Biodiversity and Ecosystem Processes in the Strandline: The Role of Species Identity, Diversity, Interactions and Body Size

By

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Abstract

In the current climate of biodiversity loss how species diversity and ecosystem process are linked is, arguably, one of the most pressing issues and greatest challenges currently facing the scientific community. Previous studies suggest that there is no universal trajectory for the relationship between diversity and ecosystem processes, the pattern depends largely on species identity and their interactions. Furthermore, the effect of reduced diversity on ecosystem process in multi-trophic assemblages is both understudied and poorly understood. Consequently, the overall aim of the present study was to investigate the role of species identity, diversity and interactions in determining ecosystem processes using the strandline as a model system. Appropriate strandline species, three species of kelp fly larvae, an amphipod and four rove beetles were were selected for use in laboratory manipulative experiments that measured decomposition as an ecosystem process. This study is one of the few to consider the affect of species interactions on ecosystem processes. The use of metabolic theory to make predictions of trophic interactions and ecosystem processes, using tractable surrogate measures of interaction strength, was also investigated. Finally, the importance of trophic interactions in affecting the connection between ecosystem processes and consumer species identity, diversity and interactions was examined.

Species identity combination explained the variability in decomposition when strandline decomposer diversity and identity were manipulated. Positive and negative interactions were identified, and the effect of diversity on decomposition was dependent on the balance of these negative and positive species interactions. A mechanism of microbial facilitation and inhibition was proposed to explain the outcome as no previously proposed single mechanism adequately described the observed effect of species identity, diversity and interactions on ecosystem process found in this study.

It was not possible to accurately predict observed predator-prey interaction strengths and ecosystem processes between strandline predators and prey and decomposition using body size as a surrogate measure of interaction strength and ecosystem processes. Although body size was an important factor explaining the variability in predator-prey interactions and decomposition, so too was species identity. The absence of a consistent relationship between size and interaction strength and decomposition was attributed to species-specific differences.

The presence of trophic interactions subtly affected decomposition of wrack by strandline detritivores. However, in the presence and absence of a predator the overall effect of detritivore diversity and interactions on decomposition remained constant.

The results of this study have implications for the fields of biodiversity ecology, metabolic theory of ecology and food web ecology. Firstly, the identification of positive detritivore-resource interactions adds to a growing body of evidence that some detritivore species may interact positively, with respect to ecosystem processes. The loss of species within a trophic group may result in a greater reduction in ecosystem processes than previously thought. If positive species interactions are prevalent, ecosystem process will decrease to a greater extent as species are lost, than that predicted from single species processing rates. By considering species interactions, future biodiversity ecosystem processing studies may better understand the effects of species diversity and identity on ecosystem process. It is also suggested that patterns and relationships uncovered in previous studies investigating the effects of species from a single trophic level on ecosystem process may still be valid in more realistic multi-trophic systems. If future biodiversity-ecosystem process studies are to make predictions concerning actual species-ecosystem process interactions in real assemblages the size of constituent species should be considered, as predator and prey size was shown to effect predator-prey interactions and ecosystem processes.

The results of this study also suggest that allometry and metabolic theory have limited capacity for making predictions of predator-prey interactions and ecosystem processes, at least at the scale investigated here. Species specific factors are more likely to explain the patterns of predator-prey interactions and ecosystem processes at smaller scales. Unless food web models consider, or allocate, non-trophic interactions correctly, erroneous predictions of energy flow and ecosystem process may result. Finally, the use of body size and allometric scaling laws to quantify food web models and energy flow through an assemblage must be treated with caution if these models are used to make predictions on interactions between species and ecosystem processes occurring at the scale investigated in this study.

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Author's Declaration

At no time during the registration for degree of Doctor of Philosophy has the author been registered for any other University award.

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CHAPTER 1: INTRODUCTION

1.1 Chapter Aims and Outline

> *"The variety of life is manifestly complex...has changed dramatically through time and is unevenly distributed through space.....For many of us these, observations may be interesting in their own right, and the study of biodiversity may be largely a heuristic exercise. But this ignores a fundamental question that, particularly against a background of unprecedented losses in biodiversity, demands both an intellectual and practical response: Does biodiversity matter?"*
>
> -Gaston and Spicer (1998)

The scientific study of biodiversity, the variety of life in all its forms, is one of the most engaging, challenging, and urgent, activities facing humankind at the beginning of the twenty-first century (Wilson 1992, Heywood 1995, Gaston 1996b). One of the key foci over the past quarter century has been the attempt to discern the relationship, if any, between what biodiversity is, and what biodiversity does, the latter referred to as ecosystem function or process (Heywood *et al.* 1995; Millennium Assessment 2005). This relationship is at the centre of the present thesis. Literature dealing with biodiversity and ecosystem process (often referred to as biodiversity and ecosystem function, BDEF) is now voluminous and wide-ranging. Therefore, it is not possible in this introductory chapter to comprehensively review that literature. Instead the more tightly-focused aims of this introductory chapter are to (a) highlight the importance of BDEF research, (b) introduce the study of biodiversity from a historical perspective, (c) briefly summarise our current understanding of this area, particularly identifying the limitations of previous investigations and current gaps in our knowledge, and in doing so provide a clear rationale for the experimental studies on BDEF presented here.

1.2 Biodiversity and Ecosystem Function - Definitions and Importance

There are in excess of ninety different definitions of the term biodiversity (Gaston and Spicer 2004). Perhaps the most important, and most influential, is the one that emerged from the Rio Convention for Biological Diversity. In the Convention for Biological Diversity, biodiversity is defined as;

"The variability among living organisms from all sources including, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems"
- (CBD 1992).

The notion of what a species is, and the organisational level at which diversity should be measured, is still highly contentious and much debated (e.g. Magurran 1988, Bisby 1995, Hawksworth 1995). For the purpose of this thesis biodiversity, unless otherwise stated, refers only to species diversity (or species richness), the number of different species. Species diversity is arguably a good integrator of many different facets of biodiversity (Magurran 1988, Gaston 1996a), it is easily measurable and permits comparability with existing literature on biodiversity and ecosystem functioning.

Differences in understanding what "ecosystem processes or functioning" means have occasionally led to confusion in the interpretation and comparison of studies, as there are subtle differences between the meanings conveyed by the use of the terms (D. Raffaelli *pers. com.*). However, ecosystem functioning and ecosystem processes are simply used interchangeably throughout this thesis and both are taken to refer to the processes operating in an ecosystem;

"...the energy transformation and matter cycling resulting from the combined activity of living organisms"
- (Ghilarov 2000).

Biogeochemical or ecosystem processes are recognized as having an economic value in that they provide ecological goods and services (e.g. Costanza *et al.* 1997,

Pimentel *et al.* 1997, Millennium Ecosystem Assessment 2005 for general assessments, Ewel *et al.* 1998 for mangroves, Moberg and Floke 1999, for coral reefs). The methods used to quantify the value of goods and services are, however, not well researched (Beaumont *et al.* 2007). Furthermore, the human population is dependent on many of these processes to provide a climate capable of sustaining human life. As the biosphere is a hugely complex, intricate system, encompassing 10-100 million species (Naeem *et al.* 2001b and references therein) to understand the functioning of the earth's systems requires not only an understanding of biogeochemical processes but also the role the biota plays in these systems.

In the current climate of biodiversity loss and climate change understanding how species diversity and ecosystem processes are linked, is arguably, one of the most pressing issues and greatest challenges currently facing the scientific community.

Current rates of species extinctions are estimated to be 100-10000 times that of pre-human times (e.g. Ehrlich and Wilson 1991, Wilson 1992, Lawton and May 1995, Sala *et al.* 2000), however some estimates predict as much as 100000 species are lost annually (see Wilson 1992, for range of estimates and problems with predictions). As the global population is predicted to expand from the current 6.5 billion to 9.1 billion by 2050 (United Nations 2004) it is possible that species extinctions may continue or even exceed these predicted rates (Millennium Assessment 2005) due to increased anthropogenic pressure on the earth's resources. Land converted for agriculture and biofuels is predicted to increase from the current 4.9 million square kilometers (in 2000) to 5.3–5.9 million square kilometers in 2050 (factoring in associated changes in consumption patterns due to additional increase in global GDP) (Millennium Ecosystem Assessment 2005). Habitat destruction has long been recognised as the main factor driving species to extinction (Wilson *et al.* 1992, Myers *et al.* 2000). Additionally a larger population will generate more waste both domestically and agriculturally, crop

nutrient application being of particular concern (Millennium Ecosystem Assessment 2005).

Changes in the environment due to climate change may also exacerbate species extinction. Thomas *et al.* (2004) predicted between 15-37% of species in the terrestrial systems they modelled would become extinct due to climate change by 2050, (although see criticisms of this report by Lewis 2006). It is not just global extinctions that will affect biodiversity but local extinctions and the well documented reductions in species distribution and abundance (Ehrlich 1988, Wilson 1988, Soule 1991, Reaka-Kudla *et al.* 1997). Consequently, biodiversity losses based on current estimates of species extinctions are likely to be minimal and modest.

1.3 A Brief Introduction to Biodiversity and Ecosystem Function Research

Initial research linking biodiversity and ecosystem function was undertaken before species loss was widely recognised as having a potential deleterious effect on ecosystem processes. Interest in linking biodiversity and ecosystem processes can be traced back at least as far as Darwin (McNaughton 1993, Hector and Hooper 2002). Most early studies focused on enhancing goods and services, specifically crop productivity, mainly from agricultural research highlighting the importance of intercropping (growing one or more crop plants together) as a means of yield enhancement (e.g. Vandermeer 1989). As the rate of biodiversity loss became widely recognised, and of increasing concern, the last decade has seen a large increase in the number of studies incorporating diversity and ecosystem process in the key words or title (see Figure 1 in Balvanera *et al.* 2006). Pioneering work by Naeem *et al.* (1994b), Tilman and Downing (1994) and Tilman *et al.* (1996), using experimental manipulations of large terrestrial grassland systems found a positive link between diversity and some ecosystem processes, or measures of stability. In doing so they

demonstrated a practical repeatable methodology through which the relationship between diversity and ecosystem processes could be investigated. The profile of BDEF research rose even further preceding the Rio Convention on Biodiversity (1992). The 103 nations that officially signed and ratified the Convention on Biological Diversity document (as of June 2000) were bound with the legal obligation to;

"(a) Identify components of biological diversity important for its conservation and sustainable use, (b) Monitor, through sampling and other techniques, the components of biological diversity identified pursuant to subparagraph (a) above, paying particular attention to those requiring urgent conservation measures and those which offer the greatest potential for sustainable use, (c) Identify processes and categories of activities which have or are likely to have significant adverse impacts on the conservation and sustainable use of biological diversity, and monitor their effects through sampling and other techniques,; and (d) Maintain and organize, by any mechanism data, derived from identification and monitoring activities pursuant to subparagraphs (a), (b) and (c) above."

- (Article 7 in CBD 1992).

BDEF research carried out to date can be split broadly into three main categories, theoretical, experimental, and predictive modelling work.

1.4 Theoretical Relationship Between Biodiversity and Ecosystem Processes

Since the early 1990s the theoretical relationship between diversity and ecosystem processes has been a topic of great interest (see Schlapfer and Schmid 1999 and references therein). The Bayreuth Conference in 2000 brought together many recognised investigators in the empirical and theoretical fields of BDEF research. A key outcome of this conference was the formal recognition of the central idea that the relationship between diversity and ecosystem processes could be described on a bivariate plane (Naeem *et al.* 2001b). The shape of the trajectory (shape of the curve on the graph) linking diversity to an ecosystem process has different theoretical underpinnings and makes different predictions on magnitude and direction of change in ecosystem processes relative to diversity. There is now in excess of 50 different

trajectories relating diversity to ecosystem process (Naeem *et al.* 2001b, Gaston and Spicer 2004). They can be categorised into five main patterns (Figure 1.1a-e).

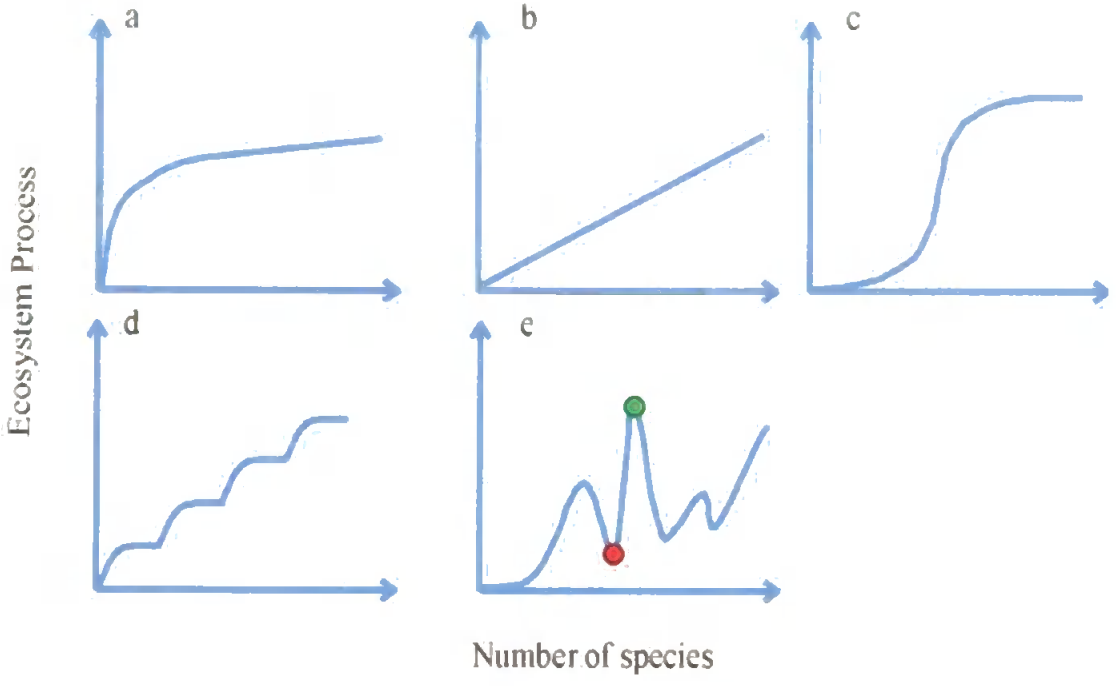

Figure 1.1 The theoretical relationship between diversity (number of species) and ecosystem processes; a- the redundancy hypothesis (Walker 1992), b- the linear hypothesis (from Spicer and Gaston 1998), c- the keystone hypothesis (from Naeem *et al.* 2001b), d- the Rivet Hypothesis (Ehrlich and Ehrlich 1981) and e- the idiosyncratic hypothesis (Lawton 1994).

The differences in the trajectories linking diversity and ecosystem processes, between the theoretical hypotheses, depend on the relative weight given to species identity, the allocation of species traits and the interactions between species.

From the redundancy hypothesis (Walker 1992) (Figure 1.1a) and the rivet hypothesis (Ehrlich and Ehrlich 1981) (Figure 1.1d) it can be predicted that as diversity decreases the remaining species are able to compensate for species loss in terms of ecosystem processes. In the case of the redundancy hypothesis, ecosystem processes

initially increase with diversity, as each additional species contributes to ecosystem functioning in a different manner, owing to differential traits and niches. However, at a certain diversity level additional species are superfluous with respect to ecosystem processes. The rivet hypothesis predicts a step-like increase in ecosystem processes with diversity. It differs from the redundancy hypothesis in that it suggests that species can be categorised, for example, into functional groups. As diversity increases ecosystem processes will increase greatly if there are no species of that functional group in the community, or to a lesser degree if there are functional conspecifics in the assemblage.

In the linear hypothesis ecosystem processes is a linear function of species diversity. This suggests that species identity is not a factor affecting ecosystem processes, rather each additional species processes resources in a different and complementary manner (niche complementarity).

In direct contrast with the linear hypothesis, the keystone hypothesis (Naeem *et al.* 2001b) predicts that the decrease in species diversity will have little effect on ecosystem processes unless a keystone species is lost. In such an eventuality ecosystem processes will be massively reduced. Thus niche differentiation is of little importance and the identity of the species lost is critical.

From the idiosyncratic hypothesis it can be predicted that ecosystem processes can increase or decrease with diversity to different degrees. This does not necessarily suggest that ecosystem processes are diversity-independent or unpredictable; rather, all the process operating in the above hypotheses may co-occur. To expand; with respect to ecosystem processes, some species may have complementary effects owing to niche differentiation, some species may be redundant and some species may have relatively greater effects, than other species. In addition to niche differentiation and allocation of traits the idiosyncratic hypothesis can be interpreted as considering species interactions,

as ecosystem processes may both exceed (Figure 1.1e, green circle), or be lower than (Figure 1.1e, red circle), additive species effects.

Derived from the results of experimental and correlative observations two further, more recent, hypotheses are worth noting. The sampling probability or selection probability effect (Aarssen 1997a, Huston 1997), although it is not directly associated with a trajectory shape it is based on positive diversity-ecosystem process correlations. This mechanisms or artifact was used to explain the empirically uncovered positive relationship between diversity and ecosystem processes found in grassland diversity manipulations. The premise behind this hypothesis is that species have uneven trait distributions with respect to ecosystem processes. Thus as diversity increases the chance of including species with a disproportionally high effect on an ecosystem process increases. Thus this hypothesis can be viewed either an artifact of experimental studies, where ecosystem processes were observed to increase with diversity and diversity treatments were constructed by random allocation of species (of different identities) to each diversity treatment (Aarssen 1997, Huston 1977), or, as a real mechanistic explanation for natural patterns of ecosystem processes and diversity (see Leps *et al.* 2001 for discussion). The second is an interference hypothesis (Jonsson and Malmqvist 2000, 2003b, Cardinale *et al.* 2002) where ecosystem processes increase with species diversity to a greater degree than species additive effects owing to intraspecific competition and interspecific facilitation.

Theoretical trajectories between diversity and ecosystem processes do not as yet have a scale; consequently the quantitative effects of species diversity on ecosystem processes and the effects of reduced species diversity on ecosystem processes cannot be inferred. Theoretical work has, however, formalised a number of potential mechanisms behind the diversity ecosystem process relationship and as such, spurred much empirical investigation into either the trajectory of the relationship or the relative

importance of species identity, niche differentiation and species diversity for ecosystem processes.

Anecdotal and/or empirical evidence for all of these trajectories now exists (see Schulze and Mooney 1993, Loreau *et al.* 2001 for reviews). Early well known studies manipulating diversity in grasslands all showed plant biomass or productivity to increase with diversity, suggesting that niche complementarily is an important factor governing the diversity-ecosystem process relationship (e.g. Tilman 1997a, b, Symstad *et al.* 1998, Hector *et al.* 1999). Likewise the well known ambitious ecotron studies of Naeem (1994b, 1995) also provides convincing evidence for the linear hypothesis and niche complementarily. Naeem (1994b) found the consumption of CO_2 and plant biomass increased with species diversity, in microcosm treatments containing different species identity and diversity. However, where nine or more species were included in the microcosms, ecosystem processes did not increase, perhaps suggesting a form of the redundancy hypothesis. Furthermore long-term decomposition, nutrient retention and water retention showed no consistent pattern. Wardle *et al.* (1997b) is one of the most cited examples to provide evidence for the redundancy and idiosyncratic hypothesis. Wardle *et al.* (1997b) found that the ecosystem processes measured (rates of litter decomposition, litter nitrogen content, rates of nitrogen release from litter and the active microbial biomass present on the litter) did not increase with increasing leaf species diversity in litter bags. However, when within-functional group diversity of leaf litter was analysed there was evidence that some species of leaf were redundant with respect to ecosystem process. However as this was not consistent for every functional group little support for the rivet hypothesis was provided. It is important that conclusions regarding the relationship between diversity and ecosystem processes drawn from the studies examined above are interpreted with caution. They all use experimental designs ***that compare the difference between ecosystem processes at different levels of***

diversity; they are not correlative type designs. Additionally, the experimental design and statistical analyses may have confounded the conclusions of studies, a point discussed in more detail in the following section. Furthermore, the absence of a scale on the theorised relationships makes generalising the results of empirically studies to fit any one particular hypothesised relationship tenuous at best. Nevertheless the studies above highlight the difficulty in categorising the data from empirical investigations into a single theoretical hypothesis, if indeed such discrete trajectories exist. From just these few examples from the terrestrial literature it is clear that the mechanistic process underpinning these trajectories are not necessarily mutually exclusive, and may differ across species and system.

1.5 Experimental Studies

Many investigations have measured diversity and ecosystem process across natural diversity gradients, finding mainly a positive correlation, higher rates of ecosystem processes in areas or sites of higher diversity (see Schlutze and Mooney 1994, Loreau *et al.* 2001b, for examples and reviews in terrestrial systems and Huryn *et al.* 2000, Jonsson *et al.* 2001 for aquatic examples). Whilst they often provide useful information on community and assemblage structure, (and occasionally patterns of succession in diversity and ecosystem processes), the relative importance of co-variables and factors that differ with separate measures cannot be disentangled from diversity effects. Most experimental studies have manipulated diversity of species belonging to a single trophic level. This has been done by randomly allocating species from a regional pool to different diversity treatments and measuring the response of one or more ecosystem processes. Initially the majority of work came from grassland studies measuring productivity and occasionally nutrient fluxes (see Loreau *et al.* 2001b and Balvanera *et al.* 2006 for reviews). Since then a plethora of studies have investigated

the relationship between diversity and ecosystem processes in many systems, measuring a wide array of ecosystem process, and collectively using a relatively wide range of species; see Worm *et al.* (2006), and Emmerson *et al.* (2001) for marine examples, Covich *et al.* (2004) for marine and fresh water examples, Bell *et al.* (2005) for bacterial examples and Loreau *et al.* (2001b), Hooper *et al.* (2005) and Balvaneria *et al.* (2006) for terrestrial examples. Despite this trend, traditional terrestrial grassland manipulative studies still dominate the BDEF literature.

BDEF research has also expanided to include additional variable temporal and spatial factors. Evidence from this research suggests that processes observed at one scale or in one system often do not generalise to other scales or systems and may be context dependent (e.g. Risser 1995, Gaston 1996a, Beck 1997, Johnson *et al.* 1996, Huston 1997, Chapin *et al.*1998, Cardinale *et al.* 2004).

There has also been debate over the correct or most suitable level at which to measure diversity (see Gaston and Spicer 2004 for an overview). Petchey and Gaston (2002) and Petchey *et al.* (2004b) provide a convincing argument for the use of functional diversity, the number of different traits rather than species number, as mechanistic explanations behind the diversity ecosystem process relationship are dependent upon the distribution of species traits. Although Petchey *et al.* (2004b) provides an excellent example of how species may be categorised by functional differences in an unbiased manner, the success of such an approach will be largely dependent upon the information available on species traits. Unless it is known *a priori* which traits can potentially affect species' ability to undertake ecosystem functions, subtle trait differences between species, that can influence ecosystem processes, may be overlooked. This latter point is exemplified in studies that have found positive diversity effects on processing rates amongst species belonging to the same functional group (e.g. Jonsson and Malmqvist 2000, 2003a). Mechanistically, the relationship between

ecosystem processes and diversity is likely to be determined by the functional differences amongst the biota. However, considering that we are rarely in a position where detailed knowledge of all species traits are available using the lowest common measure of diversity that is easily measured may prevent underestimation of the value or role of diversity in maintaining ecosystem processes.

Despite the vast amount of studies and work in the BDEF field there is still no general consensus on the form of the relationship between diversity and ecosystem process, much less a widely accepted understanding of how ecosystem process will respond to reduced species diversity. Many recent meta-analyses, reviews and large-scale experimental studies conclude that diversity does affect ecosystem processes positively (e.g. Loreau *et al.* 2001b,c, Emmerson *et al.* 2001, Covich *et al.* 2004, Bell *et al.* 2005, Balvanera *et al.* 2006, Worm *et al.* 2006). However, the incongruity and discrepancies between these and previous older studies, suggest that the form of this relationship is far from universal. Furthermore, despite the ingenuity of previous BDEF studies, most have been heavily criticised in the interpretation, significance and generality of their results (Givnish 1994, Lawton 1994, Johnson *et al.* 1996, Huston 1997, Aarssen 1997, Huston and McBride 2001).

1.6 Importance of Segregating Species Identity, Diversity and Interactions

If, as is suggested, no universal trajectory between diversity and ecosystem process exists, the effect of species diversity on ecosystem processes will depend on the relative importance of species identity and interactions. Identifying species with large effects on ecosystem processes and species which interact positively with respect to ecosystem processes may help inform and prioritise management strategies help us understand and predict the effects of reduced species diversity on ecosystem processes. The link between diversity and ecosystem processes, inferred from previous studies,

may have been confounded by the inability of many studies to segregate the effects of species identity from diversity and to empirically quantify the effects of species interactions. In experimental studies this has been attributed to the design and interpretation of results. For example, when randomly assigning species from a species pool to diversity treatments, an increase in ecosystem process with diversity may depend upon the "chance" inclusion of a species with a disproportionally high effect; the sampling effect (Huston 1997, Aarssen 1997). The sampling effect has also been expanded to include species interactions; the chance of high diversity treatments including species that interact positively is greater than that of low diversity treatments (Huston and McBride 2001). The failure to segregate the effects of species identity from that of diversity may in part explain the divergent results of previous studies. Considering that many mechanistic explanations behind the diversity-ecosystem process relationship are based on species trait distribution (species identity). Numerous investigations have argued that species identity combination rather than diversity *per se* influences ecological processes (e.g. Aarssen 1997, Hooper and Vitousek 1997, Huston 1997, Tilman *et al.* 1997a, Wardle *et al.* 1997a, Chapin *et al.* 1998, Symstad *et al.* 1998, Ruesink and Srivastava 2001, Jonsson and Malmqvist 2003b). To illustrate this, (a) Symstad *et al.* (1998) found plant functional group diversity to have a positive, negative or negligible effect on nutrient retention, depending on species identity, (b) Ruesink and Srivastava (2001) found leaf breakdown to be dependent on the identity of the stream detritivore removed and (c) Jonsson and Malmqvist (2003b) found the relationship between diversity and processing rates in aquatic invertebrates to be directly related to both the species identity and interactions between these species.

Species interactions have similarly been overlooked, despite their recognition as important factors in shaping plant assemblages (e.g. Crawley 1997, Callaway 1995, Callaway and Walker 1997, Stachowicz 2001, Bruno *et al.* 2003) intertidal assemblages

(e.g. Bertness, 1989, Bertness and Leonard 1997) and the numerous examples of synergisms in nature. Species interactions have been central in population and community ecology research, in understanding the underlying patterns of species distribution through species co-existence or competitive exclusion. In general, species interactions have been quantified, inferred or modelled based on species life history, population and community dynamics (see Raffaelli and Hall 1996, Laska and Wootton 1998, Wootton and Emmerson 2005 Woodward *et al.* 2005b). Few studies have addressed this phenomenon in the context of other biotic interactions and ecosystem processes (Bronstein 1994, Stachowicz 2001, Bruno *et al.* 2003). Even in the theoretical BDEF literature the role of competition and facilitation has only been very briefly considered (Section 1.4). Theoretically resource processing may increase with the number of species due to species interactions. If it is advantageous to complete a life-cycle stage before conspecifics, species may increase processing rates, to accelerate ontogeny. Species may also increase the palatability of a food source for conspecifics *via* their own feeding. Alternatively, species sharing a food source may allocate time to protecting the resource or to antagonistic behaviour towards other species thus reducing time available to process the resource. Thus the balance between intraspecific and interspecific competition and interference could determine the resource processing-diversity relationship. This latter example may apply to species competing for other resources such as mates and refuge, if the time spent undertaking ecosystem processes is reduced due to antagonistic behaviour.

Although initial work on diversity ecosystem processes from intercropping studies demonstrated how positive species interactions can positively enhance yield production (see Vandermeer 1989 for examples), species interactions, in the context of positive diversity-ecosystem processes mechanisms are rarely investigated. When experimental designs have allowed the identification of species interactions, positive

interactions with respect to ecosystem processes have been found, e.g. in grassland studies (Loreau *et al.* 2001b), Fungi assemblages (Tiunov and Scheu 2005) and decomposer assemblages, (Cardinale *et al.* 2002, Cardinale and Palmer 2002, Jonsson and Malmqvist 2000, 2003b).

The balance between negative and positive species interactions can affect ecosystem processes. In order to untangle the effects of positive and negative species interactions on ecosystem processes, investigations need to compare ecosystem processes predicted based on the additive affects of species in monocultures, to those observed in multi-species treatments or assemblages. This approach was initially proposed to segregate the niche differentiation effect from the sampling effect (Loreau 1998, 2001a Hector 1998, Emmerson and Raffaelli 2000). The design of most BDEF studies has not permitted this type of analysis. Although terrestrial grassland studies sometimes incorporate measures of overyielding using this type of design, species were often allocated from a random pool and species identity and diversity could not be discerned (see examples in Loreau *et al.* 2001b). Jonsson and Malmqvist (2003a) gave one of the best examples, where diversity treatments were constructed using every possible species combination and species interaction effects was measured. They found that processing rates increased, decreased or were unchanged with diversity. Overall it was the balance of species' negative, positive and additive interactions that determined the effect of diversity on processing rates was significant and positive or negative. Whilst the balance of negative and positive species interactions combined with species individual effects will clearly determine the resultant ecosystem process, how prevalent positive species interactions are relative to negative species interactions cannot be concluded from such a limited body of work.

Interpreting the importance of interspecific and intraspecific interactions in enhancing ecosystem processes is further confounded by the density and relative density

of species in different diversity treatments. There are limitations in using substitutive and additive designs to assess species interactions (Underwood 1978, 1984, 1986, Benedetti-Cecchi 2004). In substitutive or replacement designs total species density is kept constant as the number of different species (diversity) of a treatment changes. Thus, the relative density of individual species changes with diversity. Considering a simplistic situation where species interactions are the only mechanism to influence ecosystem processes, if ecosystem processes increased with diversity it could be due to either, intraspecific competitive release, or, interspecific facilitation. Substitutive designs will not allow the segregation of these two separate mechanisms. In additive designs, the relative density of each species is kept constant so that total density will increase with diversity. Again considering a simplistic situation where species interactions are the only mechanism to influence ecosystem processes, if ecosystem processes increase with diversity it could be due to interspecific facilitation, or to total species-density effects. Using modelling approaches where density-dependent effects on ecosystem processes were assumed and diversity treatments were constructed using random allocation of species identity at each diversity level, Benedetti-Cecchi (2004) found large increases in the probability of increasing Type I errors using only one of these designs (either additive or substitutive). Using a previously proposed (Underwood 1978, 1984) factorial design that involved setting up diversity treatments using both additive and substitutive experimental designs (so that density and diversity effects and interactions can be segregated) reduced the probability of Type I errors occurring, when analysing the effect of diversity on ecosystem processes (Benedetti-Cecchi 2004). Unfortunately logistical constraints may limit the number of replicas and it may not always be possible to incorporate both types of design into BDEF experiments. As such it is vital that the limitations of whichever design is used are considered when making inferences of the possible mechanisms behind observed diversity-ecosystem process

relationships. *A priori* knowledge of the system and species used will enable a clearer interpretation of the relative importance of diversity and density effects.

In conclusion, if the relationship between diversity and ecosystem process is species and system-specific, and, the trajectory reliant on species identity and their interactions, then individual species' natural history information (how these species contribute to ecosystem process and how these species interact with other members of an assemblage) is vital if the consequence of reduced diversity on ecosystem processes is to be understood.

1.7 Importance of Establishing Mechanisms

Despite the fact that the rationale and theoretical underpinnings of the relationship between diversity and ecosystem process depend on mechanisms which collectively operate between species, and between species and ecosystem processes, the mechanisms themselves are notably understudied empirically. And yet identifying and understanding such mechanisms is essential in interpreting the results of all BDEF experiments (Aarssen 1997, Huston 1997, Loreau 1998, Wardle 1999, Hector 1998, Emmerson and Raffaelli 2000, Deutschman 2001, Loreau and Hector 2001), and could provide information, that would be key to understanding the inconsistencies between species diversity-ecosystem process between and within experiments (Schlapfer and Schmid 1999, Schwartz *et al.* 2000, Loreau *et al.* 2001b). However, the emphasis in BDEF research has been in the search for a universal trajectory between diversity and ecosystem processes. The precise mechanism by which processes such as niche differentiation, negative and positive species interactions operate is rarely empirically investigated (Emmerson and Raffaelli 2000, Petchey 2003). Understanding how positive, negative or additive diversity-ecosystem processing mechanisms operate will surely enable inferences on the generality of such relationships and may even permit

predictions on where and when such processes may occur. With respect to conservation effort, identifying species and systems where positive interactions are present is of huge importance as the loss of species in these systems may result in a reduction of ecosystem services below that predicted from species-additive effects alone.

1.8 Importance of Incorporating Multi-Trophic Interactions

Another facet of BEDF research that remains relatively under-represented in the literature is the effect of reduced species loss in multi-trophic systems. Few real assemblages are comprised of single trophic levels. Food web research has highlighted the importance of trophic interactions in structuring communities, controlling population dynamics and determining stability (Raffaelli and Hall 1996, Laska and Wootton 1998, Berlow *et al.* 1999, 2004 and references therein). Both modelling and theoretical studies have generally concluded that the distribution of interactions strengths towards weaker interactions, promotes stability in, real (Laska and Emmerson 1998, deRuiter *et al.* 1995, Roxburgh and Wilson 2000, McCann *et al.* 1998) and model systems (McCann *et al.* 1998, deRuiter *et al.* 1995, Roxburg and Wilson 2000, although see Kokkoris *et al.* 2002).

A considerable amount of work investigating trophic cascades has either shown directly, or provided anecdotal evidence on, how species removal may (directly and indirectly) affect the remaining assemblage species persistence and abundance across trophic levels (see Paine 1980, Carpenter *et al.* 1985, for terrestrial examples, Estes and Palmisano 1974, Estes and Duggins 1995, Estes *et al.* 1998 for marine examples and Carpenter *et al.* 1987, Power 1990, Brett and Goldman 1996 for freshwater examples). Through trophic connectivity, loss of species can directly influence energy flow or affect species (at different trophic levels) that are responsible for controlling the ecosystem processes of interest. Further emphases on the importance of incorporating

multiple trophic levels into BDEF research comes from the well documented skew in extinction vulnerability towards species at higher trophic levels (e.g. Duffy 2003). In previous BDEF studies, species which are not directly responsible for resource processing, productivity or uptake, have been excluded from investigations (Duffy 2003) yet arguably these species are not at the greatest risk of extinction.

