 8 | 0 | 0 | 0 | 78 | 0 | 16 | 0 |
| 2 | 18 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 59 | 0 |
| 2 | 82 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 45 | 0 |
| 2 | 63 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 27 | 0 |
| 2 | 76 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 57 | 0 |
| 1 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 67 | 0 |
| 1 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 39 | 0 |
| 1 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 29 | 0 |
| 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 0 |
| 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 44 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Jun 2010

| SR | Plot | Armeria | Aster | Puccinellia | Atriplex | Limonium | Plantago | Salicornia | Triglochin | Spergularia |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 83 | 33 | 2 | 14 | 0 | 31 | 100 | 8 | 14 | 2 |
| 8 | 22 | 14 | 2 | 14 | 4 | 35 | 100 | 27 | 12 | 2 |
| 8 | 56 | 27 | 8 | 29 | 0 | 55 | 94 | 57 | 24 | 6 |
| 8 | 19 | 31 | 12 | 71 | 0 | 49 | 80 | 80 | 45 | 14 |
| 7 | 26 | 27 | 10 | 37 | 0 | 16 | 92 | 55 | 24 | 0 |
| 7 | 14 | 6 | 20 | 78 | 0 | 63 | 55 | 71 | 20 | 0 |
| 7 | 75 | 8 | 2 | 8 | 0 | 39 | 96 | 24 | 14 | 0 |
| 7 | 24 | 6 | 2 | 41 | 0 | 43 | 80 | 73 | 31 | 0 |
| 6 | 84 | 8 | 6 | 20 | 0 | 29 | 98 | 0 | 45 | 0 |
| 6 | 43 | 4 | 2 | 53 | 0 | 57 | 76 | 0 | 37 | 0 |
| 6 | 88 | 8 | 6 | 73 | 0 | 69 | 90 | 0 | 4 | 0 |
| 6 | 16 | 16 | 12 | 76 | 0 | 33 | 73 | 0 | 31 | 0 |
| 5 | 41 | 57 | 14 | 0 | 0 | 76 | 76 | 0 | 27 | 0 |
| 5 | 32 | 2 | 4 | 0 | 0 | 39 | 98 | 0 | 45 | 0 |
| 5 | 52 | 20 | 4 | 0 | 0 | 51 | 92 | 0 | 20 | 0 |
| 5 | 11 | 41 | 8 | 0 | 0 | 41 | 88 | 0 | 37 | 0 |
| 4 | 89 | 0 | 2 | 0 | 0 | 22 | 92 | 0 | 20 | 0 |
| 4 | 4 | 0 | 6 | 0 | 0 | 63 | 94 | 0 | 33 | 0 |
| 4 | 34 | 0 | 6 | 0 | 0 | 67 | 86 | 0 | 45 | 0 |
| 4 | 46 | 0 | 6 | 0 | 0 | 10 | 100 | 0 | 41 | 0 |
| 3 | 40 | 0 | 16 | 0 | 0 | 0 | 88 | 0 | 67 | 0 |
| 3 | 45 | 0 | 4 | 0 | 0 | 0 | 86 | 0 | 37 | 0 |
| 3 | 51 | 0 | 2 | 0 | 0 | 0 | 71 | 0 | 14 | 0 |
| 3 | 58 | 0 | 6 | 0 | 0 | 0 | 88 | 0 | 20 | 0 |
| 2 | 18 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 69 | 0 |
| 2 | 82 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 53 | 0 |
| 2 | 63 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 41 | 0 |
| 2 | 76 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 61 | 0 |
| 1 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 78 | 0 |
| 1 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 59 | 0 |
| 1 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 41 | 0 |
| 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 0 |
| 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |  |  |