If realistic predictions on how reductions in diversity will affect ecosystem process in real systems are to be made, then incorporating both intra- and inter-trophic interactions into BDEF studies is imperative.

Difficulties associated with conducting and interpreting the results of experimental manipulative studies investigating the loss of species diversity in multi-trophic systems has severely limited research effort in this area. Currently most experimental work investigating the effects of species diversity in multi-trophic systems is confined to microbial manipulative studies (e.g. Carpenter and Kitchell 1993, McGrady-Steed *et al.* 1997, Naeem and Li 1998, Raffaelli *et al.* 2002; although see Loreau *et al.* 2001b, Cardinale *et al.* 2006). In microbial mesocosm experiments (Carpenter and Kitchell 1993, Schindler *et al.* 1997, Cardinale *et al.* 2002, Raffaelli *et al.* 2002, Naeem and Li 1998), and pond assemblage manipulations (Downing and Leibold 2002) processing rates were seen to increase, decrease, stay the same, or follow more complex nonlinear patterns dependent on community composition, trophic structure and consumer diversity. In experimental manipulations of multi-trophic diversity there are so many variables, direct and indirect interactions, that interpreting the results of these studies is both difficult and ambiguous.

It can be concluded therefore that, owing to the practical constraints and difficulties in interpreting diversity affects on ecosystem processes in multi-trophic systems, new approaches are required if the effect of reduced diversity in real assemblages is to be assessed.

1.9 Alternative Approaches to Incorporating Multi-trophic Interactions

Using theoretical and empirical evidence from the field of food-web ecology that has concentrated on trophic interactions seems an intuitive starting point if we wish to incorporate multi-trophic interactions into BDEF research. This is not a novel concept (e.g. Brown and Gillooly 2003, Brown *et al.* 2004, Ives *et al.* 2005). However, logistically combining two fields with traditionally very disparate aims is not a trivial task. Food-web ecology has traditionally focused on the number and strength of trophic links in assemblages, whereas BDEF research has focused on the effects of diversity within a single trophic level on ecosystem processes. One recent advance in food-web ecology that may prove to be fruitful in predicting the effects of reduced diversity on ecosystem processes is that of metabolic ecology (Brown *et al.* 2004, Woodward *et al.* 2005b). Although far from a new concept (see reviews in Peters 1983, Schmidt-Nelson 1984), renewed interest in metabolic ecology has arisen from the work of Brown and colleagues (2004) who collated a vast amount of data and advocated the use of allometric scaling laws and body size to quantify trophic links as,

"...species body size may provide a relatively simple means of encapsulating and condensing a large amount of biological information embedded within an ecological network"

- (Brown *et al.* 2004).

Thus, using simple and tractable surrogate measures of interaction strength, such as body size, the trophic links in an assemblage may be quantified, and thus the energy flow and potentially ecosystem processes predicted. Although body size has been shown to be an important factor in determining predator consumption of prey in empirical, field and laboratory exclusion experiments (Eklov and Werner 2000, Hulot *et al.* 2000, Sala and Graham 2002, Ovadia and Schmitz 2002) and ingestion rate has been seen to correlate with body size (Farlow 1979, Cammen 1980), there are only a handful of cases that have empirically quantified predator: prey body size and interaction strength. Emmerson *et al.* (2005) confirmed that there were general relationships

between interaction strength and the ratio of predator: prey body mass based on allometric scaling and species trophic distributions based on empirical measures of these relationships in the Broadstone stream food web. Wootton and Emmerson (2005) combined the results of three previous studies and found good agreement between body size and interaction strength, although the significance of the relationship was not tested. The only empirical study to relate the predator and prey body size ratio to that predicted by metabolic theory (Emmerson and Raffaelli 2004) provided mixed results on the usefulness of body size as a surrogate measure. Species identity explained more of the variability in interaction strength than the relative predator and prey body sizes, although for some groups of organisms the regression between predator: prey body size and interaction strength was significant.

Despite the importance of quantifying the effects of reduced diversity on ecosystem processes in multi-trophic systems there have been no studies to date that have empirically evaluated the use of body size as a surrogate measure for trophic interaction strength and, related this to predicted effects on ecosystem processes. If species body size can be used as a surrogate for metabolic capacity, and species metabolic capacity determines interaction strength between trophically opposed species and between species and a resource, then the effects of reduced diversity on ecosystem process may be predicted by simple measures of species body sizes and trophic levels within an assemblage. Although this methodology provides an attractive alternative to incorporating multiple-trophic levels in traditional BDEF experiments the underlying assumptions, have not been tested empirically. Furthermore it is important that the plethora of information pertaining to the importance of non-trophic diversity, identity and interactions in affecting ecosystem process are not overlooked when predicting the effects of reduced diversity on ecosystem processes.

Before such approaches are widely employed to make inferences on how the biota influences and how reduced diversity may affect ecosystem process, it is vital that the assumptions underlying metabolic scaling laws are empirically tested. Furthermore it is imperative that the relative effects of non-trophic species interactions on ecosystem processes are determined in real multi-trophic systems.

1.10 Conclusions and Thesis Aim and Objectives

To date, no universal trajectory between diversity and ecosystem processes has been identified. The relationship, whilst in the main positive, appears to be species and system specific. The incongruity and discrepancies between previous studies may be due, in part, to the experimental designs used; specifically the failure to discern the effects of species identity and interactions from that of diversity. If there is no universal trajectory between diversity and ecosystem process then identifying species and species interactions which have large effects on ecosystem processes is paramount so that the effects of reduced diversity on energy matter and material cycling can be assessed. Incorporating multi-trophic levels into BDEF research is vital if predictions of the relationship between diversity and ecosystem process are to be made in real assemblages. New approaches are desperately needed to overcome the logistical and interpretative complications involved in empirically testing the BDEF relationship across multiple-trophic levels. The incorporation of food-web ecology and metabolic ecology may provide a means through which this can be achieved, although it currently lacks empirical testing.

Consequently this thesis aims to investigate the role of species identity, diversity, trophic and non-trophic species interactions on ecosystem processes using the marine strandline as a model system. The rationale and background behind the use of

the strandline as the model system, and the choice of strandline species is the subject of the following chapter (Chapter 2) and will not be repeated here.

Thus the objectives of this thesis are to:

1. Investigate the effects of species identity, diversity and species interactions on decomposition in four, co-occurring strandline detritivores (Chapter 3).

2. Investigate empirically the use of body size as a surrogate measure of interaction strength and assess the use of body size in a predictive capacity to estimate ecosystem processes by manipulating the size of four predator strandline beetles, and their kelp fly prey, whilst measuring kelp decomposition (Chapter 4).

3. Investigate the effects of a predator on diversity-ecosystem processing relationships, and the influence of a predator on the connection between ecosystem processes and detritivore identity and diversity, using three strandline larvae, and measuring decomposition across treatments of every possible species combination with and without a natural predator (Chapter 5).

CHAPTER 2: THE STRANDLINE AS A MODEL SYSTEM

2.1 Chapter Aim and Outline

The aims of this chapter are to 1) introduce strandline systems, 2) survey, describe and compare with previous strandline surveys the strandline system at Wembury, the site which provided all of the fauna and algae used in the experimental manipulations presented in Chapters 3, 4 and 5 of this thesis and to 3) to present the rationale underlying the choice of ecosystem process, decomposition and the choice of species for construction of the manipulation experiments outlined in Section 1.10.

This will be done using data from a preliminary survey of one particular strandline at Wembury First Beach, Devon, UK (48.3°N, 50.4°E) and comparing the strandline at Wembury with existing data on other strandlines in terms of their biotic and abiotic nature. The criteria by which we identify a good model system will be listed and used to show why the strandline as a habitat, and decomposition as one of its key ecosystem processes, is ideal for constructing experimental manipulations to conduct biodiversity and ecosystem process investigations. Finally a brief synopsis on decomposition in the strandline, and the natural history of the species used in subsequent chapters of this thesis will be presented.

2.2 Introduction to Strandline Systems

2.2.1 Definition of a Strandline

The term 'strandline' is often used synonymously with wrack bed and drift line. In many sandy beach classification systems the strandline is identified as the level of mean high water (MHW) the end of the zone of drying (Salvat 1964) or the seaward edge of the talitrid zone (Dahl 1952). Backlund (1945) defined 'wrack' as dead and

decayed seaweed once grown submerged in the sea now washed-up on the beach. In this study the strandline refers to the area on a beach where wrack, drift wood and inert material of marine and/or terrestrial origin is deposited.

2.2.2 Distribution and Composition

Strandlines are present on all but the most exposed shores. The type and form of the strandline differ globally as the accumulation of material is dependent on the interaction between near-shore production and physical factors. Composition depends fundamentally on the type of near-shore production. Strandline vegetation can consist primarily of kelp and fucoids, but may extend to all kinds of algae and even freshwater angiosperms, depending on the region. Laminarian kelps have a worldwide distribution in cold waters. They are an important component of strandlines forming on beaches on the Atlantic seaboard, China, Japan, New Zealand, Australia, South Africa, north-eastern Pacific, Peru, Chile and Argentina (Colombini and Chelazzi 2003), although wrack composition may differ [e.g. bull kelp in the sub Antarctic (Smith and Bayliss-Smith 1998) and the giant kelp in the north-eastern Pacific (Dayton 1985, Kirkman and Kendrick 1997)]. Seagrasses also have a worldwide distribution and, as such, can form extensive wrack accumulations, where they dominate near-shore production, in areas as geographically separated as the Seychelles (Lenanton *et al.* 1982, Brown and McLachlan 1990), East Australia (Rossi and Underwood 2002) and the southern Baltic (Persson 1999).

Physical factors relating to water motion vary both temporally and spatially. Thus the inputs of material to the strandline may also vary on temporal and spatial scales (Backlund 1945, Muir 1977, Koop and Field 1980, Koop *et al.* 1983, Stenton-Dozey and Griffiths 1983, Brown and McLachlan1990, Orr *et al.* 2005). Temporal changes in wrack volume have been noted as seaweed cast up on the shore settles

compacts and begins to decompose (Dobson 1974). The aspect of the beach will also affect the balance of wrack deposition and removal. Deposition is generally greater on reflective beaches that lack a surf zone, and have low near-shore primary production, compared to that on dissipative beaches (McLachlan 1983, Brown and McLachlan 1990).

Tidal movements determine the existence, persistence and placement of strandlines (Backlund 1945, Dobson 1974, Messana *et al.* 1977, Griffiths and Stenton-Dozey 1981, Ochieng and Erftemeijer 1999, Colombini *et al.* 2000). Strandlines have been observed to follow patterns of accumulation removal; according to tidal type (spring or neap) (Messana *et al.* 1977, Ochieng and Erftemeijer 1999) and within a tidal cycle (Griffiths and Stenton-Dozey 1981, Colombini *et al.* 2000). In contrast, the formation of extensive and permanent wrack beds with associated depth stratification has been found in relatively sheltered areas where tidal influence is minimal (e.g. Backlund 1945).

Other site-specific, physical factors may also interact with tidal cycles to alter the ephemeral nature of strandlines (Hodge and Arthur 1997, Koop *et al.* 1982a).

Wrack deposition may also change seasonally. Wrack deposition has been seen to increase either after storms (Crafford and Scholtz 1987, Balestri *et al.* 2006) or in seasons when weather conditions are more severe (Ochieng and Erftemeijer 1999, Koop and Field 1980, Stenton-Dozey and Griffiths 1983, Marsden 1991). Although storms may deposit a greater amount of material; 12% kelp biomass can break free in storms (Griffins and Stenton-Dozey 1981, Jarman and Carter 1981) and 2.5% of this amount can be deposited annually on beaches (Koop *et al.* 1982a), storms may also remove the strandline permanently.

On a smaller wrack can accumulate on different sectors of a beach (Koop and Field 1980, Hansen 1984) or adjacent to rocky protrusions (Ochieng and Erftemeijer

1999). With the exception of extensive permanent strandlines, there is probably much spatial variation within a site that is not documented in the literature as studies generally sample only the wrack deposits.

Wrack can be evenly distributed or deposited along one or more drift lines, usually at high water springs, also in bands, or in a band, down to the level of the most recent high tide (Marsden 1991, Ochieng and Erftemeijer 1999) and/or in patches from extreme high water, to mean tide levels (Marsden 1991, Colombini *et al.* 2000). The vertical elevation of the strandline has been seen to change following the high water mark through a neap-spring tidal cycle (Messana *et al.* 1977, Stenton-Dozey and Griffiths 1983, Colombini *et al.* 2000).

2.2.3 Physical and Chemical Characteristics of the Strandline

The physical and chemical characteristics of a strandline depend primarily on the type and amount of wrack material and its decomposition; decomposition being dependent on a variety of environmental factors, discussed in Section 2.5. Thus the physical and chemical nature of the strandline is complex and multifaceted (see Figure 2.1).

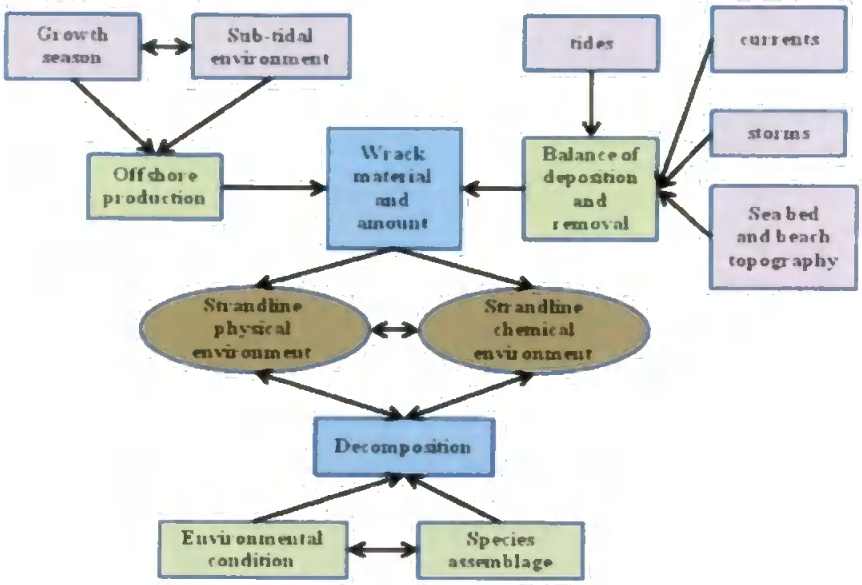

Figure 2.1 Schematic showing the key factors influencing the physical and chemical strandline environment. Arrows represent the direction of an influence.

2.2.3.1 Physical Characteristics

Backlund (1945) classified the physical characteristic of marine wrack beds recognising seven different groupings, all of which or only some of which may be present on a beach at any point in time and space;

Wrack string-small accumulations of wrack less than 15 cm wide and 15 cm deep, they do not decay and retain little moisture so become dry in dry weather.

Wrack flakes-thin carpet-like accumulations of wrack less than 5 cm deep but can be of any width, here decomposition can be rapid.

Wrack banks-large accumulations of wrack more than 15 cm wide they are moist at the bottom and can produce 'slime' through rapid decomposition.

Wrack banks often have distinct layers; the *surface layer* dries easily and retains its shape as decomposition is slow. Depth of the surface layer can vary from 5-12 cm. The *deeper layers* are always moist and rapid decomposition transforms algae to an

unidentifiable state covered with slime. These two layers are separated by the *border horizon* which itself never exceeds 1 cm and is often much thinner.

Wrack aevja- Wrack accumulated in bay or lagoons.

2.2.3.2 Chemical Characteristics

The chemical environment in the wrack bed will depend on the marine algae species present and their state of decomposition. Different marine algae species have different chemical compositions, and within a species this may also change seasonally (Backlund 1945, Goncharova *et al.* 2004). Decomposition and the type of decomposition will release, or transform, the organic and inorganic compounds in the algae thus altering the humidity, gaseous environment, water availability and pH of the strandline environment. Thus the chemical environment in the strandline is also dependent on the ability of strandline species to decompose the wrack material, and the composition of the wrack material. As wrack material decomposes, its physical form alters and changes in structure on both a macro- and microscopic scale.

The volume of wrack material may also influence the type of decomposition. If large wrack beds are formed, decomposition may be aerobic in surface layers and anaerobic in compacted bottom layers. The by-products of these two layers will differ (Backlund 1945). Although it is difficult to disentangle cause and effect, decomposition may alter depending on the biota, e.g. high abundances of detritivores will decrease wrack volume and increase surface area for microbiological decomposition, wrack deposits with fly larvae have been cited as being anaerobic (Philips and Arthur 1994) and fungal growth on wrack was not observed in the presence of *Orchestia gammarellus* (Backlund 1945).

Despite its complex and multifaceted nature there are some generalisations and characteristics that apply to all strandline habitats. Water contained in, and trapped

between, marine debris will create a more humid environment compared with that of the surrounding sandy beach. Owing to the specific heat capacity of water and the heat generating process of decomposition, accumulations of marine debris will act to stabilise temperature fluctuations within in a patch of wrack (Backlund 1945, Moore and Francis 1985, Crafford and Scholtz 1987).

2.2.4 Assemblages

The intertidal zone of sandy beaches lack extensive vegitation so wrack deposits alongside nutrient input from the adjacent pelagic zone may provide the main source of organic enrichment (McLachlan 1985). Additionally as sandy beaches are arguably homogeneous environments (McLachlan 1985) the physical disturbance caused by wrack deposits, and subsequent heterogeneity in physical and chemical habitat, may all increase overall sandy beach species diversity (in terms of the number of different species) and abundance. Wrack material is often cited as an environment providing food and refuge to a wide array of terrestrial, semi-terrestrial and occasionally aquatic animals (Backlund 1945, McLachlan and Erasmus 1983, McGywnne *et al.* 1988, Inglis 1989, Colombini *et al.* 2000 and references therein). Many animals have also been observed directly eating wrack deposits (e.g. Griffiths and Stenton-Dozey 1981, Koop *et al.* 1982a and Griffiths *et al.* 1983 for amphipods, Chown 1996 for dipteran larvae) or prey on animals that consume marine plants deposits (e.g. Backlund 1945, E. McAfee *pers. comm.* for some beetles, Ugolini 1997, Laffaille *et al.* 2001, 2006, Arcas 2004, Hample *et al.* 2005, Minderman *et al.* 2006 for predatory fish and birds). Additionally many studies have shown a high correlation between species diversity and abundance and wrack deposits (e.g. McLachlan 1980, 1985, Bigot 1970, Polis and Hurd 1996, Vilas 1986, Colombini and Chelazzi 2003). Finally wrack removal through beach

cleaning has been seen to reduce species diversity and abundance (e.g. Smith 2003, Schlacher *et al.* 2007 and references therein).

There are few studies where the strandline assemblage has been quantified in its entirety. However, strandline assemblages are generally thought to be comprised of a few eucoenic species (species indigenous to the strandline) in high abundances, with a lower abundance and frequency of occurrence for many tychocoenic species (species which occur and are adapted to strandline conditions but also thrive in other biotopes) or xenocoenic species (species which cannot live and/or reproduce continually in the biotope) (Backlund 1945, Bebenhani and Croker 1982, Griffiths and Stenton-Dozey 1981, Inglis 1989, Colombini *et al.* 2000, Jedrezejcazk 2002).

The opportunist Order Amphipoda has been found repeatedly to dominate strandline assemblages (Dugan *et al.* 2003, Colombini *et al.* 2000, Bebenhani and Croker 1982, Griffith and Stenton-Dozey 1981, Inglis 1989, Smith 2003, Backlund 1945). The relative abundance of Diptera species can be very variable. They can be important components of strandline assemblages in terms of abundance (Stenton-Dozey and Griffiths 1980, 1981, Inglis 1989, Philips and Arthur 1994, Philips *et al.* 1995, Hodge and Arthur 1997). Conversely Diptera may be absent at some sites (Colombini *et al.* 2000, Figure 2.4e). Similar to dipterans, the abundance of coleopterans in strandline assemblages differs between studies (Inglis 1989, Jedrzejczak 2002, Colombini 2000). Enchytraeids and other oligochaetes are considered important strandline taxa in terms of abundance (Backlund 1945, Behbehani and Croker 1982); however they are often not counted in samples. The contribution of meiofauna and microbes to strandline assemblages is poorly known, although on some exposed beaches dry meiofaunal mass has been found to exceed that of macrofauna (McLachlan 1985). There has been a little work on the spatial and temporal changes in strandline assemblages; although in general studies have investigated the change in abundance of only a few taxa. In terms of spatial

distribution many strandline species have been observed to migrate with the tide (Colombini *et al.* 1996, 2000, 2002), and/or follow diurnal nocturnal migration and activity patterns (for amphipods see Marsden 1991, Jaramillo *et al.* 2003; for coleopterans and isopods see Koop 1982, Colombini *et al.* 2005; for other arthropods see Colombini *et al.* 1996, 2005, Aloia *et al.* 1999, Jaramillo *et al.* 2003). Microclimatic conditions and prey activity may also determine strandline assemblage composition (e.g. Philips *et al.* 1995 Colombini *et al.* 2002). Furthermore the diversity and abundance of the strandline assemblage may alter with the size of the wrack patch (Olabarria *et al.* 2007) or the temperature and depth of wrack patch (Phillips *et al.* 1995).

Most documented patterns of strandline assemblages have been related to the temporal, usually tidal, cycle of wrack accumulation and removal. Talitrid amphipods and many species of kelp-fly larvae are often recorded as the first opportunistic colonisers of newly formed strandlines (Griffiths and Stenton-Dozey 1981, Inglis 1989, Colombini *et al.* 2000, Jedrzejczak 2002a, b). However changes in dipteran abundance and dipteral life stage may be correlated to the Diptera life-cycle (Egglishaw 1960, Dobson 1974, Inglis 1989, Hodge and Arthur 1997, Jedrzejczak 2002b). Where coleopterans have been included in analysis of strandline communities over time they generally arrived and increased in abundance a days after the initial wrack deposition (Inglis 1989, Griffiths and Stenton-Dozey 1981, Colombini *et al.* 2000).

2.3 Field Studies of Wembury Strandline

2.3.1 Introduction

The present study will attempt to quantify the strandline assemblage and physical properties of the strandline habitat at Wembury, as this strandline provided all

of the species used in the experimental manipulations in subsequent chapters of thesis. As the strandline is thought to change temporally (Section 2.2) the present study will quantify the strandline assemblage and physical habitat in different seasons and within a season over the monthly tidal cycle. The correlation between the physical properties of the strandline environment and the strandline assemblage will be investigated in an attempt to discern any underlying factors governing the faunas occurrence and distribution.

2.3.1 Materials and Methods

2.3.1.1 Collection of Animal Material, Wrack and Sediment

All samples were taken from Wembury First Beach, Devon, UK (48.3°N, 50.4°E). The high tide strandline on Wembury alone was selected for study due to time limitations and the absence of an alternative persistent strandline. The high tide strandline at Wembury was fairly persistent throughout the year with the exception of October - December 2005.

To measure any seasonal changes in the strandline assemblage the site was visited in winter, spring, summer and autumn, however as there was no visible strandline in October-November 2005 samples were only taken in winter (16.02.05-28.02.05), spring (02.06.05) and summer (19.08.05-31.05.08). Unfortunately due to time limitations replicate samples in each season from subsequent years could not be made. To quantify any temporal change in the strandline assemblage that may occur over the tidal cycle samples were taken a day after the highest tide in that month then every other day, for two weeks corresponding to the low tide in winter (16.02.05-28.02.05) and summer (19.08.05-31.05.08). Initial plans to use a randomised block design to quantify spatial variability in the strandline were abandoned as the strandline

did not always expand across the beach in its entirety. On each sampling day, five sampling sites were allocated using a random numbers table (Zar 1999) to select co-ordinates. If the tide strandline did not extend across the whole beach and the first set of co-ordinates fell on a patch of beach with out wrack coverage the random numbers table would be used to select a second set of co-ordinates, and this process repeated until the co-ordinates coincided with the wrack.

2.3.1.2 Strandline Abiotic

At each location temperature and humidity measures were taken from above the wrack and below the wrack above the sediment using a hygrometer (HANNA HI-8564). The depth of the wrack was measured using a meter ruler and the length and width of the wrack patch was measured using a 100m ruler, to estimate the patch area.

In the laboratory pH paper was used on the surface of the wrack to measure pH before the wrack and sediment from each core were placed in the Tulgren funnels.

2.3.1.3 Strandline Biota

At each sample site cores (diam. = 0.25m) were pushed into the sediment to a depth of 20 cm, if the core did not push easily into the wrack secateurs were used to cut around the outside circumference of the core before the core was pushed into the wrack and sediment. All material was carefully placed in sealed plastic bags. The bags were transported to the laboratory within a few hours of collection and fauna were extracted in the laboratory using a well-established Tulgren-funnel technique (Backlund 1945). The Tulgren-funnels used 100W light bulbs and a 1cm sieve used. All extracted material was preserved in industrial methalated spirit (IMS) 75% and identified where possible to species level. Owing to time limitations Acarina, Annelida, Nematoda and Coleptera larvae were not identified to species level.

2.3.1.4 Statistics

All statistics were undertaken using PRIMER Version 6.2.

Multi-dimensional scaling (MDS) plots were used to graphically represent the similarity between strandline samples in terms of the strandline biota (diversity and abundance) and separately abiotic data (Wrack patch size, temperature, depth, and humidity).

The similarity between the strandline abundance and diversity, from different sample seasons; winter, spring and winter was analysed using an ANOSIM Global test of similarity. A pair-wise test of similarity (ANOSIM) was then used between replicas of the strandline assemblage from each season to assess between which if any seasons the strandline assemblage differed. Within each season a separate ANOSIM, Global test of similarity was used to test for significant differences between the strandline assemblage from samples taken on different days.

A BIOENV analysis was used to analyse which if any of the measured wrack physical characteristics best correlated to the biotic assemblage.

The strandline assemblage was measure in terms of species abundance and diversity and the raw data was 4^{th} root transformed; this transformation was chosen as this down-weights the effect of abundant species so that the contributions of rarer strandline species can be assessed. A Bray-Curtis similarity matrix used as this is most appropriate measure of similarity for biotic data (Clark *et al* 2006).

The physical properties of the strandline samples, wrack patch size, depth, temperature and humidity was 4^{th} root transformed, as this down-weights the effects of large values (e.g. humidity) so that the contribution of all physical characteristics can be better assessed.

A Euclidian similarity matrix used as this is most appropriate measure of similarity for abiotic data (Clark *et al* 2006).

2.3.2 Results

2.3.2.1 Observations

After a month of easterly winds the entire beach was devoid of a strandline for the whole of October - December 2005. The position of the material also altered; extensive wrack banks formed at the west end of the beach, due to the dominance of south-westerly winds and the rock protrusion off-shore (Mewstone), but also occasionally shifted to the east end of the beach. A week or so after particularly high tides in the summer months the high tide strandline (which remained a relatively permanent feature) was accompanied by extensive wrack banks on the mid shore and sometime aevja (see Section 2.2.3.1 for a definition) at the low shore. No clear monthly or two weekly cycles in strandline persistence were observed between the years of 2001-2002 and 2003-2007 (Marsh *pers. obs.*), there were often fresh deposits of material after particularly high tides.

The Tulgren funnels were not as effective as previously thought, and despite best efforts some animals (mainly from the orders Diptera and Coleptera) escaped. Furthermore the use of the tulgren funnels resulted in a number of Annelida and possibly Nematoda worms becoming dried out and thus unidentifiable. Similarly due to the dry and tough nature of the wrack the core did not always easily push into the strandline and sicotters were used to cut around the outline of the core to aid sample collection, this and the core itself caused a deal of disturbance in at the sample site and may have resulted in the "escape" of mobile animals, especially Diptera, Coleoptera, Amphipoda and Araneae. Furthermore pitfall traps generally contained a greater density of coleopteran and Amphipoda and in the case of the former a higher diversity per area. This suggests that the coring method used, whilst initially thought to be quantitative may not measure the true diversity of the strandline.

2.3.2.2 Abiotic Characteristics of the Strandline at Wembury.

On Wembury Beach, *Fucus* spp. and *Laminaria* spp. dominated the strandline deposits (*pers. obs.*).

pH could not be measured using pH paper as the wrack was too dry. Alternative measurements of pH that involved measuring the internal pH of the wrack algae were not taken as pH measurements were only used to ascertain the environment that the strandline fauna were exposed to.

Wrack patch size was extremely variable in all seasons, and between samples on all days. In general wrack patch size was greatest in spring (mean $36.3m^2 \pm 14.3\ m^2$ s.e.) then summer (mean $16.0m^2 \pm 5.1\ m^2$ s.e.) being smallest in winter (mean $2.7m^2 \pm 0.8\ m^2$ s.e.).

Wrack depth was similar between seasons, but differed between sample sites and days. Overall the average depth of the wrack was mean 5.1cm ± 0.2 cm s.e. Maximum recorded depth was 11cm, one site in winter, 18.02.05, and minimum 2 cm at a different site on the same sampling day (18.02.05).

The humidity in the air was very variable within seasons, but on average was lower in winter (mean 53.8% ± 4.0 s.e.) than summer (mean 70.2% ± 3.7 s.e.) and was highest in spring (98.6% ± 1.4 s.e.) (Figure 2.2). Humidity within the wrack deposits was higher than that of the surrounding air and with the exception of winter was less variable than the humidity of the surrounding air; winter mean 73.2% ± 4.0 s.e., summer mean 95.7 ± 1.9 s.e., and mean 100% ± 0.0 s.e., in spring. Temperature outside the wrack deposits was lower in winter (mean 7.5 °C ± 0.54 s.e.) than spring (mean 15.6 °C ± 0.54 s.e.) and highest in summer (mean 23.8 °C ± 0.9 s.e.) (Figure 2.2). Temperature in the wrack deposits followed a similar patter to that of the air temperature (figure 2.2);

winter mean 8.5°C ± 1.9 s.e., spring mean 16.2 °C ± 0.1 s.e., and summer mean 22.1 °C ± 0.6 s.e.

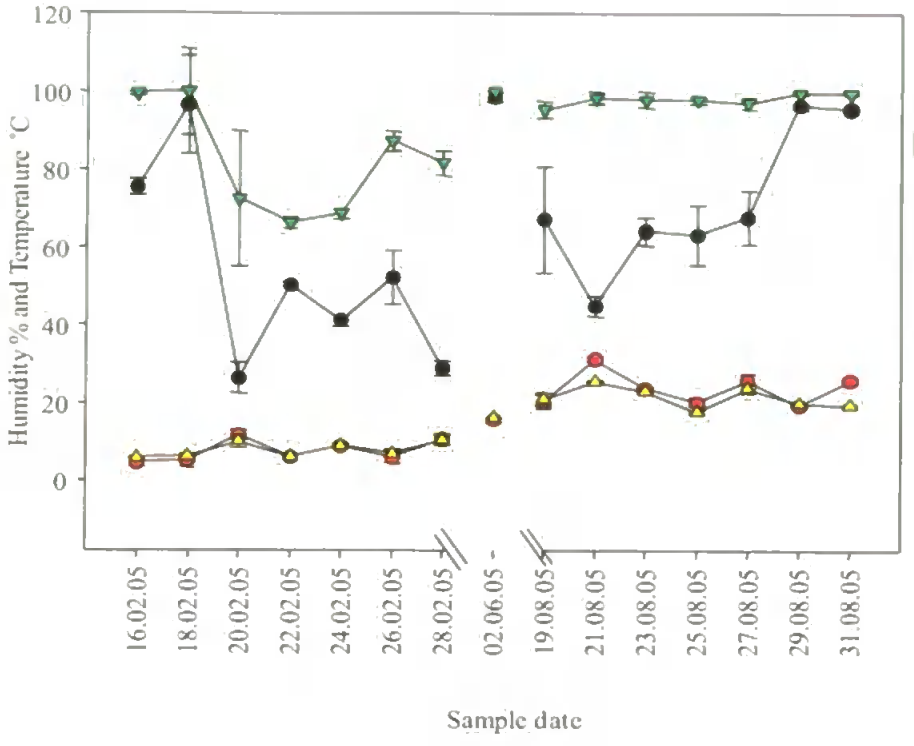

Figure 2.2 Temperature and humidity from the wrack bed on Wembury beach (Feb-Aug 2005, n=5). Values are means ± 1 s.e. Black circle = humidity above wrack, red circle = temperature above wrack, green triangle = humidity under wrack, yellow triangle = temperature under wrack.

In general the physical properties of the strandline where not different between seasons and within a season did not follow any consistent pattern from high tide to low tide. This is reflected in the MDS plot of similarity between wrack properties on sampling dates in summer and winter, there is not clustering or obvious gradients of samples by date (Figure 2.3).

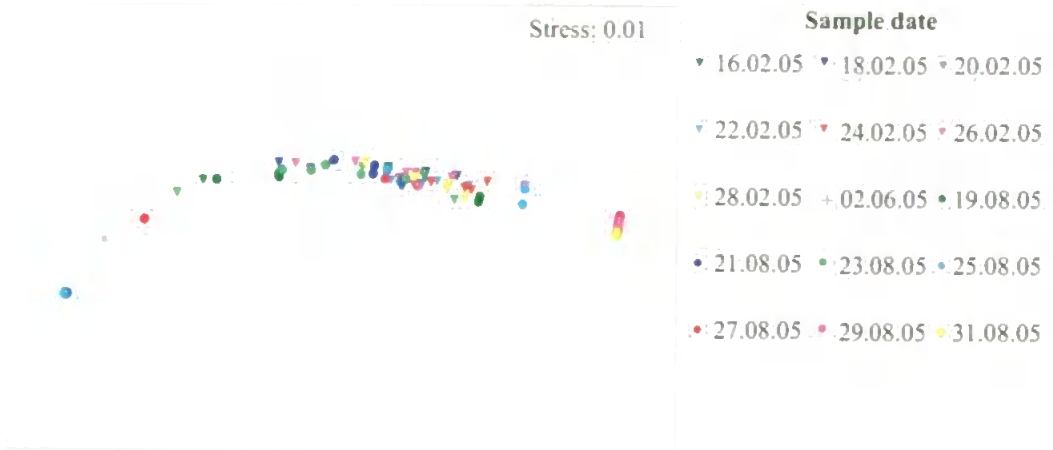

Figure 2.3 Multi-Dimensional Scaling (MDS) plot of the physical characteristic of the strandline by sampling date. Physical variables used are wrack depth cm, surface humidity %, surface temperature, humidity at depth, temperature at depth and patch dimensions and a Euclidean similarity matrix was used on 4^{th} root transformed data.

2.3.2.3 Biotic Characteristics of the Strandline at Wembury

The strandline fauna of Weburry was highly variable by both sampling season, sampling day within a season and between cores taken on the same day, this is reflected in the exceptionally high standard error of abundance for every order when samples are seperated by season (Figure 2.4). Despite this there are some generalisations that can be made for the strandline fauna of Wembury.

In the preliminary survey of Wembury beach, when all sampling dates are combined and mean abundance per core compared between orders, amphipods dominated numerically the strandline fauna constituting 60% of the total abundance. In terms of abundance the order Diptera was the second most abundant and made up 14.7% of the total species abundance, followed by Coeloptera and Annelida and Nematode which contributed 11.2% and 10.8% of the total species abundance respectively (Figure 2.4). Where species in each taxon were identified to species level, each grouping was generally dominated by one or two species (Figure 2.4). Within the

order Amphipoda *O. gammarellus* made up 95% in summer, 75% in spring and 83% in winter, this was followed by *T. deshayessi, T. saltator* only constituting more than 1 percent of the total Amphipoda abundance in winter (6.4%) (Figure 2.4). The order Diptera was massively dominated by *C. frigida and C. pilipes, C. frigida* made up 79%, 39% and 49% of the total Dipteran abundance in summer, spring and winter respectively and *C. pilipes* 13%, 30% and 35% (Figure 2.4). Only in spring did all the other Dipteran species combined contribute more than 8% to the total Dipteran abundance (30%) (Figure 2.3b). Within the order Coleoptera *C. xantholoma* and *C.littoralis* dominated the order these two species respectively made up 55% & 26%, 37% & 33% and 40% & 20% of the total order abundance in summer, spring and winter. Coleoptera larvae (not identified to species level) made up 15% and 24% of the total order abundance in spring and winter respectively all other species did not make up greater than 5% of the total order abundance in any season (Figure 2.4).

2.3.2.4 Species Seasonal Trends

At Wembury, overall species abundance was much greater in summer, then winter then spring (Figure 2.4). This was mainly due to the massive number of Amphipods collected in summer samples. The average abundance of Amphipoda per core in summer was 989 species compared to 294 species in winter and 161 species in spring (Figure 2.4). There was also a notably higher abundance of coleopteran in summer samples (Figure 2.4). Although spring samples had the overall lowest average species abundance per core, the average abundance of Diptera per core was greater than the other two seasons 201 species in spring, compared with 24 species in summer and 123 species in winter (Figure 2.4).

Despite the changes in abundance of species between summer and winter the relative contribution of species to an order remained remarkably unchanged (Figure 2.3) At

Wembury there were significant differences in the strandline assemblage between seasons (Global R: 0.535 significance level of sample statistic: 0.1%) although only samples taken in winter were significantly different from those taken in spring (Table 2.1). However, this comparison should be viewed with caution; 1) Because there is no temporal replication of seasonal samples, and 2) The strandline fauna was only collected on one day in spring minimising the number of possible permutations to eight (Table 2.1). Considering the high R value and low number of possible permutations there may be considerable differences between the fauna in spring and summer (Table 2.1). Considering the high R value and low number of possible permutations there may be considerable differences between the fauna in spring and summer (Table 2.1).

Table 2.1 Pair-wise tests of similarity between faunal samples (4^{th} root transformed) taken from Wembury in summer, winter and spring.

Comparison	R	Significance level	Possible permutations	Number of permutations	Number of observations
winter-spring	0.238	87.5	8	8	7
winter-summer	0.637	0.2	1716	999	1
spring-summer	0.565	12.5	8	8	1

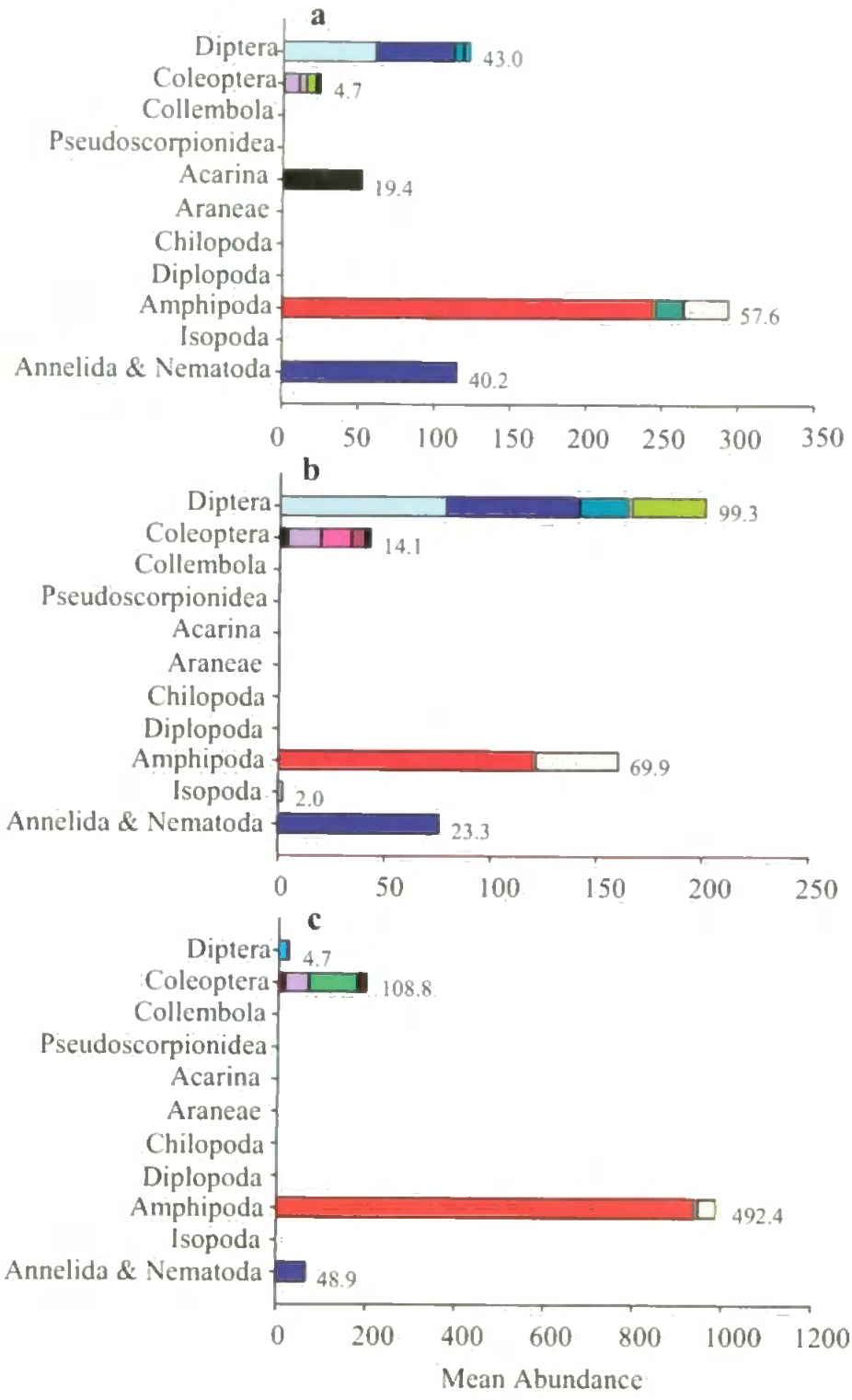

Figure 2.4 The mean abundance and standard deviation of each taxon extracted from cores taken from Wembury high tide strandline during a) summer, (19.08.05-31.08.05), b) spring (02.06.05) and c) winter (16.02.05-28.02.05). Where species were identified to species level within orders different coloured bands represent the abundance of different species within that order

2.3.2.5 Species Tidal Trends

As previously mentioned both the diversity and abundance of species in cores was exceptionally variable both between cores taken on the same day and between samples collected from different days within a season. This is reflected in the MDS plot of similarity between the strandline assemblage on sampling dates in summer and winter, based on assemblage diversity and abundance, there does not appear to be any clustering or sequential gradient of samples by sampling date (Figure 2.5).

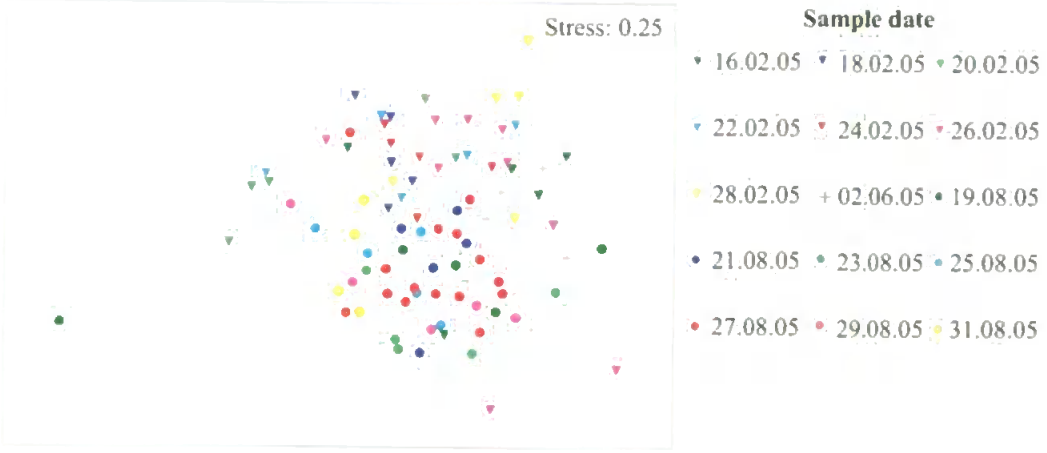

Figure 2.5 Multi-Dimensional Scaling (MDS) plot of the strandline assemblage by sampling date. A Bray-Curtis similarity matrix was used on 4th root transformed data biotic data.

The strandline assemblage was significantly different between samples taken on different dates in summer (Global R): 0.323, Significance level of sample statistic: 0.1%, but not between samples taken in winter (Global R): -0.001 Significance level of sample statistic: 46.5%.

Although the strandline assemblage at Wembury differed significantly between sampling days in summer there did not appear to be any particular pattern in species colonisation, in terms of the relative abundances of different taxa. Again this is reflected in the MDS plot where the similarity in the strandline assemblage, in terms of species

abundance and diversity, taken at subsequent days after high tide, in both summer and winter followed no clear pattern (Figure 2.5). Thus the significant change in the strandline assemblage at different sampling dates in summer is most likely due to changes in overall species abundance rather than diversity, which changed idiosyncratically over the tidal cycle (Figure 2.5).

2.3.2.6 Links between Abiotic and Biotic Characteristics of the Strandline

As previously mentioned there does not appear to be any clear patterns in the similarity of the strandline species assemblage or the biotic variables with respect to tidal cycle or season (Figure 2.3, 2.5). Furthermore the similarity between samples of the strandline assemblage and physical characteristics of the strandline does not appear to be distributed in the same manner with respect to date (Figure 2.3, 2.5). This said, the stress level for the biotic data is high (Figure 2.5) and the multi-dimensional scaling plot must be interpreted with care as the two-dimensional distances on Figure 2.3 do not represent the realised similarity between samples very accurately. A BIOENV analysis relating the physical characteristics measured to the biotic assemblage, reflects this observation; all of the physical factors measured,wrack depth, surface humidity, surface temperature, humidity at depth, temperature at depth and patch dimensions combined gave the best overall correlation to the similarity between the biotic assemblage. However, the overall correlation, 0.250, was very low; suggesting factors other than those measured determine the strandline assemblage.

2.3.3 Survey Summary

The physical characteristics of the strandline varied, in terms of temperature and patch size. Although humidity and wrack patch depth was variable, humidity was always higher and less variable inside the wrack compared to that of the surrounding air

and patch depth did not vary as much as temperature. The strandline fauna at Wembury appeared to be greatly variable, between sample sites, sampling days and seasons. On average the strandline was dominated in terms of abundance by the orders Amphipoda and Diptera, and these orders themselves were dominated by one (in the case of Amphipoda) and two (in the case of Diptera) species. The strandline fauna and physical properties of the wrack did not appear to follow any successional temporal trends with the tidal cycle. There was low correlation between the physical properties of the strandline and the strandline assemblage, suggesting factors other than those measured determined the strandline assemblage species diversity and abundance.

2.4 Discussion

2.4.1 Wrack deposition

Although only the high tide strandline was sampled a number of strandlines did form at the site in the present study, consistent with previously reported strandline formation. Marsden (1991) and Ochieng and Erftemeijer (1999) reporting on the wrack deposition on beaches in new Zealand and Mombassa found a number of different types of strandlines ranging from those where wrack was evenly distributed or deposited along one or more drift lines, usually at high water springs, to those in bands, or in a band, down to the level of the most recent high tide and/or in patches from extreme high water, to mean tide levels. Similarly Messana *et al.* 1977, Stenton-Dozey and Griffiths 1983, Colombini *et al.* 2000 observed the vertical elevation of the strandline changing following the high water mark through a neap-spring tidal cycle. However unlike the strandlines in Fennoscandia surveyed by Backlund (1945) the wrack banks formed at Wembury did not cover the entire beach and were not permanent. The discrepancy between this study and that of Backlund (1945) can be explained by the tidal regime in

Fennoscandia the formation of extensive and permanent wrack beds with associated depth stratification was found in relatively sheltered areas where tidal influence is minimal.

In this study the deposition of wrack was greatest in spring, then summer being completely absent in the autumn months. This coincides with the largest (spring) and smallest (autumn) tidal range for this area. Similarly, Behbehani and Croker (1982) reported greatest wrack deposition in the months of May to August in New England strandlines In New Zealand too, accumulation of drift wood, seagrass and two kelp species was lower in summer (Dec-Jan) than in winter (Jul) (Marsden 1991). Again constituent with the lowest and highest tides for the region, seasonal changes in strandline formation and marine debris accumulation have been observed in South Africa (Koop and Field 1980, Stenton-Dozey and Griffiths 1983). Ochieng and Erftemeijer (1999) also found greater accumulations of wrack when the tidal range was greatest, accumulation of seagrass along the beaches of the Mombasa Marine National Park and Reserve was greatest during spring tides compared with neap tides. Contrary to the present study and previous work (Ochieng and Erftemeijer 1999, Behbehani and Croker 1982) Phillips and Meredith (2002) found an increase in anthropogenic material deposition on South Wales beaches in summer (Jul-Sept) not spring months, however patterns in the volume of offshore anthropogenic material was not documented and local conditions may have contributed to the observed pattern of deposition.

Wrack deposition at Wembury does not appear to follow patterns in accumulation and removal consistent with the monthly tidal cycle. This is in contrast to previously documented patterns of wrack volume; Griffiths and Stenton-Dozey (1981) found a total kelp replacement cycle of 14 days, coinciding with the spring tide, for a kelp-dominated strandline in the Cape Peninsula South Africa; Messana *et al.* (1977) investigating a sheltered Indian Ocean beach also recorded the pattern in absence and

accumulation of marine debris resulting in the formation of strandlines that followed a 2-week tidal cycle; Fynes (*pers. comm.*) and Dobson (1974) found wrack beds persisted for 14-16 days respectively; On a Somalian beach, the seagrass strandline cycled over a 10-day period, being notably absent at the beginning and end of the semi-lunar cycle (Colombini *et al.* 2000) and finally where tidal influence is minimal extensive and permanent wrack beds have been formed (e.g. Backlund 1945).

However, as observed at Wembury, the formation of strandlines and deposition of wrack does not always follow tidal regime closely; In sampling seventeen wrack beds in north east England between June and August 1995, nine strandlines lasted less than a week, three lasted 1-2 weeks and only five lasted 25-26 days (Hodge and Arthur 1997). Koop *et al.* (1982a) estimated an 8-day cycle in strandline deposition and replacement as the exposed beach in their study was positioned behind an extensive reed bed requiring higher tides to enable transport of marine debris to the beach. Despite the diurnal tidal cycle in England of two high spring tides a month in this study and that of Hodge and Arthur (1997) factors other than tidal regime are likely to influence the deposition and removal of wrack material. Factors other than the tide regime have been seen to effect wrack deposition. Previous patterns of wrack deposition has been attributed to storms (Balestri *et al.* 2006), rough seas (Crafford and Scholtz 1987), monsoons (Ochieng and Erftemeijer 1999) and the beach and offshore topography (Koop and Field 1980, Hansen 1984, Ochieng and Erftemeijer 1999).

In conclusion, the strandline is clearly an ephemeral environment. Its persistence and position depends on the balance of deposition and removal of marine debris, itself dependent on nearshore production and water motion, both of which can alter seasonally, the latter on smaller daily and monthly tidal cycles. Although the tidal regime is clearly an important factor influencing the formation of strandline in some areas (Dobson 1974, Messana *et al.* 1977, Griffiths and Stenton-Dozey 1981, Colombini

et al. 2000, Fynes *pers. comm.*) to assume all strandlines will follow tidal cycles of deposition and removal will undoubtedly lead to erroneous predictions of the strandline environment in some cases.

2.4.2 Temperature and Humidity

Owing to the deposition of wrack, the specific heat capacity of water and decomposition within the strandline, strandlines are thought to be environments of high humidity and stable temperature. The strandline environment at Wembury was one of consistently high humidity, at least when the humidity and the variation in humidity within the wrack deposit was compared with that of surrounding air. Where humidity within strandlines has been recorded humidity was always greater in the strandlines than the surrounding air (Backlund 1945, Moore and Francis 1985).

Unlike previous studies where temperature has been less variable and generally higher than that of the surrounding air(Backlund 1945, Moore and Francis 1985, Crafford and Scholtz 1987) at Wembury beach the wrack temperature followed that of the air (Figure 2.2). Although, as in the present study Moore and Francis (1985) found temperature within wrack deposits differed between seasons and within each season diurnal oscillations in temperature were recorded, when they measured temperature in artificial strandlines placed in the supalittoral zone at a site in Scotland. However the temporal variability in temperature markedly decreased with depth in the wrack pile. The fluctuations in the temperature of the wrack deposits at Wembury may be explained by the smaller depth of the wrack at Wembury compared to previous studies. The strandline did not exceed 11cm at any site or time and had a median depth of 5 cm across replica wrack patches. Moore and Francis (1985) similarly found that the temperature 5 cm below the surface of the wrack fluctuated to a greater extent and

followed more closely the air temperature fluctuations, than the temperature in deeper (15 – 30 cm) wrack layers.

2.4.3 Species Composition

At Wembury the strandline was dominated in terms of species abundance by the orders Amphipoda and Diptera. Within these orders only a handful of species made up the majority of the abundance. Coleoptera, Annelida and Nematoda were the next most abundant orders and contributed to the overall abundance to different extents dependent on seasons. There are few studies where the strandline assemblage has been quantified in its entirety even in this study which originally aimed to quantify the strandline, in terms of species abundance and diversity time constraints limited the identification of all fauna within an order to species level. Assessing the variability and relative contributions of groups to strandline assemblage diversity and abundance between different sites is very difficult owing to the, different sampling and extraction techniques employed and the timings of the sampling. This makes comparisons across studies of the strandline in terms of its biotic components difficult. The strandline at Wembury is concurrent with previous studies were a few Orders comprising of relatively few species appear to dominate the strandline assemblage in terms of abundance (Backlund 1945, Bebenhani and Croker 1982, Griffiths and Stenton-Dozey 1981, Inglis 1989, Colombini *et al.* 2000, Jedrezejcazk 2002). To compare the percentage contribution of faunal Orders to the total abundance of strandline fauna easily Figure 2.6 was constructed, where the total mean abundance of each Order across species and sometimes spatial and temporal factors was taken from the few studies in which sufficient information of the strandline assemblage could be extracted to permit this presentation. It is clear that the strandline assemblages investigated globally generally follow the same trend of species dominance as seen in the present

study and as described above (Figure 2.6). As in the present study the opportunist order Amphipoda have been found repeatedly to dominate strandline assemblages. In Western Australia the strandline fauna was generally very depauperate with only amphipods in high abundances (Dugan *et al.* 2003). Similarly on a Somalian beach amphipods always dominated the strandline fauna and constituted 90% of the total species abundance between October and November (Colombini *et al.* 2000 Figure 2.6e). In New England, the strandline community was dominated by the amphipod *Platorchestia* (as *Orchestia*) *plantensis* and oligochaetes, constituting 49.5% and 36.5% of the total assemblage respectively (Bebenhani and Croker 1982, Figure 2.6 b). When the relative dominance of species colonising litterbags over 28 days planted in the sediment of a South African beach was observed, *Talorchestia* overall was far more numerically abundant than any other species, followed by *Coelopa* (Griffith and Stenton-Dozey 1981). As in the present study dipterans and amphipods were also the most numerically important strandline macrofauna groups colonising litter bags buried in the sediment of a beach in New Zealand. Additively these two taxa constituted 78 % of the total species abundance (Inglis 1989, Figure 2.6c). Similarly, collection of strandline macrofauna in 1999 and 2002 to monitor the effects of beach cleaning activity on a site in England showed a massive predominance of talitrid amphipods in the samples, across sites and tidal cycles (Smith 2003). Amphipods were the second most numerically dominant fauna after collembolans in strandlines surveyed around the Swedish and Finnish coasts (Backlund 1945, Figure 2.6a).

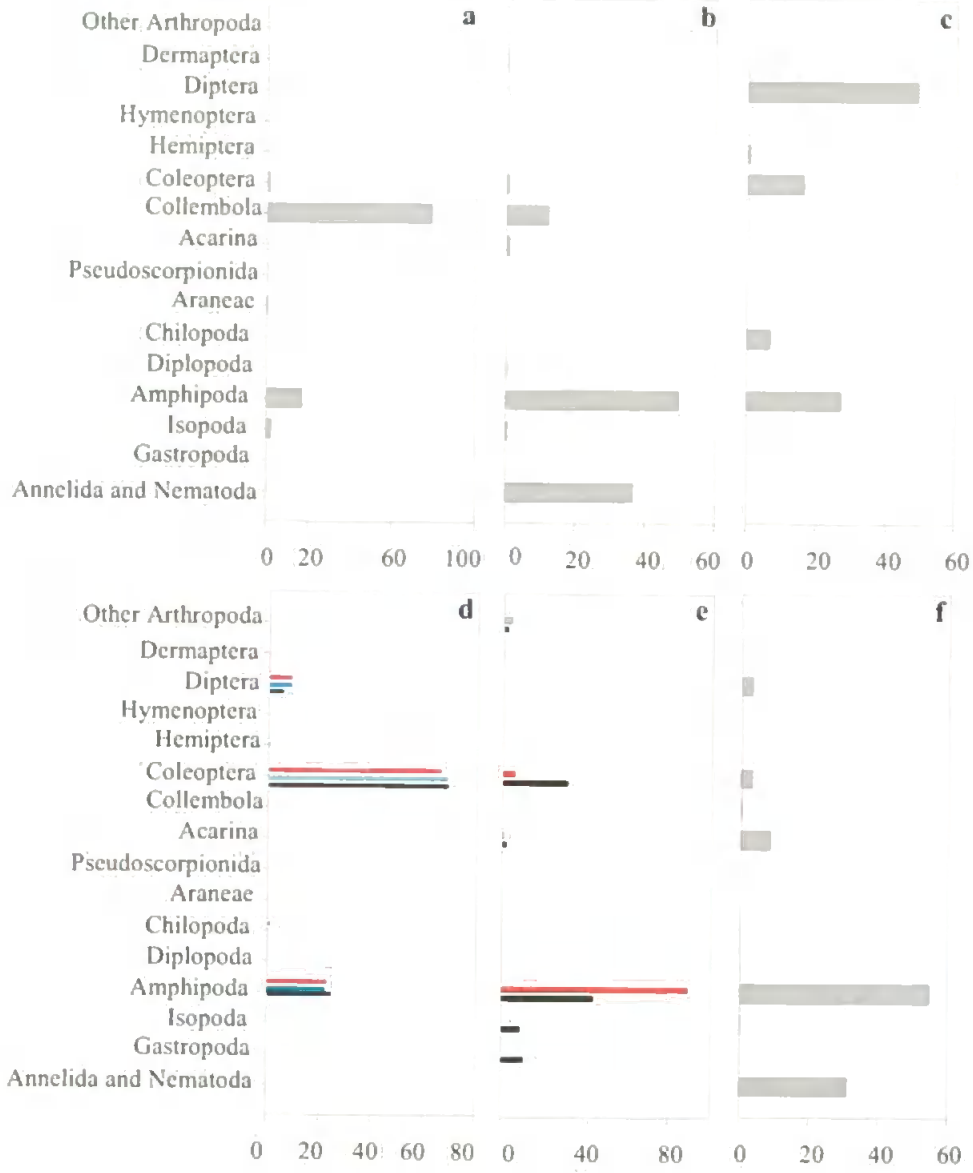

Figure 2.6 Percentage contributions of strandline Orders in terms of abundance for different strandline worldwide. Percentages are calculated based on mean abundances taken from the data presented in the study and averaged for the entire survey. a) Backlund's (1945) strandline survey of the Finnish and Swedish coast (1933-1944) at different months. It is based on the average abundance of species in each order. Species were collected using cloth bags were extracted using Tulgren funnels. Although Annelida and Nematoda and Diptera were found in high abundances they were excluded from the analysis. **b)** Behbehani and Croker's survey (1982) of 3 sites in New Hampshire, sampled using 0.04m^2 core, each month over a year in 1975. Only species

with a body size > 0.5mm were picked and counted from wrack samples. The absence of diptera is due to the selective collection of wrack samples. **c)** Inglis' survey (1989) of species colonizing buried litter bags of *Macrocystis* on a New Zealand sandy beach (Mar-Apr 1986). The abundances are based on order averages taken from litterbags of different sizes, retrieved at different times over 18 d and as such probably under represents larger animals that would have been excluded from some of the litter bags. **d)** Jedrzejczak's survey (2002) of species colonising 0.25 mm mesh litter bags of *Zostera* spp. buried at different tidal heights and vertical depths at three Polish beaches. Species were collected at different seasons and at different times up to 150 d after litter bag placement. Black bars = samples taken in 1999, turquoise = 2000 and red = 2001. **e)** Survey by Colombini *et al.* (2000) of strandline species abundance from a Somalian beach. Only species with total abundances over 100 individuals were included. Black bars represent a species captures in pitfall traps collected every other day over 2 tidal cycles red bars represent a results of a preliminary survey where species abundances were calculated from the results of small cores taken randomly along the beach in 1971. **f)** Collated faunal data from this preliminary survey of Wembury beach strandline in 2005 using the methodology described in Section 2.4.

The relatively high abundance of collembolans in Backlund's survey (1945), when compared with this survey and previous studies (Figure 2.6) may be due to the permanent nature of the strandlines sampled by Backlund (1945) or the small size of many members of this order making them overlooked in samples where only visible fauna are extracted. In the present study although humidity was always high in the strandline, the wrack was not very deep, was often dry, and was not permanent. Any collembolans living in the high tide strandline at Wembury would have been at risk from periodical low humidity conditions and when the wrack patches moved spatially, predation as well as exposure. Most collembolans use tegumentary respiration and as such are sensitive to desiccation and may not survive long in such a spatially ephemeral environment as the strandline at Wembury. As in the present study when comparing the relative abundance of Diptera between spring, summer and winter sampling seasons the overall contribution of this order to totally strandline abundance can be very variable. In New Zealand, Diptera even constituted 48.89 % of the total macrofauna abundance (Inglis 1989, Figure 2.6c). Conversely Diptera may be absent at some sites (Colombini *et al.* 2000, Figure 2.6e). The presence or absence of dipterans in some studies may be due to the short persistence of wrack deposits disturbing dipterans life-cycles (Blanche

1992). In Somalia, wrack deposits where dipterans were not found, persisted for only 10 d (Colombini *et al.* 2000). Many Diptera species require between 14 - 24 d to emerge as flies from eggs (Hodge and Arthur 1997). There is also some limited evidence that the relative abundance of species within a trophic group may be influenced by interspecific competition. The amphipod *Platorchestia platensis* has been rarely found co-exsisting with dipteran larvae (Behbehani and Croker 1982). Similarly, wrack beds on the Cornish coast were dominated by either amphipods or kelp-fly larvae, with the two groups never in equal abundances at the same time during the tidal cycle (M. Fynes and J.I Spicer *pers. comm.*). These observations, however, must be interpreted with caution as the segregation of these two taxa may be due to the environmental characteristics of the wrack banks. Kelp-fly larvae generally show a preference for anaerobic wrack (Backlund 1945, Behbehani and Croker 1982) and amphipods a preference for aerobic surface and mid layers of the wrack bed. It cannot be ascertained from such a small body of work weather the segregation of Diptera and Amphipoda in previous surveys is unique to these habitats or the co-occurrence of Diptera and Amphipoda in the present survey is a unique feature of the strandline at Wembury, this discrepancy does however highlight the variability in strandline assemblages from different sites.

Similar to dipterans, and between seasons in the present surveys the abundance of coleopterans in strandline assemblages can differ (c.f. Figures 2.6a with 2.6c, d). As many species of Coeloptera are xenocoenic (Backlund 1945, Joy 1976, D. Bilton *pers comm.*) their contribution to the overall abundance of strandline assemblages will depend on the terrestrial environment adjacent to strandlines. This may explain the discrepancies between previous studies in the relative abundance of coleopterans in strandline assemblages. As with Diptera, the time at which the strandlines were sampled may also affect the number of Coeloptera species in samples as coleopteran abundance

may follow cyclical patterns with either wrack deposition (if the species are herbivorous) or with prey items such as dipterans (Colombini *et al.* 2000).

Annelida, Nematoda and meiofauna are likely to have been under-represented in the present and previous strandline surveys. Despite the fact that enchytraeids and oligochaetes are considered important strandline taxa in terms of abundance they are often not counted in samples, or if extraction methods like the Tulgren funnels are used, their abundance and diversity may be underestimated. In this study the extraction of fauna using Tulgren funnels resulted in a number of oligochaete and possibly nematode worms becoming dried out and thus unidentifiable. The contribution of meiofauna and microbes to strandline assemblages is poorly known, although on some exposed beaches dry meiofaunal mass has been found to exceed that of macrofauna (McLachlan 1985).

Whilst the overall patterns of species dominance in strandline assemblages appears to be similar across study sites the actual contribution of species or orders to overall assemblage abundance, and indeed total abundance and diversity measures of strandline assemblages should be treated with caution. Different sampling techniques may perform differently. Pitfall traps will underestimate the abundance of non-mobile fauna, and coring methods will underestimate adult fly and flying beetle abundance. Species extraction methods will also introduce error. In this study using box cores coleopteran abundance was exceptionally low (Figure 2.4 f), yet small pitfall traps sometimes collected over 50 beetles in a 12 h period. Colombini (2000) also collected a greater abundance of coleopteran when pitfall traps were used (Figure 2.4 e). Similarly, greater numbers of amphipods were collected in cores than pitfalls, and *vice versa* for the relatively smaller xenocoenic coleopteran species (Figure 2.4). Furthermore, using box cores the amphipod assemblage was dominated by *O. gammarellus* > *T. deshayesii* > *T. saltator* (Figure 2.6 a, b). Yet when pitfall traps were laid in the high tide strandline

for 12-24 hours the relative abundance of *O. gammarellus* and *T. deshayesii* was more similar and relatively more *T. saltator* individuals were found than when using the box core method. The low abundance of Araneae in previous strandline surveys (Figure 2.4) may also be due to the inadequacy of box cores and pitfall traps to collect highly mobile species (in the case of pitfall traps Araneae may be able to escape). As previously mentioned for Diptera and Coleoptera, temporal patterns in strandline species distribution will determine their abundance in strandlines sampled at a single point in time. Temporal changes in community density have been related to population biology of dominant species (Veloso and Cardoso 2001) and species diurnal behaviour patterns have been suggested to underestimate amphipod abundance in samples taken during the day (Craig 1973, Cardoso 2004). Finally, different sampling efforts give different assemblage results (Schoeman *et al.* 2003). As noted previously the distribution of wrack deposits can be very ephemeral and variable. Thus the most abundant animal species of the strandline are thought to be opportunistic and respond to wrack deposits by colonising them rapidly.

2.4.4 Species Seasonal Patterns of Distribution

At Wembury, overall species abundance was lowest in spring and greatest in August this is surprising as the size of the wrack was greatest in spring and previous studies have shown that small wrack patches had lower abundance than medium-size and large-size patches (Philips *et al.* 1995 Colombini *et al.* 2002). However the actual difference in wrack patch size between seasons was not large and previous studies where wrack patch size has been seen to correlate with species abundance also found differences in the macrofaunal assemblage sampled from different sites and at different times (Olabarria *et al.* 2007). The high tide strandline at Wemburry was only sampled once in spring making comparisons with other seasons not statistically powerful.

Considering the two seasons in which the strandline was repeatedly sampled the abundance of species was greatest in August than February possibly reflecting the seasonal population cycles of many species. Lower amphipod abundance may be due to the fact the species found at Wembury do not mate below 10°C (Morritt and Stevenson 1993) and display bivoltine population cycles with peaks in the spring and summer months (Section 2.7.1). Adult amphipods may migrate away from the strandline and over-winter under boulders and rocks higher up on the shore (Persson 1999). Strandline beetles too may also over-winter under larger rocks and boulders higher up on the shore, in torpid state (D. Bilton *pers comm.*). There is no direct evidence to suggest this is occurring in the beetles of Wembury strandline. However, species of *Remus*, *Cafius* and *Polystoma* found in high abundance under rocks and boulders during winter months would not feed on any food source presented in the laboratory and were exceptionally inactive despite constant temperatures of 25°C and light/dark cycles ranging from 24 h light to 6 h light. The relatively higher abundance of Annelida and Diptera in winter compared to summer may reflect either the absence of predatory beetles or interspecific interference by amphipods (M. Fynes and J.I. Spicer *pers. comm.*).