| SR | Plot | Armeria | Aster | Puccinellia | Atriplex | Limonium | Plantago | Salicornia | Triglochin | Spergularia |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 83 | 39 | 4 | 18 | 0 | 24 | 100 | 8 | 10 | 2 |
| 8 | 22 | 22 | 2 | 18 | 4 | 41 | 94 | 33 | 14 | 2 |
| 8 | 56 | 29 | 8 | 31 | 0 | 53 | 96 | 55 | 27 | 2 |
| 8 | 19 | 47 | 16 | 78 | 0 | 27 | 86 | 63 | 53 | 10 |
| 7 | 26 | 27 | 10 | 39 | 0 | 20 | 96 | 55 | 22 | 0 |
| 7 | 14 | 6 | 22 | 73 | 0 | 59 | 71 | 67 | 8 | 0 |
| 7 | 75 | 20 | 4 | 14 | 0 | 27 | 100 | 37 | 16 | 0 |
| 7 | 24 | 18 | 4 | 43 | 0 | 41 | 82 | 86 | 37 | 0 |
| 6 | 84 | 16 | 4 | 20 | 0 | 22 | 96 | 0 | 45 | 0 |
| 6 | 43 | 8 | 4 | 55 | 0 | 55 | 88 | 0 | 41 | 0 |
| 6 | 88 | 8 | 8 | 82 | 0 | 57 | 94 | 0 | 10 | 0 |
| 6 | 16 | 31 | 8 | 86 | 0 | 45 | 90 | 0 | 33 | 0 |
| 5 | 41 | 67 | 16 | 0 | 0 | 63 | 90 | 0 | 31 | 0 |
| 5 | 32 | 8 | 6 | 0 | 0 | 27 | 98 | 0 | 49 | 0 |
| 5 | 52 | 31 | 8 | 0 | 0 | 29 | 100 | 0 | 16 | 0 |
| 5 | 11 | 43 | 12 | 0 | 0 | 39 | 90 | 0 | 55 | 0 |
| 4 | 89 | 0 | 2 | 0 | 0 | 24 | 96 | 0 | 29 | 0 |
| 4 | 4 | 0 | 6 | 0 | 0 | 63 | 98 | 0 | 37 | 0 |
| 4 | 34 | 0 | 20 | 0 | 0 | 67 | 90 | 0 | 47 | 0 |
| 4 | 46 | 0 | 4 | 0 | 0 | 6 | 98 | 0 | 43 | 0 |
| 3 | 40 | 0 | 20 | 0 | 0 | 0 | 84 | 0 | 82 | 0 |
| 3 | 45 | 0 | 2 | 0 | 0 | 0 | 86 | 0 | 27 | 0 |
| 3 | 51 | 0 | 2 | 0 | 0 | 0 | 78 | 0 | 14 | 0 |
| 3 | 58 | 0 | 8 | 0 | 0 | 0 | 92 | 0 | 35 | 0 |
| 2 | 18 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 84 | 0 |
| 2 | 82 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 53 | 0 |
| 2 | 63 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 49 | 0 |
| 2 | 76 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 76 | 0 |
| 1 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 88 | 0 |
| 1 | 47 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 49 | 0 |
| 1 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 41 | 0 |
| 1 | 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 35 | 0 |
| 0 | 80 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | 0 | 0 | 0 | 0 | 0 | 0 | 0 |  |  |  |

## APPENDIX B: Appendices to chapter 3.

B1. Raw \% cover values from the simulated wave exposure experiment on macroalgae communities at Penmon point.

| Time (Days) | Treatment | Ulva | Chondrus | Gracilaria | Ectocarpus | Fucus | Ceramium | Membranoptera | Lomentaria | Cladophora | Proclamium | Palmaria | Laminaria | Callithamnion |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | Control | 80 | 59 | 49 | 27 | 6 | 24 | 2 | 0 | 2 | 0 | 0 | 0 | 2 |
| 0 | Control | 82 | 47 | 49 | 24 | 14 | 12 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | Control | 43 | 82 | 61 | 0 | 6 | 27 | 22 | 0 | 0 | 0 | 0 | 2 | 0 |
| 0 | Control | 35 | 88 | 45 | 0 | 4 | 37 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | Control | 86 | 53 | 55 | 10 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 2 | 0 |
| 16 | Control | 88 | 49 | 39 | 35 | 6 | 24 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Control | 76 | 43 | 61 | 31 | 4 | 6 | 10 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Control | 51 | 78 | 51 | 12 | 16 | 14 | 29 | 0 | 2 | 0 | 0 | 0 | 0 |
| 16 | Control | 51 | 80 | 39 | 4 | 8 | 27 | 4 | 0 | 0 | 0 | 0 | 12 | 0 |
| 16 | Control | 100 | 47 | 47 | 33 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28 | Control | 88 | 57 | 57 | 29 | 4 | 12 | 2 | 0 | 4 | 0 | 0 | 0 | 0 |
| 28 | Control | 82 | 43 | 78 | 29 | 0 | 8 | 4 | 0 | 2 | 0 | 2 | 0 | 0 |
| 28 | Control | 65 | 76 | 69 | 10 | 24 | 20 | 31 | 0 | 6 | 0 | 0 | 0 | 0 |
| 28 | Control | 59 | 67 | 49 | 18 | 12 | 35 | 8 | 2 | 0 | 0 | 0 | 2 | 0 |
| 28 | Control | 86 | 57 | 76 | 20 | 0 | 0 | 12 | 0 | 2 | 0 | 0 | 0 | 0 |
| 45 | Control | 86 | 49 | 61 | 16 | 10 | 20 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| 45 | Control | 88 | 39 | 80 | 10 | 4 | 12 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| 45 | Control | 59 | 84 | 63 | 12 | 6 | 6 | 22 | 0 | 4 | 0 | 0 | 0 | 0 |
| 45 | Control | 76 | 82 | 22 | 0 | 4 | 63 | 10 | 2 | 0 | 0 | 0 | 0 | 0 |
| 45 | Control | 78 | 53 | 67 | 29 | 0 | 2 | 18 | 0 | 0 | 0 | 0 | 0 | 0 |
| 58 | Control | 90 | 49 | 76 | 27 | 6 | 53 | 10 | 0 | 12 | 0 | 0 | 0 | 0 |
| 58 | Control | 76 | 45 | 86 | 16 | 4 | 12 | 22 | 0 | 0 | 4 | 0 | 0 | 0 |
| 58 | Control | 63 | 88 | 65 | 18 | 14 | 45 | 29 | 0 | 10 | 0 | 0 | 0 | 0 |
| 58 | Control | 57 | 76 | 41 | 10 | 4 | 33 | 14 | 2 | 0 | 0 | 2 | 2 | 0 |