2.4.5 Species Tidal Patterns of Distribution

The change in the Wembury strandline assemblage over the tidal cycle did not appear to follow any particular pattern in species colonisation, in terms of the relative abundances of different orders or species. Contrary to the results of the present survey numerous studies have documented temporal changes in species assemblage composition and individual species abundance. Many mobile species have been recorded migrating with the tide (Colombini *et al.* 1996, 2000, 2002), and/or follow diurnal nocturnal migration and activity patterns (for amphipods see Marsden 1991, Jaramillo *et al.* 2003; for coleopterans and isopods see Koop 1982, Colombini *et al.*

2005; for other arthropods see Colombini *et al.* 1996, 2005, Aloia *et al.* 1999, Jaramillo *et al.* 2003). Talitrid amphipods and many species of kelp-fly larvae have frequently been recorded as the first opportunistic colonisers of newly deposited strandlines (Inglis 1989, Jedrzejczak 2002a, Griffiths and Stenton-Dozey 1981). Inglis (1989) found the amphipod/Diptera dominated assemblage to peak in total macrofaunal abundance 3 d after wrack deposition. Whilst amphipod and dipteran abundance decreased rapidly thereafter many species of predatory beetle and a centipede remained at the same abundance for 18 d. Nematodes increased in abundance rapidly after 9 d. Acarina were only present in the later stages of litter decomposition. Similar trends of initial amphipod and/ or dipteran peaks in abundance following wrack availability have been found at other sites, where the abundance of other strandline species remained consistently low or increased in abundance after 7 d (Griffiths and Stenton-Dozey 1981, Colombini *et al.* 2000, Jedrzejczak 2002b). Studies where only the dipteran larvae are quantified the change in dipteran abundance on a temporal scale may be related to the life-cycle of these species. Jedrzejczak (2002b) found a succession in dipteral life stage. Adult flies were most abundant between 2-4 d of litter bag placement and eggs most abundant between 4-10 d. Larvae increased in abundance to a 'plateau' around 8 d. Remarkably similar changing patterns of abundance between adult, egg and larval life stages of Diptera following wrack deposition have been recorded by Inglis (1989) and by Hodge and Arthur (1997). Other studies suggest that the kelp-fly can complete its larval development between successive spring tides (Egglishaw 1960, Dobson 1974, Inglis 1989) potentially following the cyclical patterns of wrack deposition.

In many studies coleopterans has been send to peak in abundance after many days or the peak in abundance of other species (Inglis 1989, Griffiths and Stenton-Dozey 1981, Colombini *et al.* 2000). This has been attributed to the preceding increase of the abundance in their prey in wrack deposits (Colombini *et al.* 2002). Xenocoenic

and tryocoenic species of beetle may only enter into the strandline habitat if food is available. However, factors other than food may play a larger role in determining beetle abundance in strandlines. The increase in beetle abundance found some period of time after wrack deposition has been attributed to their preference for drier wrack conditions following initial water loss in wrack deposits (Moore and Legner 1973, Griffiths and Stenton-Dozey 1981). In the present survey if there was not successive pattern in wrack deposition, abundance of coleopterans prey items, and at least the surface layers of the wrack were nearly always dry, this may explain the lack of a successive temporal pattern in coleopteran abundance in Wembury high tide strandline.

In previous survey there were many factors that changed with the tidal cycle most notably deposition, resulting in changes in the chemical and physical environment of the strandline, species population cycles and patterns of species colonisation resulting from changes in species interspecific interactions all of which may have influenced species distributions. At Wembury the lack of a successive temporal pattern in species colonisation is maybe due to the fact that only the high tide strandline was sampled and that the wrack of this strandline did not follow patterns of deposition and removal with the tide, but rather was ephemeral in its horizontal spatial distribution. The significant change in the strandline assemblage at Wembury, at different sampling dates in summer, is most likely due to changes in overall species abundance rather than diversity, which changed idiosyncratically over the tidal cycle (Figure 2.5a,b) and between season, possibly reflecting the ephemeral horizontal nature of the wrack distribution at Wembury.

2.4.6 Links Between the Biotic and Abiotic Strandline Environment

At Wembury there did not appear to be any clear patterns in the similarity of the strandline species assemblage or the biotic variables with respect to tidal cycle or

season. This is contrary to previously thinking, whereby the physical and chemical properties of the strandline determined the strandline assemblage. There are few studies were specific chemical and physical properties of the strandline are statistically correlated to properties of the strandline assemblage however, wrack is often cited as an environment providing food and refuge to a wide array of terrestrial, semi-terrestrial and occasionally aquatic animals (Backlund 1945, McLachlan and Erasmus 1983, McGywnne *et al.* 1988, Inglis 1989, Colombini *et al.* 2000 and references therein). Many animals have also been observed directly eating wrack deposits (e.g. Griffiths and Stenton-Dozey 1981, Koop *et al.* 1982a and Griffiths *et al.* 1983 for amphipods, Chown 1996 for dipteran larvae) or prey on animals that consume marine plants deposits (e.g. Backlund 1945, E. McAfee *pers. comm.* for some beetles, Ugolini 1997, Laffaille *et al.* 2001, 2006, Arcas 2004, Hample *et al.* 2005, Minderman *et al.* 2006 for predatory fish and birds). Furthermore many studies have shown a high correlation between species diversity and abundance and wrack deposits (e.g. McLachlan 1980, 1985, Bigot 1970, Polis and Hurd 1996, Vilas 1986, Colombini and Chelazzi 2003). The volume of wrack deposit has also been shown to positively correlate with species diversity (Olabarria *et al.* 2007). Finally wrack removal through beach cleaning has been seen to reduce species diversity and abundance (e.g. Smith 2003, Schlacher *et al.* 2007 and references therein). However as the species assemblages in wrack deposits are rarely compared to similar areas lacking deposits, explaining variation in these assemblages on the basis of wrack properties is problematic. Caution should be exercised when assuming species assemblages found in strandline samples only there due to the specific physical and chemical environment of the wrack as many species observed to dominate the strandline system have also been found in high densities on sandy beaches without wrack (e.g. talitrid amphipods on sandy beaches of the North Brittany Coast, France, J.I Spicer *pers. comm.*). There are a few studies where particular abiotic characteristics of the

strandline have been used to infer of describe the strandline assesmblage however Phillips *et al.* (1995) did link the distribution of a particular abundant strandline species to specific properties of the strandline. Phillips *et al.* (1995) found the distribution of dipteran larvae and amphipods to be highly aggregated and dependent on wrack depth and temperature. The only study to quantitatively assess the chemical and physical components of strandline environments and statistically compare these properties with the strandline species assemblage was undertaken in Australian intertidal mud flats (Rossi and Underwood 2002). Here the effect of organic enrichment was tentatively concluded to explain more of the variation in the strandline assemblage than physical disturbance caused by the physical presence of the wrack. In the present study it is likely that factors other than those measured determined the strandline assemblage. The distribution of wrack horizontally along the beach was very variable and the disturbance frequency of a wrack patch may be correlated with the strandline assemblage. As previously mentioned for a variety of reasons the strandline assemblage is thought to, and has been observed to, follow a pattern of succession preceding wrack deposition (Section 2.4.6), the wrack deposition following the monthly or two weekly tidal cycle. The strandline assemblage at Wembury may be dependent on the time lapsed preceding wrack deposition, and on other species arrival and distribution however wrack deposition and removal was not dependent on the tidal cycle but varied spatially. Thus at any one point in time a number of wrack patches of different ages may have been present on the shore, each colonised by an assemblage at a different stage of succession, leading to the overall variability in the strandline assemblage between sites on the same day. In the present study and previous studies observed seasonal changes in community density may have been related to the population biology of dominant species, rather than the change in wrack volume, or physical environment as previously reported (Veloso and Cardoso 2001).

2.4.7 Preliminary Survey Conclusions

As in previous studies the strandline assemblage at Wembury is characterised by a few species in exceptionally high abundance. As with the majority of previous surveys the Orders Amphipoda and Diptera contributed disproportionately to the overall species abundance at Wembury this is despite the geographical distance, ocean currents and climatic conditions between previous studies.

Unlike previous studies the strandline at Wembury did not appear to follow any temporal patterns in species colonization, most likely due to the pattern of wrack deposition which did not vary systematically on a temporal scale, but was, like the strandline assemblage variable on smaller spatial scales.

The abiotic properties measured in the present survey were not correlated with the strandline assemblage, and it is suggested that wrack disturbance, was more likely to effect the strandline assemblage.

This preliminary survey adds to a relatively small body of work that suggests strandlines, both in terms of the biotic and abiotic components can be exceptional variable, within and between studies. The strandline assemblage appears to be dominated by a few species but can be exceptionally transient the transient nature of the strandline assemblage depending on numerous factors associated with wrack deposition and colonisation.

2.4.8 The Process of Decomposition

In subsequent chapters of this thesis decomposition is measured as an ecosystem process. This section introduces the process of decomposition in the strandline and summarises previous work in this area.

Decomposition is likely to have great overall functional significance in coastal transition zones such as the strandline (McGwynne *et al.* 1988, Snelgrove 1997, Levin *et al.* 2001), especially on sandy shores where the sediment mobility restricts *in situ* primary production (Brown 1964, McLachlan 1985). Detritus in the sediment serves to stabilise seasonal inputs of organic matter (Pomeroy 1970) providing bottlenecks to energy flow (MacFadyen 1961). Therefore, processes like decomposition which mobilise particulate organic matter are crucial for ecosystem functioning (Hargrave 1975). The decomposed material enhances secondary production (McLachlan 1985, McMahon and Walker 1998, Trolley and Christian 1999) and provides an energy source for meiofaunal and interstitial communities (Robertson and Lucas 1983, McGwynne *et al.* 1988, Camilleri 1992). Additionally the release of nutrient and organic matter from marine debris back into the coastal intertidal and near-shore areas can be considerable (see Perkins 1974 and references therein however c.f. Koop *et al.* 1982a) and may apprently support unrelated near-shore food webs (McLachlan *et al.* 1981, Duggins *et al.* 1989, McMahon and Walker 1998).

Perhaps surprisingly the contribution of detritivores to the overall decomposition of wrack material is not well known, although they are thought to accelerate decomposition through, a) the spread of microorganisms, b) fragmentation of larger particles by feeding and burrowing activities increasing the surface area available for microbiological decomposition (Robertson and Mann 1980, Stenton-Dozey and Griffiths 1980, Harrison 1982, Bedford and Moore 1984, Inglis 1989) and c) by selectively grazing microbial communities on the detritus leading to increased microbial metabolic activity and potentially microbial decomposition (Smith *et al.* 1982). Stenton-Dozey and Griffiths (1981) estimated that grazers remove 60 - 80% of organic input from the strandline in 2 d based on standing crop mass loss and individual feeding rates. Similarly Griffiths *et al.* (1983) calculated losses of 71% of the material deposited on a

South African sandy beach due to grazing. As amphipods are found generally in the highest abundance in strandline habitats (see Section 2.3) and have one of the greatest consumption rates of strandline detritivores (Griffiths *et al.* 1983) they are certain to be important macrofaunal decomposers of wrack material. There are many examples where amphipods feed indiscriminately on any food type availible (Backlund 1945, Agrawal 1964) and owing to their low assimilation efficiencies (Griffiths and Stenton-Dozey 1981) their faeces may become sites of increased microbial activity (see Hargrave 1975 for a review), both mobilising organic matter for off-shore habitats (Griffiths and Stenton-Dozey 1981) and potentially providing a food source for other strandline species. Although dipterans may occur in high abundances in the strandline (see Section 2.3 and Figure 2.4) their overall contribution to decomposition in the strandline is not likely to be as great as that of amphipods owing to their lower biomass and feeding rates (Griffiths *et al.* 1983, Griffiths and Stenton-Dozey 1981). Griffiths *et al.* (1983) calculated the amount of kelp consumed by herbivorous or detritivorous species. Coleopterans consumed only 3.5%, amphipods 52.7% and kelp flies 14.7% of the stranded kelp. However, in some regions the dipteran contribution to decomposition may be greater. For example, Diptera is one of the dominant consumer groups on sub-Antarctic islands (Chown 1996). Although the contribution to decomposition of other Orders was not investigated, a single species, (*Paractora trichosterna*), was directly responsible for 12% of wrack degradation in a sheltered site and 20% in an exposed site (Chown 1996). *Antrops truncipennis* was responsible for an additional 3% loss in the exposed bed and 8% in the sheltered one. These fly species were therefore concluded to contribute significantly to kelp degradation (Chown 1996). Decomposition in the presence of dipteran larvae may alter the microbial assemblage which may affect decomposition. Although evidence is anecdotal; larval exudates have been noted as being wet (Backlund 1945, Egglishaw 1960, Stenton-Dozey Griffiths 1980) and wrack

decay in the presence of larvae has been cited as being anaerobic (Philips and Arthur 1994). Additionally the presence of larvae on *Laminaria* has been seen to exclude moulds (Backlund 1945). The contribution of adult Diptera to overall decomposition is less clear (c.f. Chown 1996, Stenton-Dozey and Griffiths 1980, Griffiths and Stenton-Dozey 1981, Inglis 1989), but is likely to be less significant than their earlier larval life stages as observations of strandline faunas feeding habits have shown that adult dipterans consume only wet wrack exudates (Griffiths and Stenton-Dozey 1981). Adult dipterans may however contribute to wrack breakdown through their tunneling activities, presumabaly be enhancing aeration and the physical breakdown of wrack (Stenton-Dozey and Griffiths 1980, Inglis 1989, Chown 1996).

Although the role that nematode species diversity plays in decomposition in intertidal wrack deposits has been investigated (e.g. DeMesel *et al.* 2003), the overall contribution of meiofauna to the decomposition process in strandline is largely unknown and so is poorly understood.

Microorganisms clearly play an important role in the breakdown of wrack (Koop *et al.* 1982b, Haxen and Grinley 1984,). There is evidence that microorganisms in detritivore faeces are important to the decomposition of detritus (see Hargrave 1975 for review). Similarly increased wrack decay has been attributed to the presence of bacteria enhanced by dipteran faeces (Egglishaw 1960, Rowell 1969). Furthermore, the presence of bacteria and Fungi on wrack may enhance detritivores feeding rates by making the food more palatable or themselves providing a food source for the detritivores. Evidence based on assimilation efficiencies, examination of the organic content of detritivores food and faeces and the disparity between the nutritional needs of the detritivore and that available in the detritus suggests that detritivores receive most of their nutritional value from microorganisms rather than the detritus itself (see Berrie 1975, Fenchel and Harrison 1975, for reviews). There is also evidence that amphipod

feeding rates increase in the presence of some microbes and Fungi (Darnell 1967, Odum 1967, Rong *et al.* 1995, Kneib *et al.* 1997) or that their assimilation efficiency increases with the presence of certain microorganisms (Hargrave 1970, Brenner *et al.* 1976). The importance of microorganisms for dipteran diets has been recognized for some time (e.g. Rowell 1969, Barnes 1984, Cullen *et al.* 1987). The importance of microbial (relative to macrofaunal) decomposition is not known, although there is limited evidence that in some systems microbial decomposition may be as important as detritivore degradation, in terms of wrack volume reduction. Inglis (1989) excluded macrofauna from litter bags of bull kelp tissue and found that standing crop mass loss 41-64% over 18 d was linear and as great in the absence of macrofauna as without. Similarly, Jedrzejczak (2002a) found no significant reduction in the rate of seagrass disintegration in litter-bag exclusions of macrofauna.

2.4.9 The Strandline as a Model System

The broad aims of this thesis are to investigate the role of diversity, identity and species interactions in setting rates of ecosystem processes, the role of body size as a surrogate measure of predator-prey interactions and ecosystem processes, and the role of trophic interactions in influencing non-trophic-resource interactions.

Essential to this research is that the model system must be:

- Accessible. Most strandlines form supralittorally and as such do not need specialised equipment and resources in order to access and sample in these habitats.

- Easily replicated in the laboratory. As discussed in Section 2.2.2 strandlines are heavily disturbed environments that can change volume, patch size and location, spatially and temporally according to tidal regimes and other environmental factors (Figure 2.1). At least on a small time scale, realistic replicate strandlines that are

within the range of physical and chemical conditions to which strandline species are accustomed to and can be easily constructed in the laboratory.

- Comprised of species with good survivorship under laboratory conditions. Strandline species live in highly disturbed conditions, and as such are exposed to a range of humidity, salinity and temperatures associated with the supralittoral zone as well as periods without wrack coverage and refuge. It is perhaps hardly surprising therefore that previous preliminary observations showed excellent survivorship of amphipods, beetles and larvae in plastic bags, tubs, and boxes of wrack in the laboratory.

- Comprised of species which have a range of body sizes (intra and inter specifically). In order to assess the use of metabolic theory in predicting trophic interactions based on scaling laws it is essential that predator and prey species used in manipulations represent a range of body sizes. Figure 2.7 shows the range of body sizes selected beetles and dipteral larvae.

- Comprised of a number of trophic levels. This is essential if the role of trophic and non-trophic interactions on ecosystem process is to be examined. Although there are no resolved food webs for strandline assemblages and the dietary breadth of many species is not known, the four beetles in Figure 2.7a-d, are known as adults to feed on dipteral larvae (Backlund 1945, Joy 1997, and *pers. obs.*), and the dipteran larvae on the wrack (e.g. Philips *et al.* 1995,Hodge and Arthur 1997).

Additional benefits of using a strandline system for BDEF research include:

- The range of diversity associated with the strandline. Owing to the ephemeral and transient nature of wrack deposits, the strandline can be either species rich and depauperate. Thus investigation into biodiversity ecosystem processes in such a

system may have implications for BDEF relationships in both low and high diversity systems.

- Available species-specific natural history information. For most eucoenic strandline species that occur in high abundances, perhaps with the exception of the beetles, there is in existence an amount of natural history information, thus interpreting results of experimental manipulations may be less ambiguous (Section 1.8).

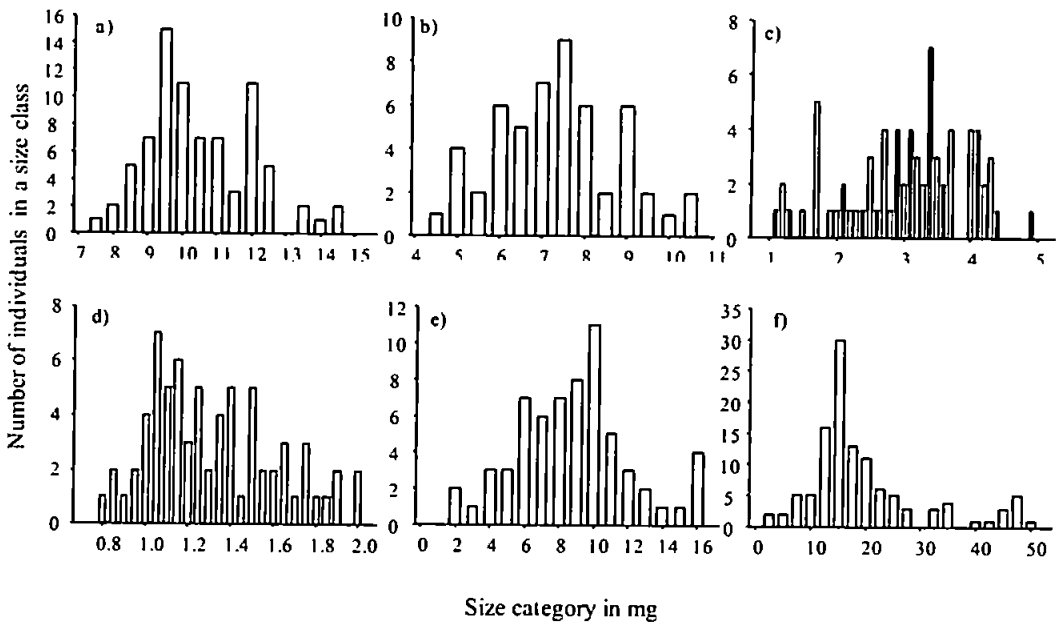

Figure 2.7 Size distribution based on wet mass of some strandline species. a) *Cafius variolosus*, based on 79 individuals taken from the strandline on the 19.10.06, b) *Cafius xantholoma* based on 53 individuals taken from the strandline on the 25.06.06, c) *Remus sericeus* based on 67 individuals taken from the strandline on the 01.10.06, d) *Polystoma algarum* based on 72 individuals taken from the strandline on the 15.07.06, e) *Dryomyza anilis* based on 64 individuals taken from the strandline on the 15.07.06, f) *Coelopa frigida* based on 52 individuals taken from the strandline on the 25.06.06 and 48 individuals taken from the strandline on the 19.10.06.

- Widespread distribution of strandlines. As strandline habitats can form all over the world (Section 2.2.2), investigations into biotic interactions and ecosystem process therein are not limited to unrealistic or rare habitats.

- The strandline is an important yet understudied system in its own right.

Despite the perceived importance of strandline habitats, the biotic interactions that occur and their link to ecosystem process remains a rich area of study, as the strandline forms the bridge between truly terrestrial and marine environments and as such is often over looked by both disciplines.

2.4.10 Rationale Underlying Choice of Species in Manipulation Experiments

In order to investigate the effects of species identity, diversity, trophic and non-trophic interactions on ecosystem processes in the strandline it is important to select species that, a) are common in strandline environments, b) whose trophic position is known and c) may play important roles in ecosystem processes. The species used in the manipulative experiments in subsequent chapters are introduced below and their importance in ecosystem processes in the strandline summarised based on published literature.

2.4.10.1 Amphipods

Talorchestia deshayesii (Audouin 1826) is an ideal test organism. As one of the most commonly occurring members of the family Talitridae in north-west Europe, it is found in great numbers in the strandline (Backlund 1945, Koop and Griffiths 1982, Stenton-Dozey and Griffiths 1983). Aside from the widespread distribution of *T. deshayesii*, *T. deshayesii* showed good survivorship in the laboratory mesocosms (Marsh and Spicer *in prep.*) and readily consumed vast amounts of algae, vegetable matter and even tissue paper when available. Additionally, talitrids are considered to be important decomposers of wrack (Griffiths and Stenton-Dozey 1981, Koop *et al.* 1982a, Griffiths *et al.* 1983). They are thought to have fast consumption rates (Griffiths and Stenton-Dozey 1980, Koop *et al.* 1982a, Griffiths *et al.* 1983), and low assimilation

efficiencies (Muir 1977, Stenton-Dozey and Griffiths 1980). Through its feeding, *T. deshayesii* will influence the size range of particulate organic matter thus increasing the availability of wrack material for a wider range of detritivores. Furthermore, talitrid amphipods are key components of strandline food webs as they provide an important food source for many species of predatory fish and birds (Ugolini 1997, Laffaille *et al.* 2001, 2006, Arcas 2004, Hample *et al.* 2005, Minderman *et al.* 2006). Although *T. deshayesii* may have a lower consumption rate than *O. gammarellus* (Dias and Hassell 2005) and *O. gammarellus* was more abundant during the box-coring survey of Wembury strandline, *T. deshayesii* was selected for use in the experiments described in Chapter 3. *Talorchestia deshayesii* is the smallest of the three amphipods, and thus its mass was more similar to the fly larvae used in Chapter 3. Furthermore it was found in high, and similar, abundances to those of *O. gammarellus* when pitfall traps were placed in the high tide strandline at Wembury. There is a relatively large amount of natural history information on strandline amphipods in general (e.g. Bulnheim and Scholl 1986, Conceicao *et al.* 1998, De Mattaeis *et al.* 2000, Ketmaier 2003, Davolos and Maclean 2005), their taxonomy and identification (e.g. Harzsch, 2004, 2006, Spicer and Janas 2006). Similarly talitrid ecophysiology and tolerance have been well defined (see Spicer *et al.* 1987 and Morritt and Spicer 1998 for reviews, also; Morritt and Ingolfsson 2000 for temperature and salinity tolerance; Ugolini *et al.* 2005, for heavy metal accumulation and tolerances; Calosi *et al.* 2005 for osmoregulation ability). A number of studies have also investigated these amphipod's orientation ability (Scapini *et al.* 1992, Borgioli *et al.* 1999, Scapini 2006, Ugolini *et al.* 2006, Papi *et al.* 2007) and diurnal activity cues and mechanisms (Fallaci *et al.* 1999, Nardi 2000, Nardi *et al.* 2003, Ammar *et al.* 2006, Ugolini *et al.* 2007). Research into the use of talitrid amphipods as biomarkers has also been well investigated (Moore *et al.* 1991, Marsden and Rainbow

2004, for *O. gammarellus*, Ugolini *et al.* 2004, for *Talitrus saltator* Fialkowski *et al.* 2003 for *T. saltator* and *T. deshayesii*, Rainbow *et al.* 1989, for all three species).

Talorchestia deshayesii is the smallest of the three amphipod species found at Wembury, with an average length of 10 mm. It occurs in sandy sediment like *T. saltator*, although there may be segregation of these two species due to grain size (Dahl 1946). When there was an absence of wrack, *T. deshayesii* was generally found lower down the shore than *O. gammarellus* and *T. saltator* (*pers. obs.*).

Although the distribution of *T. deshayesii* is less well known the three species of amphipod found at Wembury are all considered to be Mediterranean-Atlantic species, extending from the Mediterranean to Iceland and northern Norway (Dahl 1946, Lincoln 1979, Marques *et al.* 2003). *Orchestia gammarellus* and *T. saltator* are semiannual, with iteroparous females appearing to produce at least two broods per year, resulting in a bivoltine life cycle (Moore and Francis 1986, Wildish 1988, Weslawski *et al.* 2000, Marques *et al.* 2003, Anisimova 2004). Cohorts born early in the reproductive period (spring) have been found to reproduce in the same season, but will not live as long and most will probably not survive the winter. Cohorts born later in the reproductive period will live longer (throughout the winter) becoming sexually active and breeding in the next reproductive period (Marques *et al.* 2003). Although evidence of this reproductive cycle in *T. deshayesii* is lacking, a closely-related species *Pseudorchestia (*as *Talorchestia) brito* displayed the same bivoltine life cycle and breeding patterns as *O. gammarellus* and *T. saltator* (Goncalves *et al.* 2003), breeding in this species was also thought to be controlled by temperature (Goncalves *et al.* 2003).

2.4.10.2 Dipterans

The dipteran larva species used in the experiments presented in this thesis are *Coelopa frigida* (Fabricius, 1805), *Coelopa pilipes* (Haliday 1838) and *Dryomyza anilis*

(Fallen, 1820). Coelopidae and Dryomyzidae only occur on beaches with a steady supply of stranded kelp (Dobson 1974).

The dipteran species used in this thesis all displayed good survivorship in the laboratory. As with the talitrids, all three species were found to co-occur at the sample site throughout the year. All three species are obligately dependent on decaying brown algae for breeding and as adults can reach such high population densities that they are of interest as a nuisance to beach tourists (Poinar 1977). As previously mentioned Diptera can make up an important part of the strandline assemblage in terms of abundance (Section 2.3.2), although much less is known with regards to dipteran consumption rates. Wrack and associated microbes and Fungi have been identified as the food source of the two *Coelopa spp.* (Rowell 1969, Cullen *et al.* 1987, Hodge and Arthur 1997). Similarly, *D. anilis* larvae are saprophagous and can feed, grow and mature on dead animals and live fungal matter (Barnes 1984). Owing to the high abundance of *C. frigida* and *C. pilipes,* these species have been identified as important in wrack decomposition (Section 2.5). As with the amphipods, dipteran larvae provide a potentially important food source for predatory strandline beetles (Backlund 1945, Joy 1976).

Additionally, as the dipteran larvae exhibit a wide range of body sizes (Figure 2.6 e, and f, Shuker and Day 2002, Laamanen *et al.* and references therein 2003), and consume wrack, they make ideal prey items with which to test the use of scaling laws to predict trophic interactions and decomposition in Chapter 5 of this thesis.

Coelopa frigida is arguably the most widespread species of the kelp fly used in this study (Laamanen *et al.* 2001). Its range extends from Russia (Barents Sea) through the Baltic region, the North Sea, Faroe Islands and Iceland to the northernmost parts of the North American coast (Hennig 1937 in Backlund 1945). *Dryomyza anilis* is commonly distributed throughout Europe and North America (Barnes 1984). At

Wembury, all kelp-fly species aggregated in high densities in deeper anaerobic layers of the wrack, although *D. anilis* was found in slightly drier areas than the other two species. *C. pilipes* and *C. frigida* larvae were found at all instar stages and ranged between 3-20 mm in length. *D. anilis* was found at all instar stages but was often smaller than the two species of *Coelopa,* rarely was it over 10 mm length. The different species of larvae were often found in species-specific aggregations, either due to the divergence by species in oviposition, or due to interference, competition or environmental preferences.

The majority of work concerning dipteran larvae has investigated the population genetic (Day *et al.* 1983, Laamanen *et al.* 2001), sexual selection and reproductive behaviour of all three species separately (Day 1983, Day *et al.* 1987, Dunn *et al.* 2002, 2005, Blyth and Gilburn 2005). There are, however, a few studies that have investigated *C. frigida* and *C. pilipes* development and growth when reared in multi-species environments. Reproductive output and dominance hierarchy between *C. frigida* and *C. pilipes* have been shown to differ in response to the environmental conditions, the development parameters measured and density-dependent effects (Leggett 1993, Philips *et al.* 1995, Hodge and Arthur 1997). *Coelopa frigida* has been seen to inhibit the growth and reproductive output of *C. pilipes* larvae when these two species are reared together (Hodge and Arthur 1997). *Coelopa pilipes* has been observed to reach higher abundances at warmer temperatures (Backlund 1945) and warmer temperatures have been shown to increase its competitive ability (Philips *et al.* 1995). There is relatively little information available on the behaviour and interactions of *D. anilis* although Barnes (1984) gives an excellent overview of *D. anilis* larval biology and summarises previous observations and studies on this species.

2.4.10.3 Coleopterans

The four predatory staphylinid strandline beetles used in the experiments presented in this thesis belong to two sub-families; thus *Cafius xantholoma* (Gravenhorst) *Remus sericeus* (Holme) and *Cafius xantholoma variolosus* (Sharp) are Staphylinninae, while *Polystoma algarum* (Fauvel) is a member of the sub family Aleocharinae. *Cafius variolosus* is a variety of *C. xantholoma*, and is morphologically distinct, being slightly larger with a much larger head and mouth parts (Joy 1932). *Cafius xantholoma variolosus* has been classified either as a sub-species, a variety of *C. xantholoma* or a distinct species. However, for the purpose of this thesis *Cafius xantholoma variolosus* is considered as a separate species from *C. xantholoma* as the former not only has a morphology that is easily distinguishable from that of *C. xantholoma*, but its size-class distribution is also distinct from that of *C. xantholoma* (c.f Figure2.7a, b). Furthermore, in preliminary laboratory feeding trials *Cafius variolosus* was observed to behave much more aggressively to both prey and handling than *C. xantholoma*. All species are classed as rove beetles which form one of the largest families of insects in the world with over 32 000 described species. Most rove beetles are predatory and inhabit moist environments such as decomposing organic matter (Joy 19732, Campbell and Davies 1991). Many members of the subfamily Aleocharinae are obligate external parasitoids on the pupae of Diptera encased within the puparium (Campbell and Davies 1991). All the species used have been found, and/or are abundant, in strandlines across central and southern Europe and Fennoscanida (Backlund 1945, Campbell and Davies 1991).

Owing to their high abundance in the strandline, laboratory survivorship, measurable consumption rates and large range of body sizes these four species of beetle made ideal test organisms in assessing trophic interactions and ecosystem process in the strandline. The four beetle's size range, in terms of wet mass is shown in Figure 2.7.

The variability in body size both within and between species makes them ideal organisms to investigate the use of scaling laws in predicting trophic interaction strength in Chapter 5. Although there is little information on the feeding habits and diet breadth of these beetles, previous observation and preliminary trials showed them to consume considerable numbers of dipteran larvae (e.g. Orth *et al.* 1977, cited in Lavoie 1985) suggesting that they may be important in strandline food webs and that they may indirectly have a large impact on processes like decomposition. However, their overall influence on prey dynamics and ecosystem process will also depend largely on their abundance, which in Wembury (Figure 2.6) and elsewhere, can be highly variable (see Sections 2.3 and 2.4).

In terms of feeding behaviour only observational data on *Cafius* is available. Backlund (1945) fed individual *Cafius* beetles (in isolated dishes on moistened paper) a range of food items; *Cafius* were observed to feed on all dead dipteran larvae, live *C. frigida* larvae but not *Orygma luctuosa*, and neither species after they had pupated, consuming an average of 1-3 larvae a day. *Cafius* was seen to consume enchytraeid worms and smaller sized larvae preferentially. Amphipods were only consumed once dead with the exception of juvenile *O. gammarellus* which were, *"...sometime attacked but always unwillingly"* (Backlund 1945). Feeding rates in *Cafius* have also been seen to increase after 72 h starvation and 2 h of "settling time" (where they were placed in the mesocosm before introduction of prey). Using ten beetles per mesocosm more prey items and prey mass loss was observed for dead *O. gammarellus* than *C. pilipes*. *C. frigida* had the lowest average mass loss in the experimental trials (E. McAfee *pers. comm.*). When live prey was introduced into the mesocosms larvae were preferentially consumed (E. McAfee *pers. comm.*). Increasing the density of *Cafius* also appeared to increase the *per capita* consumption rates (E. McAfee *pers. comm.*) although due to statistical averaging this conclusion may be biased, as by chance alone more individuals

displaying high consumption rates would have been included in replicas with a high density of *Cafius*. Overall consumption rates were very varied but were analogous with Backlund's feeding trials (1945), 1-3 larva individuals over a 20 h period (E. McAfee *pers. comm.* and *pers. obs.*).

Very little natural history information is available on the beetle species used in this investigation and what do exist are single-point observations. Many species of insects may enter a state of torpor, during colder months where metabolism, activity and feeding are reduced (Tauber et al 1986) this has alos been observed in some species of rove beetles (Nield 1976). As previously mentioned (Section 2.4.2) behaviour akin to that expected if beetles were in a state of torpor was observed in all four species from Wembury strandline. The species were observed in much lower densities in the strandline during winter months (c.f. Figures 2.5a,b) although *Cafius* spp and *R. sericeus* were found during these periods in high abundances under large flat stones above the high tide mark, the absence of *P. algarum* from the entire shore was notable during the winter months. The species were also observed to display massive up-shore migrations during flooding tides. This was especially noticeable on particularly high spring tides when the entire beach was covered in migrating beetles and it was impossible to walk on the shore without stepping on hundreds of *Cafius* and *Remus*.

There is no previously reported information on the ecophysiology of these four beetle species. However, in preliminary mesocosm trials the physical and environmental conditions appeared to affect the consumption rates and feeding behaviour of all four species. Survival was greatest when 50ml of distilled water was added to mesocosms (*pers. obs.*) and consumption was highest when ridgid mesocosms were employed (Polypropylene containers 17cm*11.5cm*4cm, 782cm^3 V = 0.782l) rather than plastic zip seal bags (1cm by 25cm). Furthermore in many instances they did not feed

extensively when larval density was less than 12 individuals per 0.782l polypropylene container. The beetles did not feed when placed in large Petri dishes with moistened filter paper. In only one instance was a beetle (one *C. variolosus* individual) observed to consume a live amphipod (*T. saltator*).

2.5 Concluding Remarks

The strandline can be broadly characterised as an ephemeral and transient environment playing host to a wide diversity of species although dominated by a few eucoenic, opportunistic species in high abundances. There are clear temporal trends in assemblage diversity and individual species abundances in some strandlines although these patterns are not universal to all strandlines where small spatial variability may be greater than temporal changes in species assemblages.

The inputs to, and even the formation of, strandlines can be variable both temporally and spatially (by composition and volume) and the species colonizing these habitats are able to exploit, survive and flourish in very disturbed regimes. Thus the behaviour of these species in laboratory mesocosms that replicate the strandline environment is likely to reflect, or be within, their natural ranges. The strandline and its fauna provide an excellent model system to manipulate in simple laboratory mesocosms.

Despite the strandline's perceived importance as a coastal transition zone linking terrestrial and marine environments, and the importance of process like decomposition in the strandline, relatively little is known regarding the influence of the biota on decomposition. Information on energy flow in strandline habitats is limited to a handful of studies and although there is some information on individual species' feeding rates, the trophic and non-trophic interactions of strandline species and the implications of

these interactions for decomposition has not been studied. Therefore investigations into predatory and consumer strandline species interactions and feeding will contribute to our understanding of strandline trophic and non-trophic interactions and how they contribute to decomposition.

CHAPTER 3: THE IMPORTANCE OF SPECIES IDENTITY, DIVERSITY, AND INTERACTIONS FOR ECOSYSTEM PROCESS IN THE STRANDLINE

3.1 Introduction

This chapter will investigate the effect of species identity, diversity and interactions on ecosystem processes, using four commonly occurring strandline detritivores and measuring decomposition.

3.1.1 Rationale

In the current climate of biodiversity loss understanding the link between diversity and ecosystem processes is one of the most pressing issues facing scientists today (Section 1.2). The vast majority of previous BDEF studies have mainly focused on terrestrial grassland systems and consequently the effects of faunal diversity on ecosystem processes are far less studied than those of plant diversity (See Section 1.5).

Despite its importance in ecological systems, decomposition has received relatively less attention than other ecosystem processes (Section 2.5) and its study is generally confined to terrestrial habitats or stream environments, investigating the effects of leaf litter diversity on decomposition rates (see Mikola *et al.* 2001 in Loreau *et al.* 2001b for review, Blair *et al.* 1990, Wardle *et al.* 1997a, 1997b, Hector *et al.* 2000, 2002, King *et al.* 2002, Madrich and Hunter 2004, Swan and Palmer 2004, for examples). The effects of detritivore species diversity on detrital processing rates have only recently been investigated (Jonsson and Malmqvist 2000, 2002, 2003a, 2003b, Cardinale *et al.* 2002, Cardinale and Palmer 2004, Zimmer *et al.* 2002, 2005) and even then solely in terrestrial or freshwater systems. Although marine environments contribute a disproportionately large percentage of the world's biodiversity as measured

in phyla (Ray and Grassle 1991), the effect of reduced diversity on ecosystem process therein has been much less studied (see Emmerson *et al.* 2001 for a review of marine systems and Covich *et al.* 2004 for benthic freshwater and marine systems).

Despite the perceived importance of the strandline as a coastal transition zone linking terrestrial and marine environments, and the importance of processes like decomposition, relatively little is known regarding the influence of the biota on decomposition (Section 2.5). Assemblages in coastal regions are likely to experience intense stress and perturbations from increasing anthropogenic activity. Nearly 40% of the entire world's population live within 100 km of the coastal fringe making coastal population densities nearly three times that of inland areas (Millennium Ecosystem Assessment 2005). As population density and economic activity in the coastal zone increase, anthropogenic pressures on coastal ecosystems will increase, e.g. habitat conversion, land cover change, pollutant loads, and introduction of invasive species and even 'maintenance'. All these pressures can potentially lead to biodiversity loss, e.g. current practices of beach cleaning reduce species diversity and abundance (e.g. Smith 2003, Schlacher *et al.* 2007 and references therein).

3.1.2 Importance of Segregating Species Identity, Diversity and Interactions

The importance of segregating effects of species identity, diversity and interactions in BDEF research are discussed more fully in Section 1.6 and are summarised below.

1) From a purely economic standpoint, if species identity determines ecosystem processes then conservation effort should be directed at identifying and protecting species that have large influences on ecosystem processes. Conversely, if species diversity (irrespective of identity) determines ecosystem processes then conservation efforts should focus on conserving entire assemblages. Furthermore, if species

interactions determine ecosystem processes then identifying species which interact positively and negatively with respect to ecosystem processes will enable conservation effort to be allocated more effectively.

2) Without segregating the effects of species identity from that of diversity the importance of species diversity in determining ecosystem processes cannot be assessed (Section 1.6).

3) Understanding the relative importance of species identity and species interactions may also enable a better understanding of the mechanism behind diversity-ecosystem process relationships (Sections 1.6, 1.7). This is because most mechanistic explanations for how diversity and ecosystem processes are linked, are based on species identity (trait allocation between species) and/or species interactions (Sections 1.4, 1.7).

4) If, as suggested, there is no universal trajectory between diversity and ecosystem processes (Schlutze and Mooney 1994, Emmerson *et al.* 2001, Loreau *et al.* 2001b, c, 2002, Kinzig *et al.* 2002, Covich *et al.* 2004, Bell *et al.* 2005) then identifying species and interactions that have large influences on ecosystem processes is of major importance for future predictions of these processes as species become extinct.

3.1.3 Detritivore Species Identity, Diversity and Interactions

Decomposition in intertidal (Zimmer *et al.* 2002), freshwater (Crowl *et al.* 2001, Ruesink and Srivastava 2001) and marine systems (Duffy *et al.* 2001) has been shown to differ and is dependent on the identity of detritivore species. However the relative importance of species diversity (Crowl *et al.* 2001, Zimmer *et al.* 2002) and species interactions (Crowl *et al.* 2001, Ruesink and Srivastava 2001, Duffy *et al.* 2001, Zimmer *et al.* 2002) have not been investigated explicitly. In contrast, species diversity rather than species identity has also been shown empirically to affect ecosystem process

when *in situ* assemblage diversity and leaf litter decomposition was measured in the field (Jonsson *et al.* 2001, Huryn *et al.* 2002) and when invertebrate resource processing was measured in mesocosm manipulations (Jonsson and Malmqvist 2000, 2003b, Cardinale *et al.* 2002, Cardinale and Palmer 2004). However, whilst overall positive diversity-ecosystem process effects were found (without identifying the balance of positive, negative and additive interactions) the effect of single species removal on ecosystem processes cannot be discerned. [1]

There are two studies, of which I am aware, that have measured the effects of species identity, diversity and species interactions on ecosystem processes (Jonsson and Malmqvist 2003a, Zimmer *et al.* 2005). Zimmer *et al.* (2005) constructed an experimental mesocosm with isopods and earthworms in isolation and in combination, with oak, alder and mixed leaf litter separately. Although detritivore diversity was significant for every measure of decomposition, additive and negative species interactions were not consistent for every measure of decomposition and depended on the litter substrate. Jonsson and Malmqvist (2003a) manipulated different functional groups of freshwater species. They found that diversity positively affected resource processing in only two of the four functional groups manipulated. As diversity increased from one to three species, two species combinations had additive negative or positive effects on processing rates and it was the balance of these interactions that determined the overall positive or negative effect of diversity with processing rates.

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[1]Considering the case where three species (A, B and C) are manipulated and ecosystem processes at each diversity level, as an average of treatments within that diversity level show an increase in ecosystem process with diversity. All species may have equitable, single species processing rates but at the two species level, A & B may interact positively, A & C, and B & C in an additive manner resulting in an average value of ecosystem processing at the two species level that is greater than the average for single species rates. Thus despite the fact that single species identity does not effect ecosystem processes, in a three species assemblage whether species A, B or C is removed will have large implications for ecosystem processes.

3.1.4 Aims and Objectives

The present study aims to investigate the combined effect of abundant, co-occurring detritivores from the strandline on a key ecosystem process, wrack decomposition. Using all possible species combinations of single, two, three and four species permutations, in a substitutive design (maintaining constant total density and similar biomass) the effect of within functional group diversity, identity and species interactions on decomposition is tested empirically. Three dipteran larva species; *Coelopa frigida, Coelopa pilipes, Dryomyza anilis*, and one talitrid amphipod, *Talorchestia deshayesii* were used. All four species can co-occur in, and even dominate, strandline communities on NW European shores (Sections 2.3, 2.4, 2.7.1, 2.7.2) and all four species are potentially key species in the decomposition of wrack (Sections 2.5, 2.7.1, 2.7.2). *Talochestia deshayesii* was selected over the other two amphipod species that were found in the strandline as the smallest amphipod species found at Wembury. Thus its mass was more similar to that of the fly larvae than the other two amphipods. Using all possible species combinations the effects of species identity and diversity can be segregated. This design also avoids problems encountered with previous designs where species were drawn from a regional species pool and randomly allocated to different diversity treatments. In previous designs positive diversity ecosystem processing effects may be due to the "chance" inclusion of a species with a disproportionally high effect (see Section 1.6 for more detailed discussion). By comparing observed decomposition in multi-species treatments with those expected based on single-species processing rates, species that interact in a positive, negative and additive manner can be identified and the overall contribution of species interactions to decomposition inferred (Section 1.6).

3.1.5 Rationale Behind the Use of a Substitutive Design.

The substitutive design employed in this study will limit the mechanistic interpretation of species interactions or diversity effects (Underwood *et al.* 1978, 1984, Benedetti-Cecchi 2004). As diversity increases, the relative density of individual species decreases thus the effects of intraspecific and interspecific competition and facilitation on ecosystem processes cannot be disentangled (See Section 1.6). It was not logistically possible to manipulate both the relative density of individual species and the total density of all species at all diversity levels [as suggested by Underwood *et al.* (1978, 1984) and Benedetti-Cecchi (2004)] as a possible means of segregating intra and inter specific effects on ecosystem processes. Even by manipulating both relative density and total density of individual species, the exact mechanism operating behind species interactions may still be unclear if both intraspecific competition and interspecific facilitation occur simultaneously. Furthermore, using an additive design where the total number of species increases with diversity, the amount of space and resources available for each individual will decrease. Thus to limit potential bias introduced by unequivocal resources and space, at each diversity level, mesocosm and resource volume would have to increase concurrently with diversity, further increasing the number of replicates needed. Therefore a substitutive design was chosen. It is suggested that whatever mechanisms are operating to determine species interactions, realistic patterns of decomposition at reduced species diversity can be identified using this design. This assumption is based on the premise that substitutive designs may have greater relevance in predicting real effects of reduced diversity on ecosystem processes if, when diversity (the number of species) declines, the remaining species in the assemblage compensate for this loss by increasing their abundance (density compensation). Density compensation has been documented in a number of species assemblages (e.g. see Faeth 1984 for a review of insects, Janzen 1973, Faeth and

Simberloff 1981, Southwood *et al.* 1982, for insects, McGrady-Steed and Morin 2000, Jian 2007 for microbes; Parody *et al.* 2001 for birds; Case 1975 for reptiles; Kohn 1978 for aquatic gastropods; Tonn 1985 and Frost *et al.* 1995 for fish, Ernest and Brown 2001 for plant species assemblages). Parody *et al.* (2001), in reanalysing an existing avian population data set covering 50 years, found total avian abundance to remain relatively constant whilst the percentage contribution of individual species changed substantially over time. Similarly Ernest and Brown (2001) examining a long-term data set on rodent and plant populations found plant total abundance to be constant but the relative abundance of different species to change. As there was little changein overall species diversity (the number of different species) in either of these two studies it is impossible to infer whether species increased in abundance in response to other species reducing in abundance (density compensation) or *vice versa*. To expand further, Kohn (1978) in a study of gastropod populations in Easter Island and the Indo-West Pacific, found one species to have increased its abundance in sites with lower gastropod diversity (possibly in response to lower heterospecific abundance), and re-analysis of this data set by Faeth (1984) showed that total gastropod density did not differ between sites irrespective of species diversity. Tonn (1985) used mark-recapture and catch-per-effort methods to estimate species diversity and abundance in five small lakes in Wisconsin over 3 years. Whilst species richness differed between lakes total densities overall were independent of species richness. Unfortunately in all of the examples above, exactly how an assemblage would compensate (in terms of abundance) to the removal of species was not explicitly examined, and the remaining species assemblage was not measured after diversity manipulations. In contrast Case (1975), Janzen (1973) and Southwood *et al.* (1982) all found total density to increase with diversity suggesting a substitutive design where total density remains constant does not reflect the response of natural assemblages to diversity reduction. Case (1975) found the number of lizard species was

inversely correlated with total density. However, as lizard populations were examined at different sites in the Gulf of California the niche space and other factors which could control total lizard density, such as predation intensity and insect productivity, may have differed by site. Similarly, Jansen (1973) found tropical insect abundance to be inversely correlated with species number (diversity) in different sites from Costa Rica and Caribbean islands and likewise Southwood *et al.* (1982) found arthropod abundance to increase with species richness when measuring the invertebrate fauna of six tree species in both Britain and South Africa. Again, in all of these examples how an assemblage would compensate in terms of abundance to the removal of species was not explicitly examined.

The only empirical evidence that a reduction in diversity does not lead to a reduction in total species density (as assumed using a substitutive design) comes from microorganism and zooplankton studies. McGrady-Steed and Morin (2000) and Jiang (2007) set up different diversity treatments using aquatic microbes and found that overall bacterial biomass did not change systematically with species richness (McGrady-Steed and Morin 2000) or remained relatively constant (Lin 2007) irrespective of the species diversity in a treatment. Frost *et al.* (1995) manipulated the diversity of zooplankton in lakes using acidification and measured the biomass of cladocerans, copepods and rotifers. Density remained at high levels despite the reduction in diversity of each component group. How microbial and zooplankton assemblages respond in terms of abundance to reductions in diversity may be similar in strandline detritivore communities. Strandline species in this system can increase their abundance rapidly in response to inputs in wrack (Sections 2.4.2). The notion that strandline detritivores may be able to rapidly increase in abundance as heterospecifics are lost (and thus overall abundance declines) is not inconceivable. Finally as wrack, when present, is unlikely to be a limiting resource in the strandline and in these

experiments, it is unlikely that intraspecific or interspecific competition for food is an important factor and, as it is wrack consumption that we were measuring (decomposition) the substitutive design was employed in this study.

3.2 Materials and Methods

3.2.1 Collection of Animal Material, Wrack and Sediment

Fly larvae, *C. frigida*, *C. pilipes*, *D. anilis*, the amphipod, *T. deshayesii*, cast-up wrack *Laminaria digitata* and underlying sediment were collected, by hand, from spring tide strandlines on Wembury first beach, Devon, UK (48.3°N, 50.4°E) on the 21.07.05. All material was transported to the laboratory in large plastic bags. In the laboratory animal material was sorted by hand according to species and maintained in a number of separate aquaria (vol. = 8l). To mimic strandline conditions each aquarium was lined with sediment from the site (depth = 2cm), overlain with 2-3 fronds of decomposing *L. digitata*. A paper towel soaked in dilute sea water (S = 20 PSU) was placed beneath the aquaria lids to maintain a high relative humidity within. Both lid and towel also prevented escape by larvae and amphipods. All aquaria were kept in the dark in a temperature controlled room, T = 20 ± 1°C for a maximum of 3 d before being used in the experiments described below.

3.2.2 Experimental Design

Sixteen treatments (replicates n = 5) were constructed encompassing all possible combinations of one, two, three and four species and a control (no animal species present). The total number of individuals in each treatment was kept constant (n = 12). Animals of similar mass were selected so that total animal mass in each treatment was similar (mean individual mass of each species across all treatments ± s.e: *T. deshayesii*

0.076 ± 0.009g *C. pilipes* 0.084 ± 0.011 g, *C. frigida* 0.076 ± 0.009 g and *D. anilis* 0.077 ± 0.009 g).

Each replicate consisted of a mesocosm constructed from a plastic container (diam. = 20 cm, height = 10 cm), with pin-pricked air holes around the upper rim. Each container was lined with Plaster of Paris (to a depth of 1 cm), saturated with dilute sea water (S = 20 PSU). A paper towel saturated with the same dilute sea water was carefully trapped under each lid to maintain the high relative humidity essential to the survival of many strandline species (see Backlund 1945). A 2 cm deep layer of pre-autoclaved (30 min at T = 200°C) sediment very-coarse sand[2] was placed over the Plaster of Paris as the amphipod species used is fossorial, and fly larvae were often collected interstitially. To prevent individuals interfering with the Plaster of Paris, two layers of muslin netting were used to separate it from the sediment layer.

Discs (diam. = 2 cm) of pre-autoclaved *L. digitata* (30 min at T = 200°C) were cut with a cork borer and placed in each mesocosm in an overlapping pattern (preliminary observations showed larvae would not feed unless the discs were configured in this way[3]). *Laminaria digitata* was used as it was the most prevalent alga in the strandline at collection times (*pers. obs.*). Furthermore, previous observations (duration = 30 h) using other strandline algae (*Fucus* spp. and *Ulva lactusa* with *T. deshayesii*, *C. frigida* and *C. pilipes*) showed either a preference for *L. digitata* in the case of the fly larvae, or no preference in the case of *T. deshayesii* (where preference was expressed as algal mass loss in g).

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[2]This is based on the mean grain size found at Wembury hightide strandline determined from samples taken at 5 different locations (selected randolmly using a random numbers table, Zar 1999) every other day between, the 16.02.05-28.02.05 analysed using a Malvern Long-bed Mastersizer X with dry sample unit MS66 Software version: 2.19. Based on Folke and Ward's (1957) graphical parameters mean grain size Φ = 0.276 ± 0.106 s.e, and sorting = 0.95, this equates to very course sand on the Wentworth scale.

[3]  *L. digitata* disc configuration

Each mesocosm was then placed separately in a black plastic (opaque) bag in a temperature controlled room, T = 20°C ± 1°C, 12 h light/dark cycle, for the duration of the experiment (40 h). Lid removal during the experiment resulted in considerable disturbance, not least because *T. deshayesii* tended to escape. Consequently, measuring salinity, humidity, mortality and pupation continuously throughout the experiment was considered impractical. Each mesocosm was left for a period of 40 h, before the remaining kelp discs were carefully removed and weighed using a Fisher Brand PS-10 balance, accuracy 0 ± 0.01 mg. Decomposition was expressed as *L. digitata* mass loss (g) per total initial animal mass (g) over the 40 h period. Before the mass of *L. digitata* discs was determined they were rinsed in distilled water and blotted dry using absorbent paper towelling. This method was repeatable and introduced little error into the measurement of *L. digitata* mass (Appendix A1).

3.2.3 Analyses

All statistical analyses were carried out using MINITAB (Version 13.32, Minitab Inc, State College PA). ANOVA tests were used to test for significant differences between means when Levine's test was not significant and the assumption of homogeneity of variance could be upheld. If data did not initially fit the assumptions of ANOVA the data were transformed. If, after logarithmic transformation, data still did not meet the assumption of homogeneity of variance then the non-parametric Kruskall-Wallis test was used. To ensure variable rates of initial animals mass, pupation and mortality were not correlated to *L. digitata* mass loss, correlations were used. If the assumption that data were normally distributed was verified by the Anderson-Darling Normality distribution test Pearson's correlation was used. If data were not normally distributed, even after logarithmic transformation, then Spearman's' rank correlation coefficient was calculated.

3.2.3.1 Species Identity

Laminaria digitata mass loss (g.g-1) between single-species treatments of *T. deshayesii, C. pilipes, C. frigida and D. anilis* was analysed using a one-way ANOVA on untransformed data.

3.2.3.2 Species Diversity and Identity Combination

A fully-nested Type III (unbalanced) ANOVA model was used to separate the effects of species diversity from identity combination, where species identity combination (treatment) was viewed as a factor nested within species diversity.

3.2.3.3 Species Interactions

Positive, negative and additive species interactions were determined by comparing mean observed *L .digitata* mass loss rates with mean expected loss rates for all two, three and four species combinations (See Box 3.1 below).

A two-tailed test for interval difference was done for each multi-species treatment, using the global mean values of observed *L. digitata* mass loss – mean values of expected *L. digitata* mass loss ± 2.84 standard deviations (s.d.) (2.84 s.d. related to the Bonferroni corrected 0.05 significance level; eleven such tests were carried out P = 0.025/11, = 0.0023 which relates to 2.84 s.d.) (Box 3.1).

Box 3.1

Expected decomposition

Two species treatments: $We_1(X_1/W_1) + We_2(X_2/W_2)$.
Three species treatments: $We_1(X_1/W_1) + We_2(X_2/W_2) + We_3(X_3/W_3)$
Four species: $We_1(X_1/W_1) + We_2(X_2/W_2) + We_3(X_3/W_3) + We_4(X_4/W_4)$.
Where X = global means of *L. digitata* mass loss in single species treatments;
W = mass of individuals in the single species treatment;
We = mass of individual species in the mixed species treatments.

Standard deviation for observed decomposition

= variance/ ($\sqrt{}$ n).

Standard deviation for expected decomposition

Two species treatment = error MS/$\sqrt{}$n * $\sqrt{(We_1/W_1)^2 + (We_2/W_2)^2}$
Three species treatment = error MS/$\sqrt{}$n * $\sqrt{(We_1/W_1)^2 + (We_2/W_2)^2 + (We_3/W_3)^2}$
Four species treatment = error MS/$\sqrt{}$ n* $\sqrt{(We_1/W_1)^2 + (We_2/W_2)^2 + (We3/W_3)^2}$

Standard deviation for observed-expected decomposition

Two species treatment = (Standard deviation for observed decomposition)*($\sqrt{(1+((We_1/W_1)^2 + (We_2/W_2)^2)}$
Three species treatment = (Standard deviation for observed decomposition)*($\sqrt{(1+((We_1/W_1)^2 + (We_2/W_2)^2 + (We_3/W_3)^2)}$
Four species treatment = (Standard deviation for observed decomposition)*($\sqrt{(1+((We_1/W_1)^2 + (We_2/W_2)^2 + (We_3/W_3)^2 + (We3/W_3)^2)}$

Where 5 = the number of replicates, and variance was taken from the $\sqrt{}$error MS.
Where error MS = within group adjusted means squares.
Where n= the number of replicates.

3.3 Results

3.3.1 Initial Animal Mass, Larval Pupation and Mortality

Despite best efforts initial animal mass differed between treatments ($P < 0.001$, Appendix A2) and species levels ($P < 0.001$, Appendix A3). There was no correlation between initial animal mass and kelp mass loss, (Pearson correlation = -0.107, P =

0.362[4]). Total animal mass change, was very small and varied little between treatments (mean = 0.015 g ± 0.006 s.e.).

Table 3.1 Mean ± s.e. total animal mass (g) and mass change for each treatment.

Treatment	Mean initial mass (g) ± s.e.	Mass change (g) ± s.e.
C. pilipes	0.336 ± 0.019	0.023 ± 0.012
C. frigida	0.221 ± 0.016	-0.033 ± 0.023
D. anilis	0.228 ± 0.011	-0.020 ± 0.004
T. deshayesii	0.410 ± 0.013	0.017 ± 0.014
C. pilipes & C. frigida	0.331 ± 0.014	0.010 ± 0.016
C. pilipes & D.	0.393 ± 0.007	0.031 ± 0.011
C. pilipes & T. deshayesii	0.477 ± 0.035	-0.042 ± 0.029
C. frigida & D. anilis	0.534 ± 0.091	0.013 ± 0.038
C. frigida & T. deshayesii	0.958 ± 0.019	0.060 ± 0.023
D. anilis & T. deshayesii	0.615 ± 0.016	0.034 ± 0.026
C. pilipes, C. frigida & D. anilis	0.320 ± 0.034	0.073 ± 0.031
C. pilipes, D. anilis & T. deshayesii	0.364 ± 0.016	0.024 ± 0.027
C. frigida, D. anilis & T. deshayesii	0.600 ± 0.020	-0.016 ± 0.009
C. pilipes, C. frigida, D. anilis & T. deshayesii	0.451 ± 0.017	0.021 ± 0.020

No larval mortalities were observed during the experiments. The proportion of larval pupation events differed markedly both between treatment ($P < 0.001$, Appendix A4) and species level ($P < 0.001$,Appendix A5). There was no correlation between initial animal mass and kelp mass loss g.g-1 (Pearson correlation on Spearman ranked data = 0.130, P = 0.266)[5].

Talorchestia deshayesii mortality was generally very low with a median of 0 %. However, there was a significant effect of treatment ($P < 0.001$, Appendix A6) and species diversity ($P < 0.001$, Appendix A7) on *T. deshayesii* percentage mortality.

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[4] Anderson-Darling test of normal distribution *L. digitata* mass loss g.g-1. Mean = 0.8815, s.d = 0.8109, n = 75, AD = 5.098 $P < 0.005$, Log_{10} *L. digitata* mass loss g.g-1 Mean = 0.1710, s.d = 0.3131, n =75, AD = 0.274, P = 0.656 Anderson-Darling test of normal distribution Initial animal mass. Initial animal mass g. Mean = 0.4458, s.d. = 0.1885, n = 75, AD = 2.172, $P < 0.005$ Log_{10} initial animal mass g. Mean = 0.3853, s.d. = 0.17723, n = 75, AD = 0.358, P = 0.445

[5] Anderson-Darling test of normal distribution % pupation. Mean =13.93, s.d. =18.25, n =70, AD =7.128, $P < 0.005$ Log_{10}% pupation. Mean = 0.6841, s.d. = 0.7031, N = 70, AD = 6.144, $P < 0.005$ Hence non-parametric Spearmans Rank correlation coefficient test was used.

However, there was no correlation between *T. deshayesii* percentagemortality % and kelp mass loss (Pearson correlation of Spearman ranked data = -0.056, P = 0.633[6]).

Although initial animal mass, larval pupation and amphipod mortality did differ between treatments, none of these factors was correlated with decomposition so they were not considered to be factors affecting decomposition in further analyses.

3.3.2 Decomposition

Laminaria digitata mass loss was not observed in three of the five control replicates. The remaining two replicates sustained 0.001g *L. digitata* mass loss over 40 h (Figure 3.1). Thus decomposition in the absence of animal species was negligible and is discounted from the analyses that follow.

The largest mean *L. digitata* mass loss (2.398 g.g-1 animal mass) was recorded when all three larval species were placed together (Figure 3.1). Of the single species treatments the amphipod *T. deshayesii* exhibited the greatest mean *L. digitata* mass loss (1.059 g.g-1 animal mass, Figure 3.1). However, treatments containing the amphipod in two and three species combinations were generally lower than those without. Of all the two species treatments *C. pilipes & D. anilis* displayed the greatest rates of *L. digitata* mass loss (1.808 g.g-1 animal mass, Figure 3.1). This was the second highest *L. digitata* mass loss observed of all treatments across all species combinations. Interestingly, when *C. pilipes & D. anilis* were incubated in isolation, the two lowest mean *L. digitata* mass losses were recorded (0.293 and 0.321 g.g-1 animal mass, respectively, Figure 3.1).

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[6] Anderson-Darling test of normal distribution of talitrid mortality. Talitrid mortality, Mean = 2.708, s.d. = 4.172, n =40, AD = 5.906, P< 0.005 Log_{10}% talitrid mortality. Mean = 0.2979, s.d. = 0.4257, n = 70, AD = 6.274, P <0.005 Hence non-parametric Spearmans Rank correlation coefficient test was used.

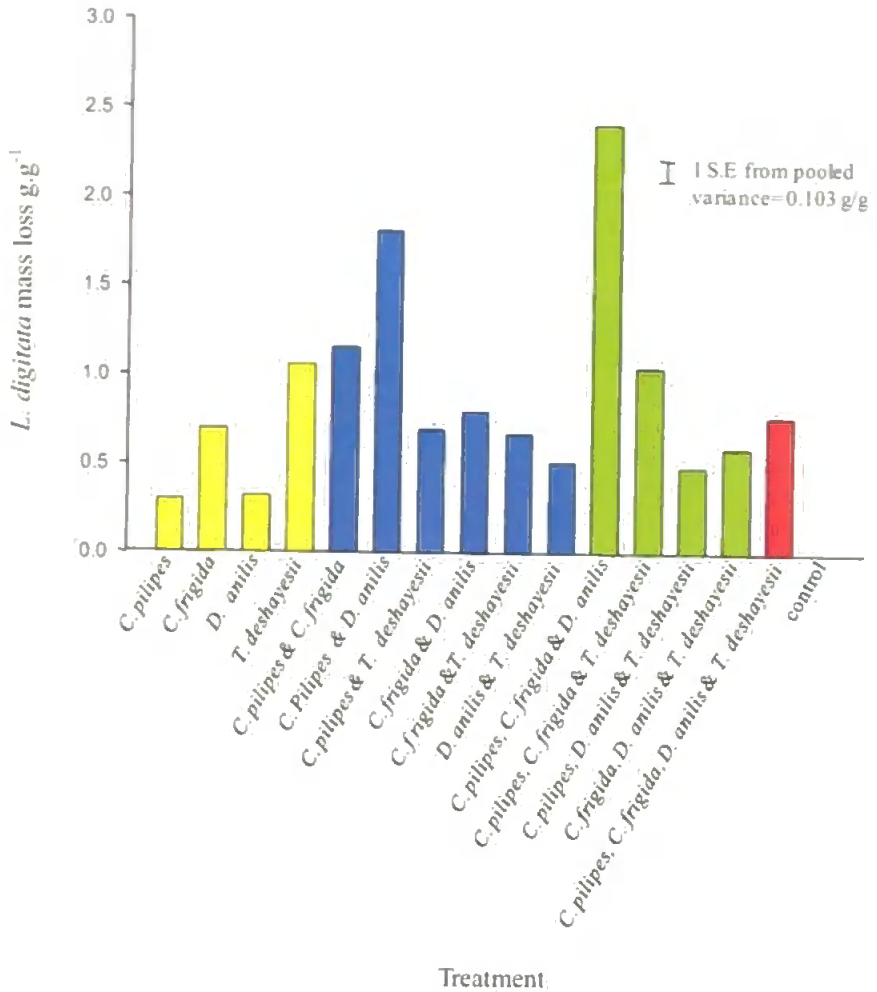

Figure 3.1 *L. digitata* mass loss $g.g^{-1}$ (mean ± s.e.). Yellow = single species treatments, blue = two species treatments, green = three species treatments, red = four species treatments.

3.3.3 Species Identity and Diversity

When species were incubated individually, *L. digitata* mass loss differed between species. The desending sequence of *L. digitata* mass loss in single species treatments was; *T. deshayesii* > *C. frigida* >*D. anilis* ≥ *C. pilipes* (Figure 3.1). The difference in *L. digitata* mass loss between single species treatments was significant ($P = 0.0011$, Appendix A8), although only the amphipod treatment displayed significantly greater mean decomposition values than *D. anilis* and *C. pilipes* ($P < 0.05$ Tukey's (HSD) *post hoc* test, Appendix A8). *Laminaria digitata* mass loss increased as more

species were included in a treatment up to the three species level then deceased when all four species were included in a treatment (Figure 3.2). The increase in *L. digitata* mass loss g.g-1 animal mass between species level one, two and three may have been due to the large *L. digitata* mass loss g.g-1 in the two species treatment of *C. pilipes* & *D. anilis* and the three species treatment including all the larval species (Figure 3.1).

Rates of *L. digitata* mass loss were very variable depending on treatment (Figure 3.1) and using a fully-nested ANOVA only nested species treatment, not species level, was significant in explaining the variation in decomposition g.g-1 (Table 3.2). Treatment or species identity combination explained 51.2% of the total variance and species diversity none.

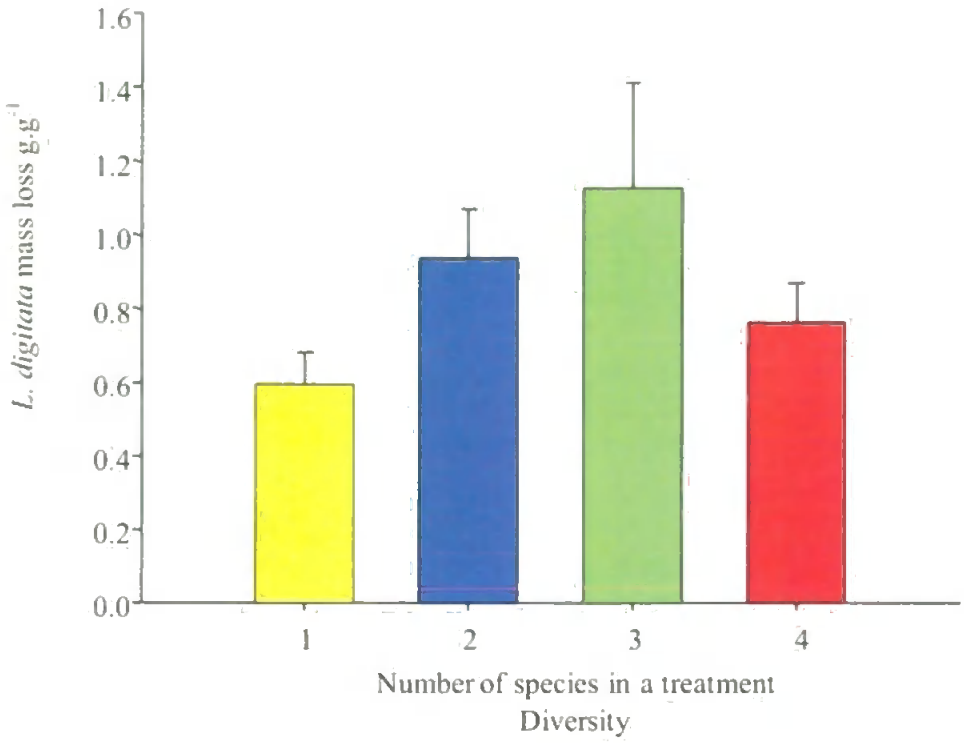

Figure 3.2 *L. digitata* mass loss $g.g^{-1}$ (mean ± s.e.) at each species level.