| 58 | Control | 86 | 65 | 92 | 18 | 2 | 10 | 22 | 2 | 10 | 0 | 0 | 0 | 0 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | Disturbed | 49 | 33 | 53 | 53 | 4 | 8 | 4 | 0 | 10 | 2 | 0 | 0 | 0 |
| 0 | Disturbed | 45 | 90 | 12 | 4 | 18 | 22 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| 0 | Disturbed | 69 | 27 | 63 | 49 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |
| 0 | Disturbed | 39 | 82 | 35 | 6 | 24 | 18 | 18 | 16 | 2 | 0 | 0 | 0 | 0 |
| 0 | Disturbed | 43 | 10 | 37 | 88 | 4 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Disturbed | 27 | 31 | 43 | 47 | 0 | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| 16 | Disturbed | 33 | 78 | 16 | 4 | 27 | 10 | 2 | 0 | 8 | 0 | 0 | 2 | 0 |
| 16 | Disturbed | 35 | 18 | 41 | 49 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | Disturbed | 53 | 92 | 24 | 6 | 24 | 18 | 12 | 4 | 0 | 0 | 0 | 0 | 0 |
| 16 | Disturbed | 4 | 12 | 20 | 67 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28 | Disturbed | 18 | 33 | 47 | 39 | 2 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| 28 | Disturbed | 39 | 94 | 20 | 4 | 20 | 31 | 0 | 0 | 6 | 0 | 0 | 0 | 0 |
| 28 | Disturbed | 31 | 27 | 43 | 18 | 0 | 4 | 4 | 0 | 2 | 0 | 0 | 0 | 0 |
| 28 | Disturbed | 45 | 92 | 41 | 2 | 20 | 18 | 8 | 2 | 4 | 0 | 0 | 0 | 0 |
| 28 | Disturbed | 8 | 20 | 35 | 47 | 8 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 |
| 45 | Disturbed | 16 | 24 | 22 | 22 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 45 | Disturbed | 16 | 71 | 8 | 4 | 14 | 31 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| 45 | Disturbed | 24 | 18 | 39 | 16 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| 45 | Disturbed | 61 | 96 | 29 | 2 | 16 | 12 | 10 | 2 | 2 | 0 | 0 | 0 | 0 |
| 45 | Disturbed | 27 | 35 | 24 | 10 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 |
| 58 | Disturbed | 27 | 27 | 43 | 31 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 |
| 58 | Disturbed | 29 | 92 | 33 | 20 | 12 | 37 | 4 | 0 | 20 | 0 | 0 | 0 | 0 |
| 58 | Disturbed | 18 | 24 | 53 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 58 | Disturbed | 31 | 98 | 27 | 35 | 6 | 18 | 14 | 2 | 10 | 0 | 0 | 0 | 0 |
| 58 | Disturbed | 16 | 8 | 27 | 29 | 0 | 4 | 0 | 0 | 14 | 0 | 0 | 0 | 0 |

B2. Population dry wt ( $\mathbf{g} \mathbf{~ m - 2}$ ) of macroalgae species. Collected during the manipulation of natural assemblages. Values are the sum of the biomass removed prior to and post ecosystem process measurements.