Table 3.2 Fully-nested ANOVA Type III showing the effect of species diversity, and identity, nested under species diversity on log_{10} *L. digitata* mass loss $g.g^{-1}$.

Source	D.F.	SS	MS	*F*	P	Variance components as % of total
Species level	3	0.6271	0.2090	0.6499	0.0599	0.00
Treatment	11	3.5378	0.3216	6.2447	<0.001	51.20
Error	60	3.0896	0.0515			48.80
Total	74	7.2545				

Levine's Test for equal variances was significant for *L. digitata* mass loss $g.g^{-1}$ between treatment test statistic = 2.196, P = 0.018. Levine's Test for equal variances was not significant for log_{10} *L. digitata* mass loss $g.g^{-1}$ between treatment test statistic species level test statistic =1.429 P = 0.168 and species level test statistic =1.046, P = 0.378.

When treatments containing only the larval species are considered there appears to be an increase in *L. digitata* mass loss as the number of larvae in a treatment increases (Figure 3.1). Larval species level was significant in explaining the variability in *L. digitata* mass loss $g.g^{-1}$ ($P < 0.001$) when *T. deshayesii* was excluded from the analysis. Diversity explained 41.09% and treatment 22.51% of the variability in *L. digitata* mass loss $g.g^{-1}$ (Table 3.3). Although *L. digitata* mass loss in single species larval treatments was significantly lower than treatments containing two or three larval species, treatments at the two and three species level were not significantly different from each other ($P > 0.05$ in each case, Appendix A9).

Table 3.3 Fully-nested ANOVA Type III showing the effect of larva species diversity, and identity, nested under species diversity, on $\log_{10}$*L. digitata* mass loss $g.g^{-1}$.

Source	D.F.	SS	MS	*F*	P	Variance components as % of total
Larval treatment	*4*	1.14013	0.28503	*4.09*	0.010	22.51
Larval species level	*2*	2.25491	1.12745	16.19	<0.001	41.09
Error	*8*	1.95002	0.06964			36.40
Total	*4*	5.34506				

Levine's Test for equal variances was significant for *L. digitata* mass loss $g.g^{-1}$ between treatments with larvae test statistic = 3.79, $P < 0.001$. Levine's Test for equal variances was not significant for $\log_{10}$ *L. digitata* mass loss $g.g^{-1}$ between treatments with larvae test statistic species level test statistic = 1.52 P = 0.137 and species level (larvae only) test statistic = 11.24, P = 0.303.

3.3.4 Species Interactions

The trend of increasing mean *L. digitata* mass loss with increasing larval diversity (in the absence of *T. deshayesii*) could be seen when observed and predicted rates of decomposition were compared (Figure 3.3). Treatments containing only larval combinations generally showed higher observed values of decomposition than predicted using the sum of single species processing rates (Figure 3.3). Observed mean *L. digitata* mass loss $g.g^{-1}$ was significantly greater than expected values, at both the 95% and

99.54% (Bonferroni corrected) significance level for all multi-larval combinations, with the exception of *C. frigida* & *D. anilis* treatments where there was no significant difference (Figure 3.3).

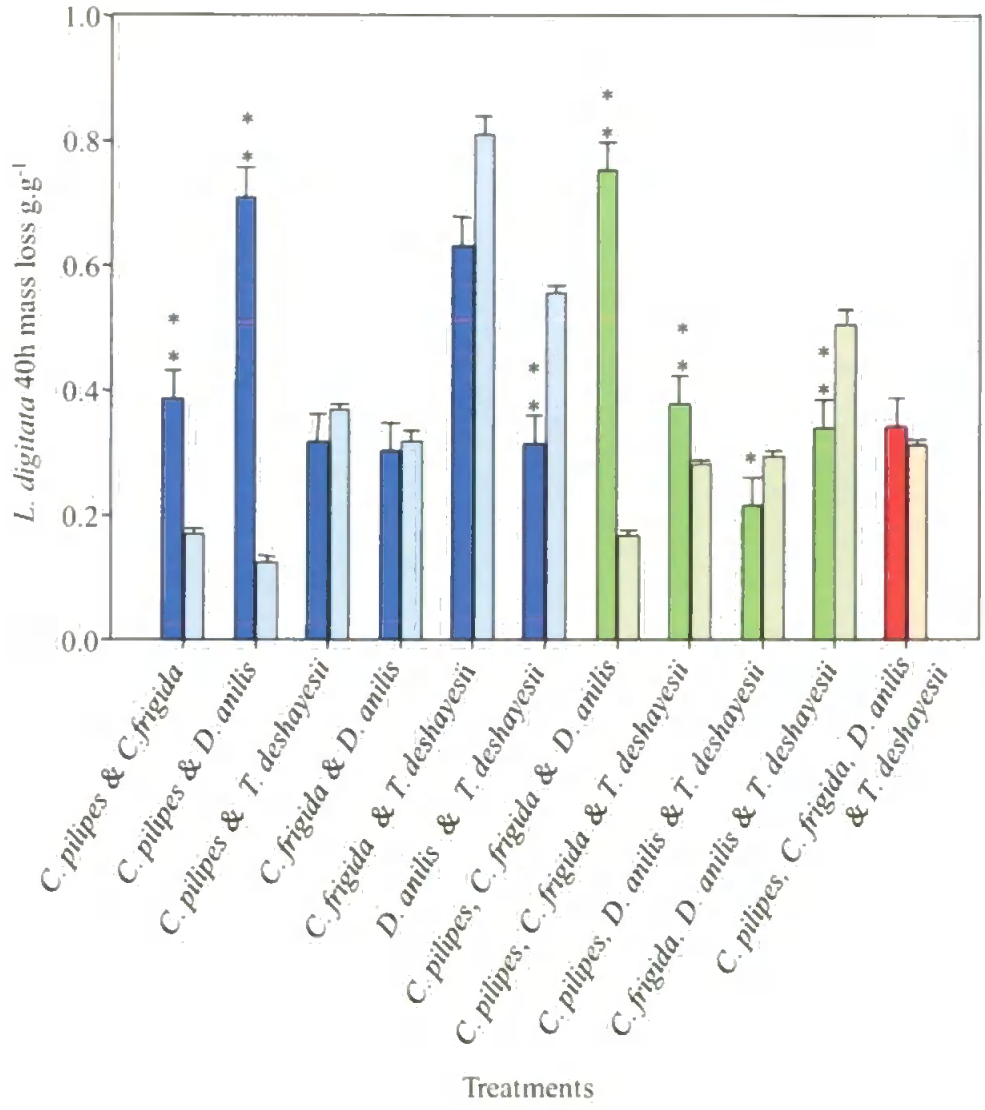

Figure. 3.3 Observed and expected values of decomposition $g.g^{-1}$ for all multi-species treatments (mean ± s.e.) over 40h. * = significant difference at the 95% significance level, ** =significant difference at the 99.54% significance level. Light coloured bars = expected values of *L. digitata* mass loss. Dark coloured bars = observed *L .digitata* mass loss g.g-1, Blue= two species treatments, green = three species treatments and red = four species treatment. s.e = (s.d/ (√ n)) (see Box 3.1).

Laminaria digitata mass loss $g.g^{-1}$ in combination treatments containing *T. deshayesii* depended largely on the other larva species in the treatment (Figure 3.3). Mean decomposition in treatments containing *T. deshayesii* were lower than expected in two treatments, one containing *D. anilis* the other *C. pilipes* & *D. anilis* (Bonferroni corrected significance level). Treatments containing *T. deshayesii* & *C. frigida*, and *T. deshayesii*, *C. pilipes* & *D. anilis* also showed lower than expected mean *L. digitata* mass losses (this was only at the 95% significance level and thus should be treated with caution due to the number of interval tests performed). Observed decomposition was only significantly greater than expected when *T. deshayesii* was incubated with *C. pilipes* & *C. frigida* (at both the 95% and Bonferroni corrected significance level, 99.54%). For the other two treatments containing *T. deshayesii*, decomposition $g.g^{-1}$ rates were not significantly different.

Owing to the large number of Students t-tests performed the chance of incurring a Type II error is increased (i.e. a false positive result). Therefore, the 99.54% significance level reflects the Bonferroni corrected significant level for the number of test employed. Whilst significant differences at the 95% significance level should be viewed cautiously, the Bonferroni correction is an extreme correction and differences at the 95% significance level are likely to be the result of real difference rather than an artifact of the test.

3.4 Discussion

3.4.1 Species Identity

Decomposition in the single species amphipod treatment was higher than any of the single species larval treatments. Previous experiments examining the effects of single species exclusions showed similar results. Litter decomposition has been shown

to be dependent on the identity of the excluded aquatic invertebrate (Crowl *et al.* 2001) or intertidal invertebrate (Zimmer *et al.* 2002). However, when all treatments are considered in this study, it was not the presence or absence of any single species but the species identity combination that explained the variability in wrack mass loss. The presence or absence of any single species did not result in significantly higher or lower *L. digitata* mass loss compared with other treatments at a particular diversity level. Although combinations of *T. deshayesii* and larvae generally resulted in lower observed than expected values of decomposition this was not consistent for all treatments and depended on the larval combination in the particular treatment. In this experiment, species interaction effects arguably played a larger role than species identity in determining processing rates. The relative importance of individual species traits, species interactions and species diversity for ecosystem processes cannot be discerned from the studies of Crowl *et al.* (2001) and Zimmer *et al.* (2002), the former only excluded or included two species of shrimp, the latter only investigated the effects of litter processing in single species isopod treatments.

Contrary to the results of this experiment, invertebrate species identity has been shown to affect leaf litter breakdown in a consistent manner in multi-species treatments (Ruesink and Srivastava 2001, Duffy *et al.* 2001). Ruesink and Srivastava (2001) removed larvae from experimental mesocosms and compared leaf breakdown in the resultant assemblages with that expected (due to the reduced metabolic capacity in the treatment). The removal of one dominant species of stonefly larva, resulted in leaf breakdown exceeding that expected and the removal of a caddisfly larva resulted in a much lower leaf breakdown by the remaining species, even when the remaining assemblage's biomass was manipulated to compensate for the loss due to species removal. Duffy *et al.* (2001) set up treatments using all possible combinations of three aquatic herbivorous crustacean species and found epiphyte grazing, seagrass biomass

and secondary production to be dependent on the species identity and their individual traits. The discrepancies between the results of this study and those of Ruesink and Srivastava (2001) and Duffy *et al.* (2001) may be due to differences in experimental design. Ruesink and Srivastava (2001) did not measure leaf processing using all possible species combinations and therefore they could not assess, whether the range and magnitude of interactions observed in this study exist for the stream detritivores they used. In the current study, if decomposition was compared between treatments containing all species, after *C. pilipes* removal, with treatments containing all species after *C. frigida* removal, similar conclusions to those of Ruesink and Srivastava (2001) may have been reached. Observed values of decomposition in the three larval species treatment, without *T. deshayesii*, was greater than expected (comparable with the removal of the stonefly larva) and treatments of all species except *C. frigida* had lower than expected values of decomposition (comparable with the removal of a caddisfly larva). As in the current study, the design employed by Duffy *et al* (2001) involved treatments of all possible species combinations, however, direct comparisons of expected litter processing based on single species processing rates and those observed in mixed species treatments were not made. Again the magnitude and consistency of negative species interactions cannot be confirmed and compared with the results of the current study. Furthermore, in the two and three species diversity treatments epiphyte levels and seagrass biomass were not significantly different from those of controls. Negative interactions may have been greater between the herbivore species investigated by Duffy *et al.* (2001) than the species used in the current experiment, or processes other than invertebrate grazing may have played a significant role in determining epiphyte accumulation and seagrass biomass.

Alternatively different mechanistic explanations behind the relationship between species identity and ecosystem processes may explain the discrepancies between the

results of the current study and those of Ruesink and Srivastava (2001). Ruesink and Srivastava (2001) attributed the mass loss in reduced diversity treatments to differences in individual species traits. As the stonefly species was a facultative, not obligate, shredder leaf consumption in treatments including the stonefly may have been reduced, as it was feeding on alternative food sources. Differences in species traits or complementary resource use cannot explain the results of the current experiment as species-specific trends in wrack processing were not consistent in multi-species treatments. Thus, it is unlikely that the species in the current study differed in traits with respect to resource use. If they did, these effects were negligible when species interaction affects were considered.

3.4.2 Species Diversity

Overall diversity was not significant in explaining the variability in *L. digitata* mass loss. However larval diversity significantly explained the increase in *L. digitata* mass loss when treatments containing *T. deshayesii* were excluded. In all but one multi-species larval treatment (*C. frigida* & *D. anilis* combined) wrack processing was greater than expected. As for the larvae in the current study, a positive effect of aquatic detritivore diversity on resource processing rates has been shown, both in the field (Jonsson *et al.* 2001, Huryn *et al.* 2002) and in mesocosm manipulations (Jonsson and Malmqvist 2000, 2003a Cardinale *et al.* 2002, Cardinale and Palmer 2002). Positive diversity-ecosystem processing relationships observed in aquatic detritivores, field studies should be interpreted with caution. Jonsson *et al.* (2001) and Huryn *et al.* (2002) measured leaf mass loss and the associated detritivore assemblage from litter bags placed in streams. Leaf mass loss was positively correlated with shredder species richness, abundance (Jonsson *et al.* 2001) and biomass (Huryn *et al.* 2002). In adopting a correlative approach to assessing diversity-ecosystem processing relationships

(Jonsson *et al.* 2001, Huryn *et al.* 2002) the effects of species diversity from that of species identity cannot be distinguished[7]. The high leaf mass loss in streams with high species abundance may be due to the increasing probability of including species with a marked influence on process rates in higher diversity assemblages; the sampling probability effect (Aarssen 1997, Huston 1997). This could be further exaggerated if species with disproportionately high effects on leaf breakdown were also the most abundant. Although species dominance was not measured in either study, Huryn *et al.* (2002) noted high species dominance in most stream types, with the identity of the dominant species changing with stream type (as did leaf mass loss). Jonsson *et al.* (2001) thought it unlikely that the increase in abundance of species with disproportionately high effects on leaf breakdown could explain the positive diversity-processing relationship they observed as biomass was not correlated with decomposition. However, the decomposer with the highest processing rates does not necessarily have the greatest mass. In this present study, wrack processing rates did not increase in the presence of the most efficient single species wrack processor, *T. deshayesii*. It is possible that if the density of the most efficient processor, *T. deshayesii*, in relation to larvae was increased an overall positive diversity ecosystem processing relationship may have been found in the current study.

Previous mesocosm manipulations that have manipulated species diversity and identity, processing rates increased with larval diversity (Cardinale and Palmer 2002, Jonsson and Malmqvist 2000). The mechanisms operating to increase processing rates with larval diversity, as proposed by Jonsson and Malmqvist (2000, 2003b), Cardinale

[7] Further caution should be taken when interpreting the results of these studies as species richness and abundance also differed with stream order (Jonsson *et al.* 2001). In the case of Huyn *et al.* (2002) the effects of shredder diversity on leaf decomposition may be an artefact of differential processing rates due to land use type and nitrate as taxonomic richness and shredder biomass also differed with land use type and nitrate was related to both land use type and leaf decomposition.

et al. (2002) and Cardinale and Palmer (2002) may be operating between the dipteran larvae investigated in the current study; this is discussed further in Sections 3.4.3 and 3.4.4. However, these mechanisms are evidently not operating between the larvae and the amphipod in the current study.

Where aquatic detritivore manipulations have shown processing rates to be diversity independent (Ruesink and Srivastava 2001, Duffy *et al.* 2001) functional differences between the individual species were used to explain the results. However, for the current study it is suggested that it was not individual species identity but identity combination and species interactions that could explain the variability in *L. digitata* mass loss between diversity treatments (see Section 3.4.1).

As previous detritivore diversity manipulations have not compared expected processing rates based on single species, additive processing rates, with observed processing rates for all species combinations, the range and magnitude of species interactions were not empirically defined. Whilst facilitative and complementary interactions may increase processing rates with larval diversity, the overall effects of diversity on processing rates will depend on the balance of positive, additive and negative interactions as seen when treatments including *T. deshayesii* are included in the analysis.

3.4.3 Species Interactions

In the current study it was the balance of species interactions that determined decomposition and also determined the overall effect of diversity and identity in determining decomposition. The overall non-significant effect of diversity on the variability in wrack mass loss reflected the range and magnitude of species interactions. Species combination effects were rarely additive and were not predictable from *L. digitata* mass loss in single species treatments. As discussed in Section 3.4.1., the

inclusion or exclusion of any single species did not have consistent effects on wrack mass loss, although general trends were evident. In all but one multi-larval treatment (*C. frigida* & *D. anilis* combined) wrack processing was greater than that expected, explaining the increase in wrack processing as the number of larva included in a treatment increased. The generally negative interactions observed when larvae and the amphipod were kept together, can explain the overall non-significant effect of diversity on wrack processing. Within multi-species treatments, observed wrack mass loss was generally lower in treatments containing *T. deshayesii,* than those without. However, not all treatments of larvae and *T. deshayesii* resulted in a significantly lower wrack processing rates than those expected. Treatments of *C. pilipes* & *T. deshayesii* had an additive affect on wrack processing and when *C. pilipes* and *T. deshayesii* were combined with a third species, the additive effect became positive or negative dependent on the identity of the third species (i.e. significantly lower *L. digitata* loss was observed than expected with *D. anilis* and significantly higher than expected with *C. frigida*). Moreover, the significantly higher than expected wrack mass loss that was observed in treatments of *C. frigida, C. pilipes* & *T. deshayesii* may have arisen as a result of the positive effect of *C. pilipes* & *C. frigida* on wrack processing overshadowing the negative interaction between *C. frigida* & *T. deshayesii*. However, if this were the case then a greater than expected wrack mass loss in treatments consisting of *C. pilipes D. anilis* & *T. deshayesii* should have been observed.

The only studies that have empirically tested interactions between the species used in the current study have been concerned with dipteran larval development and growth when reared in multi-species environments (Hodge and Arthur 1997, Philips *et al.* 1995, Leggett 1993). The conclusions reached with respect to competition and facilitation between the species was different depending on the environmental conditions and developmental parameters measured (Hodge and Arthur 1997, Philips *et*

al. 1995, Leggett 1993). Comparing previously found species interactions (in terms of their effect on population parameters) with their effect on processing rates is, at best, speculative. Unfortunately, unlike the studies of Hodge and Arthur (1997), Leggett (1993) and Philips *et al.* (1995) the current study could not measure individual species responses in multi-species treatments. However, the pattern of interspecific interactions between *C. pilipes* & *C. frigida* found in previous studies may explain the higher than expected processing rates in treatments of *C. pilipes* & *C. frigida. C. frigida, C. pilipes* and *Thoracochaeta zosterae* were seen to compete. A dominant hierarchy, *C. frigida* > *C. pilipes* > *T. zosterae*, was suggested based on output population and positive species interactions were observed. *C. pilipes* actually enhanced *C. frigida* survival and population output (on chopped seaweed) and irrespective of resource type *C. pilipes* survival and population output decreased in the presence of *C. frigida* (Hodge and Arthur 1997). Similar evidence of interspecific facilitation and competition is seen when *C. frigida* and *C. pilipes* eggs were allowed to develop, both in isolation and together, and population density measured (Hodge and Arthur 1997). *Coelopa frigida* survival increased in the presence of *C. pilipes*, *C. pilipes* survival decreased as its own density increased, although mortality increased and male wing length (surrogate for body size) decreased in the presence of *C. frigida* (Hodge and Arthur 1997). In the current study when *C. pilipes* & *C. frigida* were incubated together, higher than expected processing rates could be a result of facilitation of *C. frigida* by *C. pilipes*. *Coelopa frigida* had the highest single species wrack processing rates. Therefore, even if *C. pilipes* was inhibited, the overall processing rates in the two species treatment may have been higher. This, however, cannot explain the positive effect of *D. anilis* & *C. pilipes* on wrack mass loss as both species had equivalent single species processing rates. Not all studies have found a positive effect of *C. pilipes* on *C. frigida* populations (Philips *et al.* 1995). The contrasting results of Philips *et al.* (1995), Leggett (1993) and

Hodge and Arthur (1997), could be due to the different parameters measured, or environmental conditions (Philips *et al.* 1995) or the increased density in multi-species treatments.[8]

There are only two other studies that have quantified species interactions with respect to processing rates using detritivores (Jonsson and Malmqvist 2003a, Zimmer *et al.* 2005). Similar to the effects of larvae on wrack decomposition recorded in the current study, Zimmer *et al.* (2005) found detritivore diversity to have a significant effect on leaf mass loss. The variability in measures of microbial respiration, leaf calcium and magnesium concentration as well as soil nitrogen, organic carbon and phosphorus concentrations between detritivore diversity treatments was also significant. The importance of species interactions in determining diversity-decomposition relationships in the study by Zimmer *et al.* (2005) is difficult to ascertain as only two species of detritivores were manipulated. As observed in this study with multi-species treatments of *C. pilipes* & *C. frigida*, leaf mass loss was greater than expected based on single species processing rates when alder was used as a substrate. However, additive species effects were observed when oak litter was used and species interactions became negative when the two leaf litter species were mixed. As oak is a poor quality food source, it is possible that when the two species were combined they preferentially fed on each other's faeces rather than the leaves. Unlike the current study, Zimmer *et al.* (2005) used an additive design, where the total species number increased but the amount of litter added to each mesocosm did not. Leaf litter was only in excess in multi-species treatments when it was of a high quality (alder). Thus, in mixed and single species treatments of the poor quality litter (oak), competition for the food source

[8] The results of Philips *et al.* (1995) and Hodge and Arthur (1997) are further confounded as the species density was increased with larval species number. Density-dependent survival for both *C. frigida* and *C. pilipes* has previously been shown, at low density survival increases with density, and then decreases at a critical point (Leggett 1993, 1996).

increased (potentially both intraspecific and interspecific competition) and feeding rates were reduced as a result. This does not, however, explain why species interactions were negative when both litter types were combined, but additive when incubated only with oak. However, the importance of substrate in determining the direction of species interactions with respect to resource processing was highlighted (Zimmer *et al.* 2005).

As in the current study, Jonsson and Malmqvist (2003a) emphasised the importance of species interactions in determining overall diversity-processing relationships. They manipulated different functional groups of species, two groups of filter feeders, one grazer group, and one predator group. Mesocosms containing every possible combination of single, two and three species were constructed; keeping densities constant across species level. In all groups the increase or decrease in processing rates with diversity was non linear. As diversity increased from one to three species, two species combinations had additive, negative or positive effects on processing rates and it was the balance of these interactions that determined the overall effect of diversity with processing rates. Similar to that found for wrack processing rates with fly larvae in the current study, Jonsson and Malmqvist (2003a) recorded an increase in processing rates with diversity in one functional group, blackfly larval filter feeders. Furthermore, within the blackfly larval group species interactions affected processing rates in a similar manner as those found in the current study. When two blackfly larvae were incubated together, two pair-wise combinations significantly exceeded expected processing rates, and processing rates with one pair was not significantly different from predicted. The significant effect of one group of filter-feeding larvae on processing rates was attributed to stronger intraspecific, relative to interspecific competition, as initially proposed by Jonsson and Malmqvist (2000). The diversity-independent or negative diversity-ecosystem process relationship observed in the other functional groups from Jonsson and Malmqvist's (2003a) study could be

explained by the separate interactions between species. In Jonsson and Malmqvist's (2003a), study grazer and predator species diversity decreased processing rates, although this was only significant for the predator group. In a two and three species combinations of grazers and predators observed processing rates were significantly lower than expected based on single species additive affects, with the exception of one grazer combination and one predator combination (both were not significantly different from expected). The decrease in processing rates with diversity observed in grazer groups was attributed to resource depression by one species. The decrease in predation with predator diversity was attributed to increased interference competition in multi-species assemblages resulting in less time spent feeding. The other group of larval filter feeders showed no increase in processing rates with diversity. Although one pair combination significantly exceeded predicted processing rates, another combination significantly underperformed, and a third showed no difference from that of expected based on species additive affects. The importance of investigating species interactions when making inferences of the effect diversity has on ecosystem processes is highlighted by the current study and that of Jonsson and Malmqvist (2003a). In this study, when all treatments were considered, only species identity combination nested under diversity was significant in explaining the variability in processing rates. When species are segregated into separate groups [in the current study larva only treatments, in Jonsson and Malmqvist's study (2003a) the blackfly larvae] diversity significantly affected processing rates. Overall processing rates were determined by the range of positive and negative interactions between species.

3.4.4 Mechanistic Explanations

Most mechanistic explanations for how increased species diversity affects ecosystem processes are based on differences in species traits (Loreau *et al.* 2001b,

Schmid *et al.* 2001, Norberg 2004). The niche differentiation or efficiency effect (Vitousek and Hooper 1993, Tilman *et al.* 1997b, Tilman 1999) is the most commonly used explanation for positive species diversity effects on ecosystem process. It predicts that each species plays a different role in ecosystem functioning, and therefore, ecosystem processes in the absence of a species cannot be compensated for by the remaining species in the assemblage. For niche differentiation to explain the positive relationship observed between larvae in the current study, each larval species would need to feed on a different, or differently on a part of the kelp. Kelp would also need to be limiting so that each species could only consume up to a maximum point, thus in multispecies treatments more parts of the kelp would be consumed resulting in greater mass loss. It is unlikely that niche differentiation can explain the pattern of wrack mass loss with the species used in the current study because *L. digitata* was present in excess in all treatments. Furthermore, wrack availability is rarely limiting in the strandline (Backlund 1945). No single species had a consistent positive or negative effect on processing rates when combined with other species, and the asymmetric interaction observed when *T. deshayesii* and larvae are considered does not support the niche differentiation hypothesis.

The sampling effect or selection probability effect (Aarssen 1997, Huston 1997) provides an alternative hypothesis to explain the increase in ecosystem process in response to greater diversity. In essence, as diversity increases the chance of including species with a disproportionately high effect on ecosystem process also increases. Whilst this sampling effect provides a plausible explanation for why leaf decomposition measured in the field was seen to increase with greater species diversity (Section 3.3.3), it is unlikely to be an explanation for the observations of the current study. In the current study, all species combinations were incorporated into the methodological

design, and no single species was seen to be disproportionately responsible for increasing decomposition rates.

Positive species interactions between larval species are more plausible mechanisms to explain the positive response of decomposition to larval diversity observed in the current study. It is possible that the inclusion of the amphipod in multi-species treatments in some way interrupts or ameliorates positive larval interactions. Positive species interactions, such as facilitation, have long been cited as potential diversity-ecosystem process promoting mechanism (Loreau *et al.* 2001b, Loreau and Hector 2001). There are numerous examples of mutualism in the literature, as well as more recent evidence that facilitation between species increases a number of ecological processes: predation rates (Soluk 1993, Soluk and Richardson 1997), leaf litter decomposition (Jonsson and Malmqvist 2000), and resource capture (Cardinale *et al.* 2002). More recently, intraspecific interference (Jonsson and Malmqvist 2000, 2003b) and interspecific facilitation (Jonsson and Malmqvist 2000, 2003b, Cardinale *et al.* 2002) have been recognized as mechanisms whereby species interactions may be responsible for the increase in ecosystem processes with diversity. Both intraspecific interference (Jonsson and Malmqvist 2000, 2003b) and interspecific facilitation (Jonsson and Malmqvist 2000, 2003b, Cardinale *et al.* 2002) may explain the increase in wrack mass loss with larval diversity in the current study.

The Interaction Hypothesis (Jonsson and Malmqvist 2000) predicts that processing rates in assemblages of lower species diversity would be hampered, due to stronger interactions between conspecifics. This assumes that intraspecific interactions are more intense than interspecific interactions (as a process of fitness-related natural selection). Although in a subsequent study Jonsson and Malmqvist (2003b) demonstrated reduced resource processing as intraspecific density increased (for some of the species investigated) and some evidence of increased processing rates when

species were removed and replaced by conspecifics, they did not explicitly show the relative importance of these two mechanisms for processing rates. Furthermore, in the species replacement experiments, processing rates also changed according to the order in which conspecifics were removed and replaced. Where an increase in processing rates was observed, one of two species used in the replacement experiments was not used in the original study that demonstrated an increase in resource processing with diversity (Jonsson and Malmqvist 2000). This said the balance of interspecific and intraspecific competition may explain the increase in wrack mass loss with larval diversity and the generally lower than expected wrack mass loss in the presence of the amphipod, found in the current study. Interspecific competition may be greater than intraspecific competition between larval species and the reverse may be true for the amphipod. Alternatively, increased processing rates as larval diversity increases may be due to interspecific facilitation between the three species of larvae, which, in the presence of the amphipod, is interrupted.

Using the design employed here, and also in Jonsson and Malmqvist's study (2000), interpreting positive species diversity ecosystem processing effects as evidence of facilitation or intraspecific and interspecific competition without additional evidence is difficult. Using substitutive designs, where overall species density is maintained equal, means that, the relative density of individual species decreases as diversity increases. Thus, positive effects of diversity on ecosystem processes due to intraspecific competitive release and interspecific facilitation cannot be discerned (see Section 3.1.3 for a more detailed discussion). Intraspecific competition between dipteran shredders may arise due to limited amounts of leaf detritus (Jonsson and Malmqvist 2000). However, in the current experiment, wrack was not a limiting resource, thus raising doubt on the role of species intraspecific competition for food. Additionally, pupation rates were not significantly reduced in mixed larva treatments. If pupation rates

increased in multi-species larva treatments, where intraspecific density was reduced, this would be indicative of a reduction in competition. Larvae often pupate in non-optimal conditions (Rowell 1969). Cardinale and Palmer (2002) provided evidence that the positive effect of three species of caddisfly larvae on resource capture was attributed to species-facilitated habitat modification (by increasing the catchnet area and thus increasing the amount of organic matter captured). Supporting the conclusions of Cardinale and Palmer (2002), that species facilitation not complementary resource was the mechanism underlying the positive effect of diversity on resource capture, increasing the diversity of the same three species increased the amount of suspended particulate matter (SPM) removed only when SPM was not limiting (Cardinale *et al.* 2002). A similar mechanistic explanation to that proposed by Cardinale *et al.* (2002) may be used to explain the generally greater than expected wrack mass loss observed in multi-larva treatments found in the current study. Heterospecific larval assemblages in the current study may facilitate processing rates through resource conditioning. This is discussed further below. However, in the presence of the amphipod either this facilitation process does not occur or other process are simultaneously operating to result in the generally lower than expected wrack mass loss when the larvae and amphipod are combined.

None of the previously proposed hypotheses can adequately explain the different wrack mass loss in treatments of different species. The presence or absence of any particular species did not affect wrack processing in a consistent way and wrack mass loss in multi-species treatments was not predictable from single species treatments. Therefore, a hypothesis of microbial facilitation and inhibition is tentatively proposed, to explain these results.

The positive effect of larval diversity on *L. digitata* mass loss may be due to increased microorganism diversity, if a different microbial assemblage was associated

with each species of larva. Thus, in multi-species larval treatments it would be predicted that a greater diversity of microorganisms would be found. If these assumptions are correct, decomposition should be greater in treatments containing a higher diversity of microorganisms, through complementary resource use of the wrack by the bacteria and/or increased larva feeding rates induced by a higher diversity of microbes. The reduced *L. digitata* mass loss in the presence of *T. deshayesii* and larvae could also be attributed to the microorganism assemblage in mixed species treatments. Larvae may increase anaerobic conditions and anaerobic decay through the introduction of their faeces. Thus when larvae are present aerobic bacteria and moulds may be excluded. *T. deshayesii* feeding rates may be depressed in the absence of aerobic bacteria and moulds as these groups themselves may constitute an important part of the amphipod diet, and/or increase the palatability of the wrack for the amphipod. The evidence supporting such a mechanism is largely anecdotal. Microorganisms play a role in the breakdown of wrack (Griffiths *et al.* 1981, Koop *et al.* 1982a, Haxen and Grinley 1984). There is evidence that bacteria in other detritivore faeces are important to the decomposition of detritus (see Hargrave 1975 for a review). Furthermore, increased wrack decay has been attributed to the presence of bacteria induced by *C. frigida* and *C. pilipes* faeces (Egglishaw 1960, Rowell 1969).

Evidence that detritivores receive much of their nutritional value from microorganisms rather than the detritus itself has come from examination of the organic content of detritivores food and faeces and the disparity between the nutritional needs of the detritivore and that available in the detritus (see Fenchel and Harrison 1975, Berrie 1975 for reviews). Moreover, microorganisms are thought to constitute a major part of larvae diets (Rowell 1969, Barnes 1984, Cullen *et al.* 1987,) and microbial colonisation of larvae guts is thought to be essential to larvae survival (Backlund 1945, Rowell 1969, Cullen *et al.* 1987). The co-occurrence of *C. pilipes* and *C. frigida* on wrack has been

accredited to differential digestion and absorption of wrack components (Egglishaw 1960). If larvae defaecate different microorganism, wrack mass loss in multi-larval treatments may have been facilitated through differential resource use by the higher diversity of microorganisms. The increase in microorganism diversity may have stimulated larvae feeding rates. A high diversity microorganism assemblage may encompass a wider range nutritionally, and through differential, extracellular digestion could have resulted in more of the *L. digitata* becoming palatable to the larvae. The *L. digitata* used in this experiment was sterilised and thus microorganisms introduced through the larvae themselves would have been likely to play a large part in both the decomposition and nutritional value of the *L. digitata* for the larvae.