| SR | $\mathbf{0}$ | $\mathbf{0}$ | $\mathbf{1}$ | $\mathbf{1}$ | $\mathbf{2}$ | $\mathbf{2}$ | $\mathbf{3}$ | $\mathbf{3}$ | $\mathbf{4}$ | $\mathbf{4}$ | $\mathbf{5}$ | $\mathbf{5}$ | ALL |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Species |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Chondrus | 28.93 | 1.48 | 275.03 | 307.00 | 140.18 | 298.95 | 159.63 | 29.53 | 70.13 | 88.18 | 194.03 | 149.35 | 175.10 |
| Gracilaria | 48.08 | 19.80 | 39.60 | 14.53 | 209.93 | 19.70 | 32.85 | 3.30 | 57.25 | 72.25 | 17.00 | 37.45 | 68.38 |
| Ceramium | 7.70 | 10.08 | 21.85 | 57.73 | 42.10 | 40.73 | 19.33 | 6.23 | 44.40 | 16.43 | 14.85 | 41.93 | 55.13 |
| Ectocarpus | 7.45 | 5.93 | 0.48 | 4.20 | 64.13 | 9.58 | 2.98 | 32.65 | 38.55 | 32.43 | 3.63 | 11.83 | 5.50 |
| Ulva | 3.60 | 0.80 | 23.93 | 5.00 | 1.18 | 18.58 | 19.43 | 22.15 | 16.33 | 2.03 | 9.13 | 20.28 | 4.23 |
| Fucus | 0.00 | 11.25 | 0.00 | 1.60 | 104.38 | 25.58 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 0.08 |
| Membranoptera | 0.85 | 0.00 | 7.68 | 11.10 | 7.98 | 0.58 | 9.88 | 0.00 | 6.23 | 10.15 | 6.23 | 5.75 | 1.68 |
| Cladophora | 0.43 | 1.28 | 0.00 | 0.10 | 0.00 | 0.20 | 0.00 | 13.83 | 0.00 | 0.00 | 0.00 | 0.40 | 0.03 |
| Polysiphonia | 1.20 | 0.13 | 0.03 | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.75 | 0.38 | 0.63 |
| Lomentaria art | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.95 | 0.00 | 0.00 |
| Palmaria | 0.03 | 0.13 | 0.00 | 0.40 | 0.00 | 0.33 | 0.00 | 0.00 | 0.10 | 0.00 | 0.00 | 0.23 | 0.00 |
| Lomentaria clav | 0.05 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.50 | 0.38 | 0.00 | 0.00 | 0.15 | 0.13 |
| Calithamion | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.58 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Proclamium | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.38 | 0.00 | 0.10 |
| Laminaria | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 |
| Delesseria | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 0.00 |

B3. R2 values obtained from estimating the fluxes of key nutrients and oxygen during measurement of ecosystem processes in the natural macroalgae assemblage. Values obtained from the relationship between $\mathrm{NH}_{4}^{+}$(Ammonium), $\mathrm{NO}_{3}{ }^{-}$(Nitrate) concentrations and time in minutes. Community respiration and Net
Community Productivity values represent the $\mathrm{R}^{2}$ from the relationship between $\mathrm{O}_{2}$ concentration and time in during dark and light measurements respectively.


## APPENDIX C: Appendices to chapter 4.

C1. Calibration curves used to convert total wet weight to dry tissue weight for sessile invertebrates.
Ascidiella aspersa


Balanus crenatus


Mytilus edulis


## C2．Raw population wet weight data $\left(\mathrm{g} \mathrm{m}^{-2}\right)$ for species identified from tiles during the hypoxic disturbance of 2009 ．

| Treatment | $\begin{gathered} \text { Time } \\ \text { (days) } \end{gathered}$ | Species |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  | $\begin{aligned} & \text { g } \\ & \text { 䯧 } \\ & \text { 亮 } \\ & \text { 离 } \end{aligned}$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  | $\begin{aligned} & \text { 言 } \\ & \text { B } \\ & \text { 足 } \\ & \text { un } \end{aligned}$ | $\begin{aligned} & \text { m } \\ & 0 \\ & 0 \\ & \text { un } \\ & \stackrel{0}{c} \\ & E \\ & \text { 흠 } \end{aligned}$ |  |  |  |  |  |
| Control 1 | 0 | 9.99 | 1.89 | 0.94 | 4.11 | 0.29 | 0.00 | 0.00 | 0.00 | 0.00 | 0.46 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 1 | 0 | 7.64 | 0.46 | 0.25 | 0.61 | 1.02 | 2.92 | 0.14 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 1 | 0 | 6.71 | 2.19 | 0.84 | 1.34 | 0.15 | 0.21 | 0.01 | 0.00 | 0.42 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 1 | 0 | 6.39 | 3.10 | 0.65 | 2.34 | 2.07 | 0.13 | 0.00 | 0.05 | 0.21 | 0.09 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 2 | 3 | 11.60 | 1.19 | 0.40 | 1.27 | 0.66 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.00 | 0.33 | 0.40 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 2 | 3 | 7.05 | 1.57 | 0.91 | 3.21 | 0.37 | 0.00 | 0.00 | 0.00 | 0.07 | 0.03 | 0.00 | 0.08 | 0.03 | 0.00 | 0.93 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 2 | 3 | 8.66 | 1.49 | 0.88 | 3.11 | 0.55 | 0.00 | 0.17 | 0.00 | 0.00 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.26 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 2 | 3 | 5.88 | 2.21 | 0.22 | 2.19 | 0.34 | 0.00 | 0.03 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 3 | 7 | 8.05 | 2.19 | 1.10 | 2.11 | 1.13 | 0.00 | 0.00 | 0.00 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.62 | 0.00 | 0.00 | 0.30 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 3 | 7 | 4.85 | 2.16 | 0.48 | 1.27 | 1.33 | 0.00 | 0.00 | 0.00 | 0.09 | 0.10 | 0.01 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.32 | 0.00 | 4.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 3 | 7 | 9.35 | 1.68 | 0.43 | 2.20 | 0.45 | 0.00 | 0.04 | 0.00 | 0.39 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control 3 | 7 | 8.53 | 2.35 | 0.39 | 0.52 | 0.23 | 0.00 | 0.10 | 0.02 | 0.24 | 0.07 | 0.00 | 0.43 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1 | 1 | 4.06 | 0.46 | 0.06 | 0.39 | 0.82 | 0.00 | 0.01 | 0.01 | 0.24 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 0.00 | 0.00 | 0.00 |
| 1 | 1 | 6.12 | 1.56 | 0.63 | 1.60 | 0.60 | 0.00 | 0.04 | 0.04 | 0.10 | 0.06 | 0.00 | 0.00 | 0.27 | 0.00 | 0.00 | 0.00 | 0.15 | 0.28 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.16 | 0.18 | 0.00 |
| 1 | 1 | 9.51 | 1.30 | 0.43 | 2.12 | 0.01 | 0.00 | 0.01 | 0.00 | 0.01 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1 | 1 | 7.41 | 2.82 | 0.51 | 0.82 | 0.54 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 |
| 2 | 2 | 7.58 | 0.72 | 0.30 | 0.10 | 0.66 | 0.00 | 0.00 | 0.00 | 0.05 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 2 | 3.35 | 3.53 | 0.41 | 1.05 | 1.58 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 2 | 5.12 | 1.73 | 0.18 | 0.69 | 0.23 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 2 | 6.38 | 2.85 | 0.28 | 0.72 | 0.90 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 3 | 4.50 | 2.07 | 0.18 | 1.05 | 1.59 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |


| 3 | 3 | 6.79 | 0.73 | 0.18 | 0.29 | 0.30 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 3 | 3 | 7.95 | 0.57 | 0.14 | 0.17 | 0.64 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 |
| 3 | 3 | 7.36 | 0.00 | 0.16 | 0.40 | 0.66 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 4 | 1.72 | 0.00 | 0.00 | 0.00 | 0.31 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 4 | 7.33 | 0.00 | 0.00 | 0.00 | 0.84 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 4 | 8.46 | 0.18 | 0.11 | 0.00 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 4 | 8.21 | 0.00 | 0.23 | 0.00 | 0.24 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 7 | 4.04 | 0.00 | 0.00 | 0.00 | 0.48 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 7 | 3.29 | 0.00 | 0.00 | 0.00 | 0.43 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 7 | 7.18 | 0.00 | 0.00 | 0.00 | 0.29 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

C2．Raw population wet weight data $\left(\mathrm{g} \mathrm{m}^{-2}\right)$ for species identified from tiles during the hypoxic disturbance of 2010.