Evidence that wrack decomposition in the presence of larvae results in a microbial assemblage that is either unpalatable or acts as a deterrent to amphipod feeding is again anecdotal. Larval exudates have been noted as being wet (Backlund 1945, Egglishaw 1960, Stenton-Dozey Griffiths 1980) and wrack decay in the presence of larvae has been cited as being anaerobic (Philips and Arthur 1994). The presence of larvae on *Laminaria* has been suggested to exclude moulds (Egglishaw 1960). Amphipods have been shown to have high assimilation efficiencies for mould (Behbehani and Crocker 1982). Fungi and mould has been seen as an important part of amphipod diets (Backlund 1945, Philips 1979, Rong *et al.* 1995) and the importance of fungi for ecological performance has been empirically tested (Kneib *et al.* 1997). Philips (1979) found fungal assimilations in *Orchestia grillus* highly negative, suggesting selective ingestion of fungi. Rong *et al.* (1995) highlighted the importance of Fungi to the diet of a freshwater leaf shredding amphipod *Gammarus pseudolimnaeus*. The amphipod had little endobacteria compared to the two larval species investigated and the highest food selectivity (Rong *et al.* 1995). As the amphipod had a gut pH close to 7 this would enable the survival of fungi which could digest leaf protein and phenolics

(these substances themselves contain bonds that are hard to dissociate with a neutral gut pH). Backlund (1945) believed *Orchestia gammarellus* fed on mould as the growth of mould on various algae was negligible in its presence. Behbehani and Croker (1982) in laboratory feeding trials observed high assimilation efficiencies of *Platorchestia (Orchestia) platensis* for mould. Kneib *et al.* (1997) found the ecological performance of a salt marsh amphipod to be reduced when fed on senescent sheaths of cord grass; only when sheaths were not washed did the male to female ratio approach 50:50. However the lack of moulds and nutritional value of the food is unlikely to inhibit amphipod feeding rates as there are many examples where amphipods feed indiscriminately on any food type (Backlund 1945, Agrawal 1964). Therefore, we suggest the absence of aerobic decay due to moulds may prevent the breakdown of components of *L. digitata* that act as a deterrent to amphipod feeding. The absence of Fungi and moulds may indirectly act as a deterrent to *T. deshayesii* feeding. Accumulation of fungal proteins and lipids has been linked to declining concentrations of organic phenolic compounds (Barlocher 1985, Cargill *et al.* 1985, Hanson *et al.* 1985, Suberkropp 1992). Barlocher and Newell (1994) found compounds that are feeding deterrents to *Orchestia grillus* and *Melampus bidentatus* (specifically cinnamic, ferulic and p-coumaric acids) abundant on cord grass, but readily decomposed by the dominant Fungi. Furthermore lignicolous and non-lignicolous Fungi strains that are able to decompose *Laminaria* spp. and alginate have been isolated from decomposing brown algae.

If larvae increase anaerobic conditions, excluding aerobic bacteria and Fungi which decreases the palatability of the wrack for the amphipod, why wrack processing in treatments of *C. pilipes* & *T. deshayesii* and *C. pilipes*, *T. deshayesii* & *C. frigida* are not significantly lower than expected is unclear. It has been suggested, albeit based on little hard evidence, that *C. pilipes* has a greater need for microorganisms owing to its

preference for higher temperature wrack (Philips *et al.* 1995). If *C. pilipes* removed more anaerobic microorganisms this may increase the substrate available for fungi and moulds, thus increasing *T. deshayesii* feeding rates.

Larva-induced microorganism facilitated decay and feeding rates plus simultaneous inhibition of *T. deshayesii* feeding may play a large or small part in explaining the positive effect of larval diversity on wrack processing and the generally lower than expected wrack processing rates in treatments of the larvae with the amphipod. The evidence is largely anecdotal and, without examination of the microorganism assemblage in the guts and on the wrack from single species and mixed species treatments, little more can be said. Complex behavioural responses may likewise play a large or small part in explaining the suite of interactions observed with respect to *L. digitata* mass loss. [9]

3.4.5 Conclusions and Limitations

Using the species, and under the experimental conditions employed in this study,[10] the importance of species interactions in determining wrack decomposition in

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[9] As individual species contributions to *L. digitata* breakdown in mixed species assemblages was not measured, reduced *L. digitata* mass loss g.g-1 in treatments of species combinations cannot be attributed to the inhibition of any or all species. Therefore it is possible that *T. deshayesii's* feeding rates may not decrease in the presence of larvae, but larvae may reduce theirs in the amphipods presence. If the amphipod induces a behavioural response in the larvae similar to that of a predator, the larvae many allocate more time into predator avoidance than feeding in the presence of the larvae. No behavioural studies on the response of larvae to the amphipod or predators have been undertaken so this is hard to confirm. Although if this response was occurring it would be expected to be less pronounced in *C. pilipes* treatments, as previous studies show a preference of *Cafius xantholoma* one of the most abundant predator at Wembury for *C. frigida* over *C. pilipes* (Backlund 1945) and thus may explain the additive affects of *C. pilipes* and *T. deshayesii*, and higher than predicted affects of *C. pilipes*, *C. frigida* and *T. deshayesii* on *L. digitata* mass loss.

[10] As with all laboratory studies the results of this study are obviously species and system and condition specific, and limited by the number of replicates used in the ANOVA analysis (Zar 1999). How decomposition will be effected by species interactions, species identity and diversity as relative species densities change cannot be discerned from this study. Furthermore, as highlighted by Zimmer *et al.* (2005), the diversity- decomposition response found in this study and the patterning of species interactions with respect to decomposition may differ when mass loss on substrates other than *L. digitata* are considered. However, as *L. digitata* was the most abundant strandline algae at Wembury beach, followed closely by other Laminariales. Thus although it has not been explicitly deomonstrated it is

the strandline is clearly highlighted. The decomposition in multi-larval treatments was higher than expected. Decomposition in treatments of the larvae and amphipod combined was equal to or less than expected, dependent on species identity combination. The results of the current study demonstrate the dangers of predicting an ecosystem processes such as decomposition, based on the additive effects of single species on processing rates. Using the species and conditions in this experiment, predicting decomposition based on single species rates will result in erroneous conclusions of energy flow and available resources for secondary production in the system as a whole. It is suggested that in coastal transition zones such as the marine strandline, it is imperative that future investigations (incorporating natural abundance and species distributions) take species interactive effects into consideration.

This study has important implications for future diversity-ecosystem process studies. Whilst individual species traits may explain diversity process patterns, it is clear that, in the strandline system investigated in this study, species interactions are important in the pattern of processing rates. By empirically segregating species interactive affects from those of individual species, the seemingly idiosyncratic and unpredictable response of ecosystem processes to diversity found in previous studies may be accounted for and misleading conclusions regarding the effect of diversity on processes will be avoided. Furthermore, if there really is no overall relationship between diversity and ecosystem process, then only by understanding the contribution of individual species and their interactive affects will the consequence of reduced diversity for ecosystem process be fully understood. Anecdotal evidence suggests that, in the current study, the presence of facilitative (between the larvae) and inhibitory (between

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tentatively suggested that the effects of diversity, identity and species interactions on decomposition as found in this study will not change massively when decomposition in the strandline at Wembury as a whole is considered.

larvae and amphipod) species interactions determine the overall rates of decomposition. Irrespective of mechanism, it is clear that, under the conditions in this experiment, reducing larval diversity reduces decomposition, and that the presence or absence of the amphipod will also have big implications for wrack decomposition. How species interact and the mechanisms behind these interactions may provide more useful information for the state of our ecosystems if current extinction rates persist, and species diversity declines. The role of microorganisms in wrack decomposition and how microbial assemblages differ with consumer diversity may prove a fruitful avenue for further research into understanding the link between species identity, diversity and interactions and ecosystem processes in the strandline.

This current investigation also highlights the dangers of assuming non-trophic interspecific interactions are equal when energy flows through food webs are modelled. As empirical investigations into predator-prey interaction strength are beginning to emerge it is potentially critical that the relative importance of non-trophic interaction strengths are empirically defined when energy flow and ecosystem process in assemblages are predicted.

CHAPTER 4: THE USE OF BODY-SIZE AS A SURROGATE MEASURE OF PREDATOR-PREY INTERACTION STRENGTH AND ECOSYSTEM PROCESSES IN THE STRANDLINE

4.1 Introduction

This chapter investigates the use of species body size to predict predator-prey interactions and ecosystem processes, using strandline species, four beetles and their prey, and measuring decomposition as an ecosystem process.

4.1.1 Rationale

If predictions are to be made regarding the effect of reduced diversity on ecosystem processes in natural assemblages, it is imperative that trophic interactions are considered. Little is known about the effect of species occupying higher trophic positions on ecosystem processes. Yet it is these species that are most at risk of extinction (Dobson *et al.* 2005). If, as suggested previously (Chapter 1) there is no universal trajectory linking diversity to ecosystem processes, understanding how species trophic interactions affect ecosystem processes is a vital step towards understanding the effect of reduced species diversity on those processes.

There are a number of problems with incorporating multiple trophic levels in traditional BDEF studies that measure ecosystem processes at different diversity levels; the large number of replicates required is both time consuming and often not logistically possible, and the results from such experiments are often difficult to interpret (Section 1.8).

Alternative approaches are desperately needed if the effect of trophic interactions on consumer populations and ecosystem processes are to be understood. Both the prediction and quantification of trophic interactions may enable the

construction of food web models in which trophic links are quantified. In the future such models may be used to infer the effects of reduced diversity on ecosystem processes, overcoming problems encountered when using traditional BDEF experiments to predict the effects of reduced diversity on ecosystem processes in multi-trophic assemblages.

4.1.2 Species Interaction Strength

Interaction strength is a term used to estimate the magnitude of the effect one species has on another. It is commonly used in both experimental and theoretical studies aimed at investigating the effect of predators on their prey (trophic interactions) (Laska and Wootton 1998, Wootton and Emmerson 2005). The distribution of trophic interactions (in terms of their strength) amongst species in food webs has long played a central and contentious role in ecology and studies of population dynamics (Laska and Wootton 1998, Berlow *et al.* 1999, 2004 Wootton and Emmerson 2005 and references therein). The direct and indirect effects of interaction strength on ecosystem process are rarely examined. Previous research has focused mainly on the effect that interaction strength distribution has on population dynamics and assemblage stability. Modelling and theoretical studies have generally concluded that a skew in the distribution of interaction strengths towards weaker interactions promotes stability, in both real (deRuiter *et al.* 1995, Roxburgh and Wilson 2000, McCann 2000) and model systems (McCann *et al.* 1998, Ruiter *et al.* 1995, Roxburg and Wilson 2000, although see Kokkoris *et al.* 2002).

Empirical measures of interaction strengths have been less frequently investigated. Wootton and Emmerson (2005) identified four basic approaches to estimate interaction strength based on empirical measurements; field experiments, laboratory experiments, observational approaches and the analysis of system dynamics.

Empirical measurements of interaction strength have been made between single predator and prey species in removal experiments. These studies have generally been based on comparative measurements of prey population dynamics with and without a predator. The majority of these studies have found predator and prey interaction strengths to be weak (Fagan and Hurd 1994, Navarrete and Menge 1996, Wootton 1997, Pain 1992, Raffaelli and Hall 1996). Although strong interaction strengths occurred between relatively few predator and prey species, when present they greatly altered the entire assemblage dynamics (Paine 1992, Navarrete and Menge 1996, Raffaelli and Hall 1996, Wootton 1997).[11]

Experimental approaches to estimate interaction strength have been heralded as the most accurate way to assess interaction strength (Bender *et al.* 1984, Pain 1992, Berlow *et al.* 1999). However, segregating direct and indirect interactions from experimental manipulations is difficult and has often confounded interpretation of the results (Wootton and Emmerson 2005). Laboratory experiments such as those undertaken by Abrams (2001) and Vandermeer (1969) may overcome this problem as they allow the isolation of single species interactions. In addition these experiments were undertaken over shorter time scales thus the interpretation of results may be increased (Wootton and Emmerson 2005). However, the validity of inferring interaction strengths estimated from laboratory studies that manipulate few species to those

[11] The majority of experimental manipulations have been attempted using intertidal rocky shores systems (Navarrete and Menge 1996, Wootton 1997, Paine 1992, Raffaelli and Hall 1996). As such it is possible that they may not reflect interaction strength distribution in other systems. On rocky shores most interaction strengths between species were weak, strong interaction strengths between predator and prey occurred between relatively few species although they greatly affected the whole assemblage dynamics when present (Navarrete and Menge 1996, Wootton 1997, Paine 1992, Raffaelli and Hall 1996). This said, similar weak interaction strengths between predators and prey have also been observed between mantid predators and their arthropod prey in terrestrial open field exclusion and inclusion plots (Fagan and Hurd 1994). Mantids reduced or increased arthropod density to different degrees depending on initial arthropod density). Additionally interaction strengths have been calculated at different prey densities (Raffaelli and Hall 1996, Fagan and Hurd 1994, Menge *et al.* 2004) and attempts to quantify the variability in these strengths over different temporal and spatial scales have been made (Berlow and Naverattee 1997). Unfortunately direct comparisons between previous studies are difficult as interaction strength has been defined, in a number of different ways (see Berlow *et al.* 2004 for a review) (c.f. Navarrete and Menge 1996, Fagan and Hurd 1994, Wootton 1997, Paine 1992, Raffaelli and Hall 1996, Berlow and Naverattee 1997, Menge *et al.* 2004).

occurring in natural assemblages has not been extensively examined (Skelly 2002, Tyler *et al.* 2002).[12]

Observational information based on species-specific natural history information such as feeding rates, abundance and life history parameters have been used to estimate interaction strength (Wootton and Emmerson 2005). Wootton (1997) gives probably the best example of an observational approach to estimate interaction strengths. In a comprehensive study of the rocky intertidal, estimates of interaction strength were based on behavioural observations (mainly feeding) and were compared to population measures of interaction strength based on field exclusion experiments. Wootton (1997) found excellent agreement between observational-based measures and field exclusion measures of interaction strength, but the measure of interaction strength was species- and system-specific. [13]

Analysis of system dynamics (modelling of interaction strength based on the variation in species abundance or biomass over time) has been used to model ecosystem parameters such as stability (Ives *et al.* 1999, 2005) and is dealt with extensively by Wootton and Emerson (2005). Whilst good agreement has been found between modelled interaction strengths and actual measured interaction strengths (Laska and Wootton 1998) some studies (e.g. Pascual and Kareiva 1996, Ives *et al.* 1999, 2005) have not validated the measure of interaction strength that was used. Further criticisms of this method and possible solutions to overcome difficulties in using this approach to estimate interaction strengths are given by Wotton and Emmerson (2005).

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[12] It is worth noting here that Schmitz (1997) tested the validity of a multi-species model parameterised by laboratory interactions of grasshopper feeding rates and plant nutrient uptake rates. The model that predicted consequences of nutrient enrichment on the species was in agreement with the long term field manipulations of nutrients.

[13] This approach is limited in its universal use and practicality as the observations were time consuming, and the natural history information necessary (population dynamics) is not always available for all species.

Based on empirical measures, interaction strength has been estimated to be skewed towards weak interactions, where only a few species interact strongly. Similarly in modelling studies the stability and persistence of theoretical assemblage dynamics has been increased by including many weak and a few strong interactions or a skew in interaction strength distribution towards weak interactions (McCann *et al.* 1998, HilleRisLambers and Dieckmann 2003, Emmerson and Yearsley 2003).

In both empirical studies and modelling studies the measure used to estimate interaction strength differs between studies (see Berlow *et al.* 1999, 2004 for review). The performance of these measures, e.g. their inherent bias towards estimating weak or strong interactions, may have influenced the conclusion reached regarding the patterning of strengths.

The results of previous studies cannot be used to identify dynamically important species or species important with respect to ecosystem processes as, in both empirical and modelling studies the use of surrogate correlates of interaction strength have not been investigated. Modelling studies mainly consist of theoretical species and assemblages thus the extrapolative power of modelling studies to real assemblages and species is, unsurprisingly, weak.

Finding tractable ways of measuring interaction strength between all species in an assemblage and realistic means to parameterise interaction strengths in model food webs remains a challenge. Easily measurable surrogate measures of interaction strength are required if the effects of reduced diversity on species assemblages and ecosystem process can be determined using food web models where links are quantified. A different approach to predicting interaction strengths using species' body sizes has emerged from renewed interest in metabolic scaling and allometry. Body size may have great potential to be used as surrogate measure of interaction strength.

Using body size to predict interaction strength and ecosystem processes assumes, a) energy demands underpin species' interactions, b) a species' metabolic rate determines its rate of consumption and c) body size can be used as a surrogate for metabolic rate. If these assumptions are valid, the size distribution of species could be used to predict consumption rates, and so indicate species interaction strengths and ecosystem processes such as energy flow throughout an assemblage. In the case of energy flux the body size of the constituent species of an assemblage may be used as a proxy for that assemblage's metabolic demand, thus ingestion or feeding rates can be determined. Metabolic theory and scaling laws may provide a useful tool to predict species interactions and energy flow in assemblages and may even provide a tractable way in which to predict the effects of reduced diversity on ecosystem processes (Brown and Gillooly 2003). However, the fundamental assumptions behind such an approach must be upheld if such an approach is to have any predictive capacity. The following section examines the theory and evidence underpinning the notion that body size can be linked with metabolic rate and how metabolic rates may determine energy flow and ecosystem processes.

4.1.3 Metabolic Theory and Interaction Strength

4.1.3.1 Metabolic Theory Overview

The compilation of over a decade of work by Jim Brown and colleagues (Brown *et al.* 2004) has resulted in an outline for a metabolic theory of ecology—a proposal for a unifying theory of ecology. Whatever else it achieved it has reinvigorated interest and placed body size and metabolism at the forefront of ecological research once again. Brown *et al.* (2004) statistically demonstrated that metabolic rate scaled with body size to the power ¾, using existing data from a wide range of phyla covering a large range of

body sizes. Furthermore, Brown *et al.* (2004) demonstrated that metabolic rate was temperature dependent, and also showed how stoichiometry can be intrinsically linked to species metabolism. In some ways there is little new in the conclusions reached by Brown *et al.* (2004). The idea that metabolic rate scales with body size is not new (e.g. Rubner 1883, Kleiber 1932- in Peters 1983, Prothero 1986, Klingenberg 1998).[14] There is a general, though not universally accepted, view that basal metabolic rate scales with body mass to the exponent ¾ or $^{0.67}$ (see reviews in Peters 1983, Schmidt-Nelson 1984, Brown *et al.* 2004, Gillooly *et al.* 2003 and also Rubner 1883, White and Seymour 2003). However, measurements and data compilations of body size data show a wide variation in exponent from 0.3 – 1.0 (Winberg 1960, Paloheimo and Dickie 1966, Dodds *et al.* 2000 White and Seymour 2003, Speakman 2005, Reich *et al.* 2006).

Previous and recent work in the field of metabolic theory has invoked controversy and lively debate. The universal generality of scaling exponents linking body size to metabolic rate (Boddington 1978, Smith 1980, Dodds *et al.* 2000, Hooper and Weibel 2005, Reich *et al.* 2006) and the statistical analysis, interpretation, generality and thus significance of results relating body size to metabolic rate have been heavily contested (Ricker *et al.*1973-from Martin *et al.* 2005, Smith 1980, Martin and Barbour 1989, Riska 1991, Harvey and Pagel 1994, Batterham *et al.* 1997, Torres *et al.* 2001, Clarke 2004, Savage 2004, Nagy 2005, White and Seymour 2005, Cohen *et al.* 2005, Martin *et al.* 2005, Suarez and Darveau 2005). Furthermore, irrespective of the exponent used there is, as yet, no general consensus as to why metabolic rate should scale with body size. A number of theories have been proposed to explain such an important allometric relationship (McMahon 1975, West *et al.* 1997, 2003, Banavar *et*

[14] Originally Max Rubner (1883) empirically established that there was a relationship between body mass and 'basal' metabolic rate in dogs which scaled to the power $^{0.67}$. In 1924, Huxley (see Prothero 1986, Klingenberg 1998) proposed a more general perspective to scaling problems and set the foundations of what became known as 'allometry' where not only metabolism but nearly all organisms traits were shown to scale with body size. Kleiber (1932) later claimed that basal metabolic rate scaled with body mass raised to the power not of $^{0.67}$ but $^{0.75}$.

al. 1999, 2002, Bejan 2000, Gillooly *et al.* 2001, Darveau *et al.* 2002, Hochachka *et al.* 2003, West and Brown 2005). Nearly all the mechanisms proposed to date have come under heavy scrutiny and criticism (see arguments in Bejan *et al.* 1999, 2002, Brown *et al.* 2002, Banavar *et al.* 2002, 2003, Darveau *et al.* 2003,West *et al.* 2002, 2003, 2005).

All of the contention notwithstanding, the relationship between body size, interaction strength and ecosystem processes has not been empirically tested. Furthermore, species size distributions have rarely been considered as a parameter in BDEF studies, although species size is a factor that intuitively has the potential to affect both species interactions and processing rates.

4.1.3.2 Body Size and Interaction Strength

Theoretically the link between body size and interaction strength can be inferred from previous correlations between body size and factors linked to interaction strength, such as ingestion or consumption rate. Consistent relationships have been found between body size and consumption rate in arthropods (Reichle 1968) and crustaceans (Sushchenya and Khmeleva 1967), although the exact scaling exponent of these relationships was not determined in either case. Farlow (1976) is probably the most cited study that provides evidence for the scaling of body size with ingestion rate. To make inferences on the metabolic type and trophic dynamics of dinosaurs, Farlow (1976) marshalled data on food intake and body mass of caged and free living birds and mammals. The log-log relationship between body mass and food intake (expressed as energy equivalents -Calories) was significant and similar between carnivorous and herbivorous birds and mammals. The relationship could be described by the power exponent 0.71, for herbivorous birds and mammals (0.72 for mammals alone) and 0.71 for carnivorous birds and mammals (0.69 for mammals alone). Similarly, Cammen

(1980) suggested that the ingestion rate of a range of aquatic deposit feeders and detritivores scaled with body mass to the exponent 0.74 (log-log relationship).

Analyses of food web parameters and energy flow in real food webs have supported the use of scaling exponents to determine both energy flow and quantify trophic interactions between species based on species body size. Cohen *et al.* (2003) constructed one of the first food webs to consider the link between food web structure, body size and species abundance. Cohen *et al.* (2003) investigated patterns in abundance, body size and trophic position from previous empirical data from a pelagic small lake food web. Perhaps the most interesting finding was that body mass was inversely related to numerical abundance and energy flow. In accordance with allometric theory, the conversion efficiency of prey to predator biomass was roughly similar over a wide range of predator body sizes, and the abundance of predators and prey was positively correlated to the predator: prey mass ratio, although the exact relationship between predator: prey body size ratios, interaction strength and/or energy flow was not defined.

Hulot *et al.* (2000) demonstrated the importance of size in determining population dynamics. The effects of press perturbations (rapid nutrient enrichment) on the modelled assemblage were reflected accurately in mesocosm lake assemblages when size and diet information were used to delimit functional groups in a multi-trophic non-linear food web model. The results also highlighted the importance of indirect interactions and trophic level diversity in determining the assemblage response to added nutrients. The importance of consumer size in determining interaction strength and resource uptake was shown by Diehl (1993). The model showed that if intermediate consumers were large, predators preferentially preyed on them and the direct impact on resources was reduced. When top and intermediate consumers are of a similar size, the impact on a resource can increase as top predators fed directly on the resource itself and

also removed less intermediate consumers through direct predation (Diehl 1993). However, they were unable to test this theory on empirical data as the size of organisms were not defined or measured. Both Cohen *et al.* (2003) and Woodward *et al.* (2005b) found trivariate relationships between body size, abundance and web structure; body size could be used to parameterise and quantify dynamic links within a food web. Woodward *et al.* (2005b) also provided some justifcation for the use of body size for quantifying energy flow within a food web. In an exceptionally ambitious study combining previous data with field collected data, an exceptionally detailed connectance web for Broadstone Stream (UK) (131 species) was constructed. They further attempted to quantify the links in the food web using gut contents analysis of an impressively large number of different species from the Broadstone Stream. In accordance with metabolic theory when Woodward *et al.* (2005b) plotted log (body size of a species) against log (total consumption of that species by all predators within the web), the latter being their measure of interaction strength, the relationship between body size and interaction strength was negative. Smaller species suffered greater predation than larger species. However, the exact relationship was not quantified and whether it was significantly different from that predicted by metabolic theory of ecology cannot be determined.

Empirical field and laboratory exclusion experiments have also shown the importance of body size in determining predator-prey interactions and have provided mixed evidence for the use of body size as a surrogate measure of interaction (Eklov and Werner's 2000, Sala and Graham 2002, Ovadia and Schmitz 2002). In field exclusion experiments and Ovadia Schmitz (2002) found that treatments containing smaller grasshoppers suffered greater mortality than those containing larger grasshoppers when presented with a predatory spider, in accordance with metabolic theory (e.g. to fulfil metabolic requirements a predator will eat more prey items of a

small size than larger conspecifics). However, contrary to metabolic theory in the predator-free controls the three size-classes of grasshoppers did not differ significantly from each other in their reduction of grass or herb biomass (Ovadia and Schmitz 2002). Ovadia and Schmitz (2002) suggested that this was due to increased *per capita* foraging by smaller grasshoppers that are at greater risk of not completing their development by the end of their annual life cycle. Furthermore, the importance of resource identity and behavioural changes in resource use when predicting ecosystem processes across trophic levels was highlighted, as grasshoppers fed less on herbs than grasses in the presence of spiders. Eklov and Werner (2000) provide evidence both for and against the use of body size as a surrogate for interaction strength in an experimental investigation of the effects of bluegill sunfish and odonate larval predators on bullfrog and green frog tadpole prey. Experimental aquaria were constructed with each predator separately (lethal and non-lethal presence) and in combination with the non-lethal presence of the other. Non-lethal inclusion of a predator was maintained by its caged presence such that it could not consume prey. Each treatment was replicated for each prey species at 5 different prey densities. Predation rates by both predators decreased with increasing tadpole size, potentially supporting the prediction that consumption decreases as predator: prey body size ratio decreases (the metabolic requirements of predators could be met by less prey items if they were larger). However, predation rates were also affected by the non-lethal presence of the other predator and predator identity, indicating that behavioural responses of predators may be as important as size in determining predator: prey interaction strength.

Counterintuitive to metabolic theory the attack rate on amphipod prey by large benthic isopod predators has been seen to increase with prey size (Ajetlawi *et al.* 2004). Although, as predicted by metabolic theory maximum attack rates with small prey were observed when small predators were used (Ajetlawi *et al.* 2004).

In all of these examples (Eklov and Werner 2000, Sala and Graham 2002, Ovadia and Schmitz 2002, Ajetlawi *et al.* 2004) predator and prey body size were not concurrently manipulated. Furthermore, the relationship between predator: prey body size and ingestion rate or, interaction strength was not investigated or compared to that predicted by metabolic theory (log-log relationship raised to the power 0.75 or 0.69). Thus, although there is evidence that size is related to interaction strength, evidence that predator: prey body size ratios can be used to predict interaction strength is limited. The exact relationship between predator: prey body size ratios and interaction strength, the relative importance of species identity, and non-direct interactions in affecting this relationship remains unclear.

There are three examples in the literature where the relationship between predator: prey body size and interaction strength has been examined. Emmerson *et al.* (2005) used metabolic theory to derive three simple and general relationships between interaction strength and the ratio of predator: prey body mass. 1) log(trophic energy transfer) / log (predator prey body size relationship) should scale$^{-1/4}$ [15], 2) biomass flux from a prey species to a predator species can be calculated by predator total ingestion rate*relative abundance of that prey in the predator's diet, which is proportional to the mass of predator raised to 0.75 / mass of prey raised to 1 [16], and 3) *per capita* effect of a

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[15] Emmerson *et al.* (2005) assumed metabolic rate to scale with body mass to the power 0.75 and species ingestion rate scales metabolic rate to the power 0.75 thus ingestion of a single prey item by a predator = predators total ingestion rate subdivided among its prey species (calculated using the relative density of that prey item divided by the total density of all prey items). Relative densities of prey items were constant such that, the ingestion rate of any one predator will scale with the total prey density. This assumption was confirmed by gut content analysis of predators and measures of prey density from species in the Broadstone Stream. Density of prey was calculated taking into account, a) that the density of prey is proportional to mass raised to the power $^{0.75}$ (as predicted by metabolic theory), b) the energy efficiency transfer across trophic levels and, c) the ratio of predator:prey body mass, so that the density of prey= the mass of that species raised to the power $^{[(\log(\text{mean efficiency energy transfer}))/(\log(\text{predator:prey body mass}))]*-0.75}$. The assumption that log (trophic energy transfer) / log (predator prey body size relationship) should scale$^{-0.25}$, was confirmed by empirical data from the Broadstone stream where log energy transfer = 0.342, and mean predator:prey = 0.67 thus log (trophic energy transfer) / log (predator prey body size relationship) scaled with the exponent $^{-0.254}$.[15]

[16] Combining the assumptions of scaling with body mass of ingestion rate and abundance, the ingestion rate of biomass flux from a prey species to a predator species could be calculated by; Predator total ingestion rate*relative abundance of that prey in the predators diet which is proportional to the mass of

predator on a prey population in terms of biomass rate of prey growth can be assumed to follow the same equation as that of ingestion rate described in 2)[17]. Empirical measures of some of the assumptions underlying these relationships were then taken from the species living in the Broadstone Stream, U.K. and the theoretical predictions were confirmed, providing strong evidence for the role of metabolic theory in predicting interaction strengths and energy flow in food webs.

Investigating the community wide distribution of interaction strengths in giant kelp forests, Sala and Graham (2002) found a positive relationship between herbivore body size and interaction strength (as defined by sporophyte density in aquaria with predators divided by sporophyte density without predators, accounting for experimental time and predator density). However, the relationship between herbivore size and *per capita* interaction strength was limited in its applicability across all body sizes. The relationship fitted a hypothetical Michaelis-Menten saturation curve reaching a plateau at high predator body sizes. Thus as predator: prey body size ratios increased, the efficiency at which herbivores can remove sporophytes becomes limited. Although the effects of herbivore identity and size could not be distinguished it is worth noting that small sea urchins (*Strongylocentrotus purpuratus*) removed less sporophyte than larger individuals and both lay on the line fitted by the theoretical Michaelis-Menten saturation curve.

Emmerson and Raffaelli (2004) empirically investigated predator: prey body size ratios and interaction strength whilst considering both predator and prey identity. Four predator species, a crab, a shrimp, and two fish were split into three size-classes and every predator species size-class was incubated separately in mesocosms with the

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predator raised to ¾ / mass of prey raised to 1. This was confirmed for each trophic link empirically measured in the Broadstone Stream food web.

[17] Empirical data from the Broadstone food web supported this assumption (Emmerson *et al.* 2005).

mud-dwelling amphipod *Corophium volutator*. Treatments were then repeated for three distinct size-classes of amphipod. Additionally each predator size-class was incubated separately with three additional prey species (only one size-class of prey was used). In accordance with metabolic theory predator size and prey size were shown to be significant in explaining the variability in interaction strengths, however so was predator identity, and also the interaction between predator identity* predator size and predator identity * prey size. The importance of species identity was further confirmed by individual regression analysis of each predator with the amphipod. Predator: prey body size ratios scaled significantly with interaction strength for the shrimp and crab predators (the power regression exponents were not significantly different from 0.75). However, separate regressions between each fish predator: prey body size ratio vs interaction strength were neither significant nor positive. Emmerson and Raffaelli (2004) provide evidence both for and against the use of predator: prey body size relationships to predict interaction strength. However, the general applicability of such a technique cannot be determined from the outcome of just one experiment. It is unclear whether the fish species used were a special exception to the rule, whether fish in general are an exception to the rule, or whether the two crustacean predators are the exception, and predator: prey body size ratios cannot be widely used to predict interaction strength.

Finally by combining the results of Wootton (1997), Sala and Graham (2002) and Emmerson and Raffaelli (2005), a study by Wootton and Emmerson (2005) found a good agreement between body size and interaction strength. The relationship between *per capita* interaction strength and prey: predator mass was described by the equation *per capita* interaction strength $^{0.25}$= 0.14+0.85*(prey: predator mass)$^{0.25}$, R^2 = 0.50 (Wootton and Emmerson 2005). However, when data from individual experiments were examined this relationship was not general. The authors suggested this trend was biased

towards the patterning of interaction strengths found by Wootton (1997). The bird species used in Wootton's experiment (1997) were of a much greater size than the invertebrate species in the studies of Sala and Graham (2002) and Emmerson and Raffaelli (2005). As previously mentioned Sala and Graham (2002), found a decrease in sporophyte density with increasing predator mass (relative to prey mass), and for at least two of the estuarine predators used by Emmerson and Raffaelli (2004) found that there was no relationship between predator: prey body size ratio and interaction strength.

The universal nature of the relationship between body sizes, interaction strength and ecosystem process remains unclear. The use of surrogate measures such as body size for determining both species interactions, and ecosystem processes therefore remains unproven. If, as suggested, allometric scaling principles can be used to parameterise the food web models that make predictions on the stability and functioning of assemblages (Brown and Gillooly 2003) it is important to test the validity of these underlying assumptions. If easily tractable surrogate measures of interaction strength, such as body size, can be used to predict species interactions and ecosystem processes, the effect of reduced species diversity on species assemblages and ecosystem process may be easily ascertained. This method may offer an alternative approach to assessing the response of ecosystem processes to reduced species diversity, where previous attempts to uncover a universal trajectory have failed.