| Treatment （days） | Species |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \text { o } \\ & \text { U } \\ & 0 \\ & 0 \\ & \text { u } \\ & \text { on } \end{aligned}$ | $\begin{aligned} & \text { B } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\begin{aligned} & \text { 劫 } \\ & \text { n } \\ & 0 \end{aligned}$ | $\begin{aligned} & \text { In } \\ & \text { N } \\ & \text { N } \\ & \text { N } \end{aligned}$ |  | $\begin{aligned} & < \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\begin{aligned} & \infty \\ & \stackrel{\infty}{0} \\ & \text { 号 } \\ & \text { in } \end{aligned}$ | $\begin{aligned} & \text { U } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | 0 0 品 응 응 | vวu．uvo plo！sp．ivmpg | （1） 0 0 0 0 0 0 | $\begin{aligned} & 0 \\ & 0 \\ & 3 \\ & \frac{1}{3} \\ & \hline \end{aligned}$ |
| 0 | 1.39 | 0.02 | 0.10 | 19.19 | 0.09 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 | 0.06 | 0.21 |
| 0 | 0.37 | 0.01 | 0.00 | 13.17 | 0.03 | 0.00 | 0.00 | 0.09 | 0.00 | 0.00 | 0.30 | 0.00 | 0.00 |
| 0 | 0.39 | 0.01 | 0.00 | 14.06 | 0.06 | 0.30 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 |
| 0 | 0.43 | 0.06 | 0.13 | 15.02 | 0.02 | 0.79 | 0.00 | 0.00 | 0.00 | 0.00 | 0.93 | 0.31 | 0.00 |
| 0 | 0.65 | 0.00 | 0.12 | 12.93 | 0.01 | 0.95 | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 | 0.00 | 0.00 |
| 0 | 0.21 | 0.01 | 0.02 | 12.97 | 0.01 | 0.59 | 0.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 0.00 |
| 0 | 0.62 | 0.03 | 0.18 | 8.68 | 0.04 | 2.56 | 0.00 | 0.00 | 0.04 | 0.00 | 0.04 | 0.24 | 0.00 |
| 0 | 0.45 | 0.05 | 0.19 | 16.47 | 0.30 | 1.48 | 0.00 | 0.00 | 0.00 | 0.00 | 0.12 | 0.38 | 0.00 |
| 1 | 0.87 | 0.05 | 0.02 | 6.63 | 0.03 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1 | 0.55 | 0.08 | 0.26 | 3.83 | 0.04 | 0.46 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1 | 1.63 | 0.00 | 0.21 | 4.77 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1 | 0.45 | 0.03 | 0.09 | 0.12 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 1 | 0.45 | 0.02 | 0.14 | 15.44 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 1.40 | 0.00 | 0.37 | 3.63 | 0.04 | 0.71 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 0.61 | 0.01 | 0.02 | 5.54 | 0.01 | 0.44 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 0.31 | 0.08 | 0.09 | 5.58 | 0.05 | 0.66 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 0.74 | 0.01 | 0.25 | 18.06 | 0.08 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 2 | 1.76 | 0.08 | 0.05 | 6.75 | 0.10 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 0.00 | 0.01 | 0.33 | 7.23 | 0.06 | 1.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 0.11 | 0.10 | 0.05 | 8.77 | 0.20 | 1.86 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 0.22 | 0.01 | 0.05 | 10.05 | 0.03 | 0.54 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 0.39 | 0.05 | 0.01 | 16.29 | 0.01 | 0.17 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 0.00 | 0.02 | 0.10 | 7.58 | 0.02 | 0.68 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.19 | 0.01 | 0.00 | 4.04 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.29 | 0.00 | 0.04 | 12.68 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.17 | 0.02 | 0.00 | 5.52 | 0.00 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.00 | 0.00 | 0.00 | 10.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 0.14 | 0.06 | 0.00 | 12.08 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | 0.11 | 0.04 | 0.00 | 0.46 | 0.01 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | 0.02 | 0.05 | 0.00 | 2.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | 0.42 | 0.01 | 0.00 | 17.66 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | 0.00 | 0.12 | 0.00 | 5.36 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | 0.31 | 0.00 | 0.00 | 13.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

C3．Population dry tissue weight $\left(\mathrm{g} \mathrm{m}^{-2}\right)$ of species identified and quantified during the manipulation of species richness to simulate hypoxia in the 2009 fouling invertebrate assemblage．Values are the sum of species removed prior to and post measurement of community clearance rate．

| Species <br> Richness | Species |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \text { E } \\ & \text { 令 } \\ & \text { 俞 } \\ & \end{aligned}$ | $\begin{aligned} & \text { 合 } \\ & \text { 会 } \end{aligned}$ |  |  |  |  | 5 5 0 0 |  |  |  |  |  |  |  |  |  | $\begin{aligned} & \text { 焉 } \\ & \text { 荙 } \\ & \text { En } \end{aligned}$ |  |  |  |  |  |  |  |
| 1 | 20.91 | 133.40 | 15.10 | 9.85 | 2.42 | 9.70 | 0.00 | 5.15 | 0.23 | 0.98 | 0.00 | 0.00 | 0.00 | 0.61 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.38 | 0.00 | 0.00 | 0.00 |
| 3 | 8.86 | 177.72 | 0.88 | 2.20 | 3.56 | 0.00 | 0.00 | 0.00 | 0.53 | 0.38 | 3.11 | 0.00 | 0.00 | 0.08 | 1.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 5 | 7.58 | 168.85 | 52.96 | 15.46 | 5.00 | 0.61 | 0.00 | 0.15 | 0.23 | 3.79 | 0.68 | 0.00 | 0.00 | 0.15 | 0.45 | 22.96 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.76 | 0.00 | 0.00 |
| 2 | 6.06 | 105.19 | 4.84 | 7.50 | 2.58 | 0.00 | 0.00 | 0.00 | 0.00 | 0.45 | 0.00 | 2.05 | 0.00 | 0.08 | 0.00 | 0.00 | 1.21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 0 | 5.08 | 149.93 | 18.42 | 9.47 | 6.06 | 20.00 | 0.00 | 0.00 | 0.15 | 2.20 | 0.00 | 0.00 | 0.00 | 0.15 | 3.71 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control | 26.59 | 66.33 | 0.00 | 4.62 | 11.44 | 0.00 | 0.00 | 0.00 | 0.00 | 13.49 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 5.53 | 0.45 | 0.00 | 0.00 | 1.52 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 23.94 | 108.17 | 17.32 | 21.36 | 7.27 | 4.02 | 0.00 | 4.85 | 0.00 | 5.91 | 1.21 | 0.00 | 0.00 | 0.45 | 3.86 | 4.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.30 | 0.00 | 0.00 | 0.00 |
| 0 | 10.61 | 170.02 | 11.75 | 24.39 | 2.50 | 5.08 | 0.00 | 1.59 | 0.38 | 3.67 | 0.00 | 0.00 | 0.00 | 0.38 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 |
| 1 | 14.70 | 108.39 | 23.27 | 14.32 | 3.26 | 3.94 | 0.00 | 0.00 | 0.00 | 4.32 | 0.98 | 0.91 | 0.00 | 0.45 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.61 | 0.00 | 0.00 | 0.15 | 3.06 | 0.08 |
| 2 | 5.83 | 92.06 | 18.12 | 2.05 | 1.97 | 0.00 | 0.00 | 0.00 | 0.08 | 3.56 | 0.00 | 0.00 | 0.00 | 0.00 | 1.89 | 0.00 | 2.58 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 20.38 | 125.28 | 20.74 | 24.17 | 9.55 | 9.77 | 0.00 | 0.00 | 0.61 | 0.91 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.08 | 6.21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.76 | 0.00 | 0.00 |
| 3 | 10.08 | 61.98 | 5.24 | 7.73 | 10.15 | 1.67 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 11.44 | 7.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.14 | 0.00 | 0.08 |
| 5 | 7.12 | 134.55 | 12.93 | 6.14 | 5.38 | 0.00 | 0.00 | 0.00 | 0.00 | 1.21 | 0.00 | 0.00 | 0.00 | 0.23 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.67 | 0.08 |
| Control | 15.46 | 150.22 | 17.47 | 10.61 | 6.06 | 2.80 | 0.00 | 0.00 | 0.00 | 0.83 | 0.00 | 0.61 | 0.00 | 0.53 | 0.00 | 1.06 | 0.61 | 0.00 | 0.00 | 0.23 | 0.00 | 0.00 | 0.00 | 0.83 | 0.08 |
| 0 | 9.17 | 161.81 | 19.22 | 17.05 | 3.18 | 1.89 | 0.00 | 2.80 | 0.00 | 0.83 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.38 | 0.00 | 0.23 | 0.00 | 0.00 |
| 2 | 17.65 | 147.42 | 14.00 | 33.56 | 4.02 | 6.59 | 0.00 | 0.08 | 0.08 | 0.68 | 0.00 | 0.83 | 0.00 | 0.00 | 2.12 | 4.02 | 0.00 | 0.00 | 0.00 | 0.61 | 0.00 | 0.00 | 0.00 | 1.74 | 0.00 |
| 1 | 17.73 | 142.56 | 6.07 | 7.80 | 1.89 | 3.33 | 0.00 | 0.00 | 0.00 | 1.89 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 14.92 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 16.14 | 105.24 | 18.21 | 36.82 | 12.95 | 8.11 | 0.00 | 0.68 | 0.00 | 8.26 | 0.00 | 0.00 | 0.68 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Control | 29.55 | 116.11 | 64.22 | 7.20 | 11.21 | 2.95 | 0.00 | 0.00 | 0.00 | 2.58 | 0.00 | 0.00 | 0.00 | 0.15 | 3.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 5 | 13.49 | 121.00 | 4.23 | 22.80 | 4.92 | 4.92 | 0.00 | 0.00 | 0.00 | 2.88 | 0.00 | 2.95 | 0.00 | 0.00 | 0.00 | 8.71 | 0.00 | 0.00 | 0.00 | 1.06 | 0.00 | 0.00 | 0.08 | 0.00 | 0.00 |
| 4 | 15.68 | 164.93 | 13.47 | 20.15 | 12.95 | 8.03 | 0.00 | 0.00 | 0.00 | 5.68 | 0.00 | 1.29 | 0.00 | 0.38 | 0.00 | 18.71 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.89 | 0.00 | 0.00 |

C4. Population dry tissue weight $\left(\mathrm{g} \mathrm{m}^{-2}\right)$ of species identified and quantified during the manipulation of species richness to simulate hypoxia in the 2010 fouling invertebrate assemblage. Values are the sum of species removed prior to and post measurement of community clearance rate.

| Species Richness Treatment | Species |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { \% } \\ & \text { 气 } \\ & \\ & \text { n } \end{aligned}$ | ps.วdse vllग!p!วSV | $\begin{aligned} & \text { I } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | $\begin{gathered} \text { § } \\ \text { U } \\ \text { U } \\ \tilde{0} \\ 0 \end{gathered}$ | $\begin{aligned} & 0 \\ & 0 \\ & 0 \\ & 0 \\ & \text { N } \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | I \# \# 0 0 0 0 0 0 0 |
| Control | 102.92 | 7.66 | 1.02 | 8.64 | 30.56 | 4.45 |
| 5 | 72.35 | 14.94 | 0.98 | 5.12 | 20.87 | 9.45 |
| 4 | 52.33 | 8.67 | 1.30 | 0.85 | 3.59 | 5.36 |
| 3 | 53.05 | 14.80 | 1.15 | 0.64 | 0.00 | 2.37 |
| 2 | 55.14 | 11.04 | 3.49 | 5.73 | 31.09 | 9.91 |
| 1 | 99.16 | 11.51 | 1.80 | 0.00 | 20.01 | 0.00 |
| 0 | 31.80 | 1.10 | 1.04 | 0.00 | 0.00 | 7.73 |
| Control | 88.78 | 0.75 | 0.80 | 0.00 | 35.14 | 14.18 |
| 5 | 58.32 | 9.19 | 3.29 | 1.79 | 7.80 | 2.09 |
| 4 | 31.59 | 5.83 | 0.34 | 2.35 | 13.50 | 12.00 |
| 3 | 83.13 | 3.32 | 0.35 | 0.00 | 14.27 | 1.36 |
| 2 | 49.94 | 3.55 | 0.62 | 0.00 | 30.32 | 3.82 |
| 1 | 69.03 | 4.64 | 0.39 | 0.00 | 2.13 | 0.55 |
| 0 | 70.83 | 3.80 | 0.08 | 0.00 | 0.00 | 5.09 |
| Control | 57.69 | 14.63 | 0.64 | 1.60 | 15.31 | 15.73 |
| 5 | 80.65 | 5.71 | 0.39 | 2.16 | 5.45 | 3.09 |
| 4 | 77.60 | 3.56 | 0.30 | 1.51 | 19.02 | 0.36 |
| 3 | 74.95 | 1.61 | 1.08 | 1.13 | 76.90 | 4.27 |
| 2 | 56.89 | 7.15 | 1.65 | 0.76 | 17.88 | 3.09 |
| 1 | 68.20 | 5.71 | 0.84 | 0.00 | 4.30 | 4.82 |
| 0 | 21.63 | 4.24 | 0.41 | 1.27 | 32.57 | 2.73 |
| Control | 87.58 | 0.54 | 1.16 | 4.46 | 9.30 | 13.27 |
| 5 | 70.82 | 14.37 | 2.67 | 2.45 | 13.24 | 1.91 |
| 4 | 65.86 | 5.02 | 0.67 | 4.70 | 38.57 | 0.00 |
| 3 | 53.50 | 5.07 | 2.93 | 0.33 | 0.00 | 4.18 |
| 2 | 95.84 | 5.44 | 0.16 | 1.58 | 40.94 | 15.45 |
| 1 | 53.85 | 7.65 | 1.08 | 0.00 | 6.36 | 3.36 |
| 0 | 89.86 | 6.11 | 0.92 | 1.44 | 15.19 | 3.27 |

C5. $\mathbf{R}^{2}$ values obtained from quantifying the decline in microalgae cell concentration during community clearance rate measurements in 2009 and 2010. R2 values are plotted against species richness treatment. Each point represents an individual replicate.


Species Richness

2010


Species Richness


[^0]:    ${ }^{1}$ Experiments performed on the assemblage which colonised between 2009 and 2010 was part of an M degree project conducted by Joe Kenworthy at Bangor University (see Kenworthy 2010). Experimental work was supervised by Thomas W. Davies (author of the current text) and Dr Jan Hiddink. The analysis presented here is entirely the work of the author, Thomas W. Davies.