4.1.4 The Present Study

4.1.4.1 Aims and Objectives

The aim of this chapter is to empirically measure the response of interaction strength and an ecosystem process to manipulated predator: prey body size ratios and to

compare these observed measures with those expected based on allometric scaling principles. The identity and size of four ubiquitous predatory strandline beetles (*Cafius xantholoma, Remus sericeus, Polystoma algarum* and *Cafius variolosus*), and three species of ubiquitous kelp fly larvae (*Coelopa frigida, Coelopa pilipes* and *Dryomyza anilis)* were manipulated in a laboratory-based mesocosm study. Interaction strength and *L. digitata* mass loss (a measure of decomposition) were then measured. In this way the effect of predator: prey body size ratios on *per capita* interaction strength and ecosystem processes (kelp decomposition) could be measured. The interaction between predator and prey was measured for different predator and prey identities. The relationships between predator and prey size, *per capita* interaction strength and the ecosystem process were predicted based on allometric scaling laws and compared to those observed in mesocosm manipulations.

The following assumptions underlying the use of predator and prey body size as a surrogate for interaction strength and ecosystem processes were tested;

H_1 Prey mass loss scales with predator mass $^{0.75 \text{ or } 0.67}$,

H_2 Predation depends on the size of predator and prey irrespective of identity,

H_3 Predation can be predicted using predator and prey body size,

H_4 *L. digitata* mass loss scales with prey mass after predation $^{0.75 \text{ or } 0.67}$,

H_5 *L. digitata* mass loss can be predicted using predator and prey,

H_6 Prey predation is not affected by prey identity.

4.1.4.2 Species Selection

Species were selected primarily due to their abundance, and their survival ability under laboratory conditions. All three species of larvae naturally co-occurred in the Wembury strandline. At least one species of larva was always available in high abundance, and with an appropriate range of body sizes, after a large deposit of stranded

material on the beach. *Coelopa* species may be important in the decomposition of wrack (Sections 2.5 and 2.7.2) and have been recorded as important constituents of wrack beetle diets (Section 2.7.3). Preliminary trials showed that larval species repeatedly consumed measurable quantities of wrack material over short time periods, without high mortality. Similarly all species of beetle employed here were shown, in preliminary trials, to consume individual larvae over similar, relatively short time periods. Using pitfalls traps the beetle species used were commonly found occurring in high abundance in the strandline at Wembury. They survived well under laboratory conditions, and killed and consumed larval prey in mesocosms. Furthermore, in terms of wet mass each species had a body size distribution which covered 1.5-2 orders of magnitude, and species differed from one another in terms of body size distribution (Figure 2.7).

4.2 Materials and Methods

4.2.1 Collection of Animal Material, Wrack and Sediment

Fly larvae, *Coelopa frigida*, *Coelopa pilipes*, *Dryomyza anilis*, and the beetles *Cafius xantholoma*, *Polystoma algarum*, *Remus sericeus* and *Cafius variolosus* were collected by hand from within and beneath the spring tide strandline at the top of the shore, Wembury First Beach, Devon, UK (48.3°N, 50.4°E) (Tables 4.1 and 4.2). At the same time cast-up wrack *L. digitata* and sediment from beneath the wrack bed were also collected. All material was transported to the laboratory in large plastic bags. In the laboratory the animal material was separated according to species and size. The larvae were held in separate aquaria (vol. = 8 l). To mimic strandline conditions each aquarium was filled (to a depth of 2 cm) with sediment, overlain with two or three fronds of *L. digitata*. A paper towel soaked in distilled water was placed under the aquarium lids to maintain a high relative humidity within. Both the lid and the towel also prevented the

animals escaping. All aquaria were maintained in a controlled temperature facility (T = 20°C ± 1°C) before being used in the experiments described below. In the laboratory individual beetles were placed in separate mesocosms, with the exception of *P. algarum* and *C. variolosus* used in prey preference experiments. These two species were kept for 7 d in identical conditions to those described above for larval species. Here they were supplied with larvae. Sufficient numbers and sizes of *P. algarum* and *C. variolosus* were not found in and around the strandline at Wembury immediately preceding the prey preference experiments that used these two species and as such previously collected species had to be used (Table 4.1).

4.2.2 Mesocosm Construction

Mesocosms used for all treatments and replicas were constructed from containers (17 cm x 11.5 cm x 4 cm, vol. = 782 cm^3) made from polypropylene. To prevent beetles and larvae escaping the lids of each mesocosm were sealed to the containers using PVA glue. A small hatch (3 cm x 2 cm) was cut in the centre of the lid of each mesocosm, through which species were added to the mesocosm. After the addition of species the hatch was closed flush with the lid, preventing beetle and larval escape but also permitting a fresh air supply. As beetles and larvae were often found deep within wrack material or sediment, each container was partially-filled with sediment (vol. = 40 ml). All sediment had been previously autoclaved to remove any bacteria (30 min, T = 200°C). The sediment was classed as very coarse sand (see Section 3.2.2). 5 ml of distilled water was added to the sediment in each mesocosm. Preliminary observations showed maximum beetle survival when distilled water (vol. = 5 ml), was added to each mesocosms to maintain humidity throughout the experiment.

Each sediment-filled container was supplied with wrack (*L. digitata*, one of the most prevalent algae in the wrack beds at Wembury Beach). Preliminary experiments (duration = 30 h) using other strandline algae (*Fucus* spp. and *Ulva lactusa* with *C. frigida* and *C. pilipes*) showed that *C. frigida* and *C. pilipes* separately showed no preference (determined as algal mass loss) for any particular wrack bed alga. Discs of *L. digitata* (diam. = 2 cm) were cut, using a cork borer, from sections of the blade of a similar thickness showing no visible signs of previous decomposition. These discs were placed in each mesocosm, in an overlapping circular pattern (see Section 3.2.2).

In each treatment prey density was constant n = 12. *L. digitata* mass loss was measurable at this larval density and larval pupation/mortality was minimal.

Each mesocosm was then placed separately in a black plastic (opaque) bag in a temperature controlled room at T = 20°C ± 1°C 12 h light/dark cycle. This temperature was the equivalent to summer temperatures experienced on Wembury beach, and also promoted measurable feeding rates.

All beetles were starved in isolation in the mesocosms (24 h) before prey items were added as this promoted feeding as soon as prey items were added to the mesocosm (*pers. obs.* and E. McAfee *pers. comm.*). All experiments ran for a period of 35 - 53 h (Table 4.1)[18].

4.2.3 Interaction Strength

There are a number of different ways of calculating interaction strength depending on the particular aims of the study. Each method has strengths and weaknesses (Berlow *et al.* 1999, 2004). To avoid limiting the experiment to a particular measure of interaction strength the number of individual larvae killed was measured.

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[18] This enabled a measurable *L. digitata* mass loss. The beetles ate, but few larvae pupated and predator and prey mortality (not through consumption) was negligible.

Most measures of interaction strength rely on a measure of prey density in the presence and absence of a predator. This measure forms the basis of a number of interaction strength indices (Berlow *et al.* 1999), including those used in Lotka-Volterra equations to model food webs (for the use of Lotka-Volterra equations in food web models see Pimm 1982). Furthermore, the number of individual larvae killed provides a potentially easy way of predicting ecosystem processes from size analysis of communities. Finally it is possible to measure this parameter empirically.

4.2.4 Kelp Mass Loss, Prey Mass, Prey Mass Loss, Beetle Mass

Kelp mass loss was determined as dry kelp mass loss in grams divided by the experimental duration. Each disc was wet weighed after blotting before and after the experiment [19](Mettler Toledo AT201 balance, accuracy ± 0.01mg). To estimate dry kelp mass the kelp remaining at the end of the experiment was dried for 48 h at 50°C. The relationship between wet kelp mass and dry kelp mass was determined using Ordinary Least Squares linear regression analysis (OLS) and the linear equation used to back calculate initial dry kelp mass (see appendix A10 for individual caculations). The inferred initial dry kelp mass and measured final dry kelp mass was then used to infer dry kelp mass loss $g.h^{-1}$. For each replicate dry beetle mass was determined by drying individual beetles for 48 h at 50°C at the end of each experiment. Dry prey mass was inferred from measurements of at least 100 individuals of each larval species before and after drying for 48 h at 50°C. OLS regression analysis was used to determine the linear relationship between wet and dry mass measurements for each larva species. This relationship was then applied to all wet prey mass measurements taken, thus prey mass loss was a function of initial inferred dry prey mass-final inferred dry prey mass (see appendix A10 for individual caculations).

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[19] Repetitive measures showed wet weighing after blotting was repeatable and precise (Appendix A1).

Owing to the large number of replicates required and time necessary to process beetles and larvae[20] this study was divided into eight separate experiments.

4.2.5 The Effect of Predator: Prey Body Sizes and Predator Identity on Prey Mass Loss, Interaction Strength and *L. digitata* Mass Loss

The first four experiments manipulated the size of four predatory beetles and one prey species (Table 4.1). Predators and prey were sorted into three size-classes, large medium and small, based on the size range of species collected that day (Table 4.2). As larval and beetle identity and size range on the strandline was temporally variable, each predatory beetle was not incubated with the same larva species. For each predator nine treatments were set up so that all possible pair-wise combinations of predator size and prey size were investigated. For each predator species five controls were also set up, each larval size category in the absence of predators, predators only (medium size-class was used here) and without predators or prey so that *L. digitata* mass loss with each size category of prey, *L. digitata* mass loss with predators only and *L. digitata* mass loss without predators and prey could be ascertained. A minimum of five replicates was used for each treatment and control. A minimum of three replicas were used for treatments of larvae in isolation (large, medium and small size-classes) and predators in isolation (large, medium and small size-classes)

4.2.6 The Effect of Prey Identity on Interaction Strength

To investigate the effect of prey identity on *per capita* interaction strength four further experiments were set up using the same four predatory beetles (Table 4.1). The effect of larval identity on *per capita* consumption rates were measured for each beetle species when incubated separately with each larval species. It has been shown that in

[20] Some days not all beetle or larva species were found at Wembury in sufficient numbers and/or sizes.

order to make valid statistical conclusions of species feeding preferences the difference in consumption must be analysed for each species pair separately (Liszka and Underwood 1990, Underwood 1997). Each beetle species was also incubated with all three prey items together and the effect of larval identity on *per capita* consumption rates measured. This was so that conclusions on the prey preference of beetles in their natural environment (when exposed to all species simultaneously) could be made. Prey density was always 12 individuals so that when all three prey species were incubated with the predator each individual prey species was present as four species.

Table 4.1 Dates and times of species collection, predator isolation, prey addition and experiment termination for both experiments.

Experiment	Predator	Prey	Species collected	Predators start isolation	Prey added	Experiment end point
Predator: prey body size experiments	*Cafius xantholoma*	*C. frigida*	24.06.06 08.00-11.00	25.06.06 08.00-14.00	26.06.06 08.00-14.00	27.06.06 19.00-23.30
	Remus sericeus	*C. pilipes*	01.10.06 10.00-13.00	02.10.06 08.00-14.00	03.10.06 08.00-15.00	05.10.06 13.00-19.00
	Polystoma algarum	*D. anilis*	15.07.06 08.00-15.00	16.07.06 08.30-10.00	17.07.06 08.30-12.00	19.07.06 12.30-18.00
	Cafius variolosus	*C frigida*	19.10.06 09.30-11.00	19.10.06, 12.30-18.30	20.10.06 12.30-18.30	22.10.06 17.30-22.00
Prey identity experiments	*Cafius xantholoma*	*C frigida, C. pilipes, D. anilis*	03.07.06, 10.00-16.00	04.07.06 8.00-18.00	05.07.06 8.00-18.00	06.07.06 19.00-22.00
	Remus sericeus	*C. frigida, C. pilipes, D. anilis*	04.10.06 09.30-10.00	05.10.06 10.30-17.00	06.10.06 10.30-17.00	08.10.06 11.30-17.00
	Polystoma algarum	*C. frigida, C. pilipes, D. anilis*	15.09.06 10.00-13.00 (*P. algarum*) 19.09.06 8.00-9.00 (larva species)	20.09.06 08.30-16.00	21.09.06 08.30-16.00	23.09.06 12.30-16.00
	Cafius variolosus	*C. frigida, C. pilipes, D .anilis*	19.10.06, 9.30-12.00 (*C. variolosus*) 31.10.06 9.00-11.30 (larva species)	01.11.06, 14.00-18.30	02.11.06 14-18.30	04.11.06 14.00-18.30

4.2.7 Statistical Analyses

All non-parametric regressions were undertaken using StatsDirect version 2.3.7 (http://www.statsdirect.com, Copyright 1990-2007 StatsDirect Limited). The non-

parametric technique is a distribution-free method for investigating a linear relationship. The slope b of the regression (Y=bX+a) is calculated as the median of the gradients from all possible pair-wise contrasts of the data. This analysis does not assume that all the errors are only in the y-direction, or that either the x- or y-direction errors are normally distributed. Furthermore, this method is less affected by the presence of outlying data points (Conover 1999). The specific non-parametric technique used can be found in Conover (1999). The significance of the regression is determined using 95% confidence intervals based upon Kendall's τ.

All other statistical analyses were carried out using MINITAB (Version 13.32, Minitab Inc, State College PA).

4.2.7.1 Predator Dry Mass and Prey Mass Loss

To test the assumption that log (predator ingestion) scales with log (predator mass), the relationship between predator dry mass and prey mass loss was analysed using linear regression techniques. In order than the results could be compared between experiments and with the relationship predicted by metabolic scaling theory, raw predator dry mass and prey mass loss ($g.h^{-1}$) was log transformed and power regression used to fit the line.

When the results from all experiments were combined and for each predator: prey experiment the relationship between predator mass and prey mass loss was investigated. The normality of residual distribution was tested using Anderson-Darling tests and if significant non-parametric techniques were used.

4.2.7.2 Interaction Strength

For all experiments, the combined effect of beetle size-class, larval size-class and predator: prey identity (experiment) on the variability in the number of individual

larvae killed was calculated using a fully-factorial ANOVA where initial beetle mass and initial larval mass are covariates.

The effect of beetle and larval size on the number of individual larvae killed was analysed separately for each experiment using four one-way ANOVA's and Tukey's (HSD) *post-hoc* test of difference.

To investigate the validity of using predator mass and prey mass to predict interaction strength or predation rate the observed relationship between the number of individual larvae killed and predator mass was compared to that predicted by metabolic scaling using the Students t-test. Where there was a significant relationship between log(predator dry mass) and log(prey mass loss), the predicted values incorporate the observed y intercept from regressions of observed log(prey mass loss) *vs* log(predator mass) (Box 5.1, Equation 2).

4.2.7.3 Decomposition

Decomposition was calculated as dry *L. digitata* mass loss divided by experimental duration. For all experiments combined the effect of beetle size-class, larval size-class and predator: prey identity (experiment) on the variability in *L. digitata* mass loss per hour was calculated using a fully-factorial ANOVA with initial beetle mass and initial larval mass as covariates. The relationship between final prey mass and *L. digitata* mass loss.h^{-1} was analysed using linear regression techniques. In order that the results could be compared between experiments, and with the relationship predicted by metabolic scaling theory, raw data of mean final prey dry mass (g) /individual and *L. digitata* mass loss ($g.h^{-1}$) was log transformed and a power regression used to fit the line. Where the relationship between log(final prey dry mass) and log(*L. digitata* mass loss) was investigated, the normality of residual distribution was tested using Anderson-Darling tests and if significant non-parametric regressions were used.

To test the validity of the assumption that prey consumption scales with prey mass the observed relationship of *L. digitata* mass loss ($g.h^{-1}$) were compared to those predicted by metabolic scaling based on actual values of mean final prey using a Students t-test, predicted values were calculated according to Box 4.1, Equation 3. This comparison was only performed if significant regressions between log(final prey dry mass) and log(*L. digitata* mass loss) where found. To investigate the usefulness of predator mass and prey mass in determining ecosystem process, the observed relationship of *L. digitata* mass loss $g.h^{-1}$ were compared to those predicted by metabolic scaling based on predator and prey mass using a Students t-test. Predicted values incorporate the observed y intercept from regressions of log(observed prey mass loss) *vs* log(predator mass) this was only calculated for those predator-prey experiments where there was a significant relationship between log(predator dry mass) and log(prey mass loss) (Box 4.1, Equation 4).

Box 4.1

Equation 1.

Predicted prey mass loss g/experimental duration = a*Predator dry mass g $^{0.75 or 0.67}$)
Where a = y intercept of the observed regression between log(predator dry mass g) and log(prey mass loss g/h).

Equation 2.

Predicted total number of individual larvae killed = (a*Predator dry mass g $^{0.75 or 0.67}$)*experimental duration h/prey mass g .
Where a = y intercept of the observed regression between log(predator dry mass g) and log(prey mass loss g/experimental duration).

Equation 3.

Predicted *L.digitata* mass loss g/individual = (a*mean final prey mass g/individual $^{0.75 or 0.67}$).
Where a = the y intercept of the observed regression between log(mean final prey mass/individual) and log(*L.digitata* mass loss g/h/individual).

Equation 4.

Predicted *L.digitata* mass loss g/ experimental duration = 12- ((a* Predator dry mass g $^{0.75}$)/ mean prey mass g)*mean prey mass g $^{0.75}$.
Where a = y intercept of the observed regression between log(predator dry mass g) and log(prey mass loss g/experimental duration).

((a* Predator dry mass g $^{0.75}$)/ mean prey mass g) is rounded up to the nearest integer. This equation estimates the number of prey killed based on the predator dry mass and prey mass, then calculates the remaining prey mass, which according to metabolic law should predicted prey ingestion and thus kelp mass loss.

4.2.7.4 Effect of predator and prey identity on interaction strength

The significance of prey identity and beetle identity in determining interaction strength (number of individual larvae killed) was determined by combining all experimental data using two fully-factorial ANOVAs. The first considering the number of individual larvae killed when the beetles were exposed to each larva species separately, the second when beetles were incubated with all three species together. In both cases beetle mass and larval mass were covariates. The significance of prey identity and beetle identity in determining predator predation (number of individual larvae killed) for each predatory beetle species was determined using a one-way

ANOVA. Where appropriate Tukey's (HSD) *post-hoc* tests were used to determine which larva species was predated on to a greater or lesser extent.

4.3 Results

4.3.1 General Observations, Feeding, Mortality, Pupation and Behaviour

Within 5-10 min of adding any beetle predator to the mesocosms the predator was observed to stop skirting the mesocosm perimeter and either move underneath *L. digitata* discs out of sight or commence attacking larvae.

With the exception of *R. sericeus* and large larval size-classes, all beetles in all replicates fed. In the case of *R. sericeus* and large larvae, no feeding was observed in 75 % of medium and small beetle size-class replicas and 66 % in large beetle size-class replicas.

In some instances beetles killed many larvae and did not fully consume all larvae killed.

In all experiments mortality and pupation was zero for controls. Larvae in the absence of predators consumed more kelp and larger size-classes of larvae consumed more than smaller size-classes. Kelp mass loss in the presence of beetles was greater than kelp only controls but less than any treatment with larvae.

Non-predatory mortality and larval pupation was low across all experimental treatments. In the body size experiments combining *C. xantholoma* and *C. frigida*, in one replicate of small beetle and small larval size-classes, three larval individuals suffered non-predatory mortality and as such were removed from further analysis. In *R. sericeus* and *C. pilipes* experiments there was no non-predatory mortality. However in some replicate, larvae in the large size-class did pupate, although pupation was never greater than 36 %. When *P. algarum* and *D. anilis* were combined two larval treatments

suffered non-predatory mortality, in one replicate of a large beetle with small larva, the other in a replicate of a medium beetle with medium larvae, in the latter replicate 50 % of the larva species suffered non-predatory mortality. D*ryomyza anilis* pupation was much greater than for any other larvae in other treatments. This was confined to medium and small larval size-classes, the former never exceeding 24 % in any one replicate, and the latter 36 %. In *C. variolosus* and *C. frigida* experiments there was no beetle or larval mortality. Two species of larva pupated in one replicate of small beetle and small larval size-class, and only two other individuals pupated throughout the experimental duration; one in a replicate with a medium beetle and medium larvae, the other in a replicate with a medium beetle and large larvae.

Depending on the size-distribution of predatory beetle and larval prey on the date of collection, small, medium and large size-classes differed between predator and prey across experiments (Table 4.2). In terms of mean beetle mass this was, *C. variolosus* > *C. xantholoma* > *P. algarum* > *R. sericeus*. This resulted in a 6.2 order of magnitude difference between the smallest size-class of the smallest beetle (*P. algarum*) and the largest size-class of the largest beetle (*C. variolosus*). The range of size distributions differed between each species. This resulted in mean beetle mass differences of 1.56, 1.53, 1.51, 1.33 orders of magnitude between smallest and largest size-classes for *C. xantholoma, R. sericeus, P. algarum* and *C. variolosus* respectively (Table 4.2). Larvae generally differed to a greater extent in terms of size; 2.76[21], 2.58 and 2.25 orders of magnitude between largest and smallest size-classes for *C. frigida, C. pilipes* and *D. anilis* respectively, reflecting the order of largest to smallest larva (Table 4.2).

[21] 2.76 reflects the mean order of magnitude difference between *C. frigida* smallest and largest size-classes in experiments where *C. frigida* was combined with *C. xantholoma* and *C. verilosus* separately. When combined with *C. xantholoma C. frigida* differed by 2.81 orders of magnitude between largest and smallest size-class and with *C. verilosus* by 2.71 orders of magnitude.

Table 4.2 Mean mass (dry mass mg) and standard error for each beetle and larval species.

Species	Predator size-class (dry mass mg)			Prey size-class (dry mass mg)		
	Large	Medium	Small	Large	Medium	Small
C. xantholoma & *C. frigida*	3.95 ± 0.10	3.30 ± 0.05	2.53 ± 0.08	3.46 ± 0.91	2.22 ± 0.38	1.23 ± 0.31
R. sericeus & *C pilipes*	1.48 ± 0.05	1.20 ± 0.02	0.97 ± 0.02	3.48 ± 0.57	2.27 ± 1.61	1.35 ± 0.36
P. algarum & *D. anilis*	2.13 ± 0.06	1.41 ± 0.06	0.89 ± 0.06	3.04 ± 0.66	2.27 ± 1.61	1.35 ± 0.36
C. variolosus & *C. frigida*	5.53 ± 0.12	4.52 ± 0.03	4.16 ± 0.03	6.00 ± 2.71	3.26 ± 1.09	2.21 ± 0.96

4.3.2 Predator Mass and Prey Mass Loss

Across all experiments prey mass loss was seen to increase as predator mass increased (Figure 4.1). For each individual beetle and prey combinations and when data from all experiments were combined, the residuals of the regression of log(predator dry mass g) *vs* log(dry prey mass loss $g.h^{-1}$) were not normally distributed as determined using the Anderson-Darling normality test (Appendix A11). Consequently, non-parametric regression analysis was used to obtain the line of best fit.

When all experiments were combined $\log_{10}$(prey mass loss) scaled with $\log_{10}$ (predator mass) to the exponent 1.076. Despite the low and high values of prey mass loss relative to predator mass in replicates where the predator *R. sericeus* was combined with *C. pilipes*, and the very low values of prey mass loss relative to predator mass loss seen in two replicates, *P. algarum & D. anilis*, and *C. variolosus & C. frigida* (Figure 4.1). This regression was significant ($P < 0.05$) (Table 4.3).

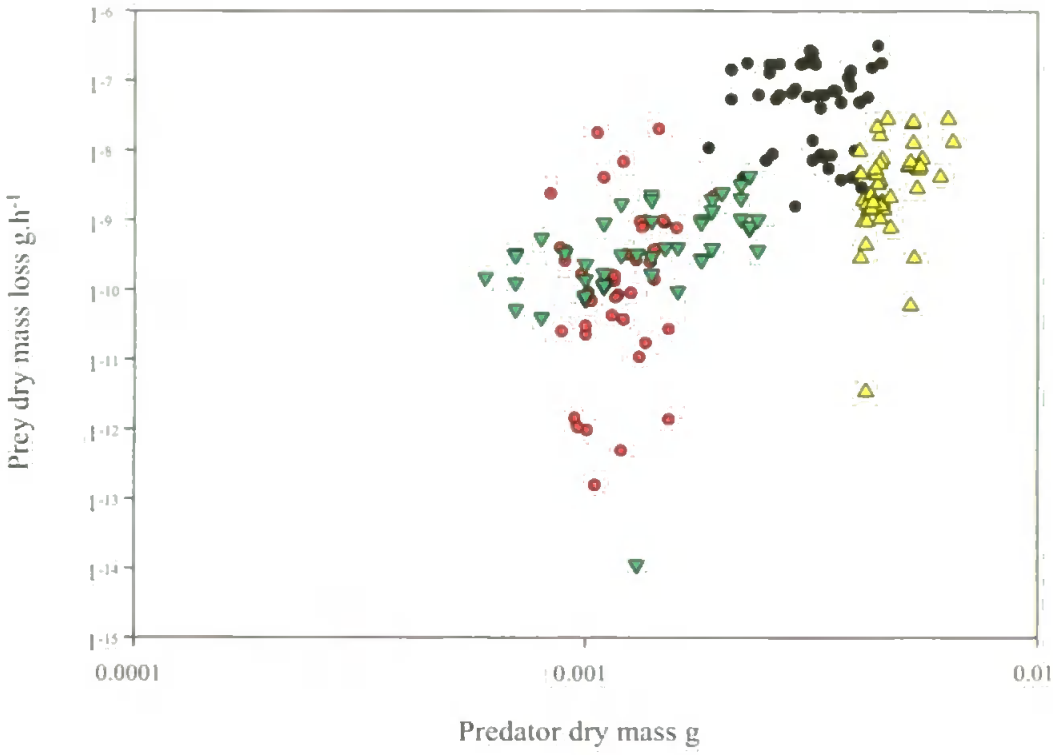

Figure 4.1 Predator dry mass g plotted against dry prey mass loss $g.h^{-1}$, for each separate beetle and larva species body size experiment. All experiments combined $Y=0.108491x^{1.076552}$ **(s)**. Black circles = *C. xantholoma* & *C. frigida* $Y=0.000637x^{0.02257}$ **(n/s)**, red circles = *R. sericeus* & *C. pilipes* $Y=11.19023x^{1.82434}$ **(n/s)**, green triangles = *P. algarum* & *D. anilis* $Y=0.021385x^{0.85036}$ **(s)**, yellow triangles = *C. variolosus* and *C. frigida* $Y=8.585943x^{1.959069}$ **(s)**. Where **s** = significant relationship, **n/s** = no significant relationship (see Table 4.3).

The exact relationship between predator mass and prey mass loss differed between experiment and is reflected in the range of exponent values of the power regression when log-predator mass is plotted against log-prey mass loss, 0.023 - 1.960 (Figure 4.1), with the exception of *C. xantholoma* & *C. frigida* and *R. sericeus* & *C. pilipes* the relationship between log-predator mass and log-prey mass loss was significant (Figure 4.1, Table 4.3). Whilst the relationship between predator mass and prey mass loss when all experiments are combined can be viewed as reflecting the average relationship it does not represent the relationship between prey mass loss and predator mass in any single predator-prey experiment.

Table 4.3 Results of Kendall's rank correlation coefficient (on a two-sided continuity corrected z) and 95% confidence intervals non-parametric line of best fit of predator dry mass *vs* prey mass loss $g.h^{-1}$.

Experiment	95% Confidence intervals	Kendall's rank correlation coefficient tau b	P
All experiment combined	0.959173 1.208595	0.421855	<0.0001
C. xantholoma* & *C. frigida	-0.785677 0.686252	-0.009333	0.9342
R. sericeus* & *C. pilipes	-0.175015 3.253811	0.182557	0.0798
P. algarum* & *D. anilis	0.493942 1.198914	0.442871	<0.0001
C. variolosus* & *C. frigida	0.658986 3.283553	0.290929	0.0051

4.3.3 Predicted Prey Mass Loss

Where the regression between prey mass loss and predator mass was significant the relationship was compared with that predicted by metabolic theory. In all cases predicted values of prey mass loss based on a scaling exponent of 0.75 or 0.67 differed significantly from those observed (Table 4.4 a, b). In all cases the predicted mean dry prey mass loss $g.h^{-1}$ was significantly greater than observed.

Table 4.4 Results of 2 sample t-test of observed dry prey mass loss $g.h^{-1}$ and predicted dry prey mass loss $g.h^{-1}$; a) based on the scaling exponent 0.75 and b) based on the scaling exponent 0.67.

a)

Factors	*n*	*Mean*	*Standard deviation*	*Standard error*	D.F.	*t*	P
Observed All species combined	182	0.0003	0.0003	0.0000	300	-19.97	<0.001
Predicted All species combined	182	0.0012	0.0005	0.0000			
Observed *P. algarum*	45	0.0001	0.0001	0.0000	87	-7.30	<0.001
Predicted *P. algarum*	45	0.0002	0.0000	0.0000			
Observed *C. variolosus*	45	0.0002	0.0001	0.0000	44	-67.33	<0.001
Predicted *C. variolosus*	45	0.1548	0.0154	0.0023			

b)

Factors	*n*	*Mean*	*Standard deviation*	*Standard error*	D.F.	*t*	P
Observed All species combined	182	0.0003	0.0003	0.0000	361	-8.82	<0.001
Predicted All species combined	182	0.0006	0.0003	0.0000			
Observed *P. algarum*	45	0.0001	0.0001	0.0000	77	-14.47	<0.001
Predicted *P. algarum*	45	0.0003	0.0001	0.0000			
Observed *C. variolosus*	45	0.0002	0.0001	0.0000	44	-75.73	<0.001
Predicted *C. variolosus*	45	0.2374	0.0210	0.0031			

4.3.4 Interaction Strength

The number of larvae killed varied greatly according to larval size-class and predator-prey combination. Within each beetle size-class, the number of individual larvae killed increased as larval size-class decreased, however for *P. algarum* & *D. anilis* treatments this trend is only apparent in small beetle size-classes (Figure 4.2 a-d). However the actual number of larvae killed differed between experiments (Figure 4.2 a-d). The number of larvae killed in each beetle size-class did not differ greatly and was inconsistent between experiments (Figure 4.2). There is some indication that the number of individual larvae within a size-class appears to decrease with beetle size-class, although this trend is not consistent for all larval size-classes in all experiments (Figure 4.2 a-d).

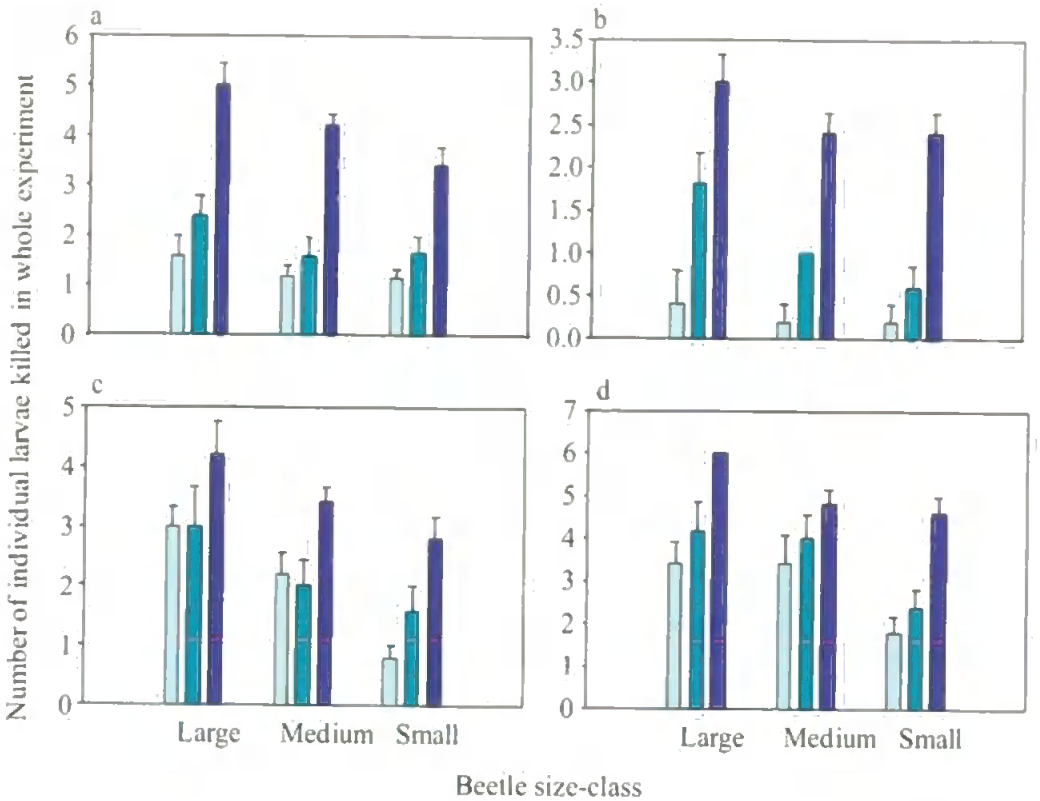

Figure 4.2 a-d Number of individual larvae killed, by each predator size-class over the entire experimental duration (mean ± s.e.). Turquoise = large larval size-class, teal = medium larval size-class, dark blue = small larval size-class. a) *C. xantholoma* & *C. frigida*, b) *R. sericeus* & *C. pilipes*, c) *P. algarum* & *D. anilis* and d) *C. variolosus* & *C. frigida*.

The fully factorial ANOVA combining all experiments supported these observations. Individually beetle size, larval size and the identity combination of beetle and larva were significant in explaining the variability in the number of individual larvae killed. However only larval size-class* identity combination were significant in explaining the variability in the number of individual larvae killed when factors were combined (Table 4.5) (the number of individual larvae killed is standardised for experimental duration).

Table 4.5 General Linear Model showing the effects of beetle size-class, larval size-class and beetle, larval identity combination on the number of individual larvae killed/h, for all predator- prey body size experiments combined where initial beetle dry mass and initial larval dry mass are covariants.

Source of variation	Number of individual larvae killed.h^{-1}					
	D.F.	SS	Adjusted SS	Adjusted MS	*F*	P
Beetle dry mass	1	0.0663	0.0000	0.0000	0.00	0.982
Larval dry mass	1	0.0843	0.0007	0.0008	2.10	0.150
Beetle size-class	2	0.0015	0.0035	0.0018	4.74	0.010
Larval size-class	2	0.0171	0.0160	0.0080	21.51	<0.001
Identity combination	3	0.0148	0.0094	0.0031	8.36	<0.001
Beetle size-class*Larval size-class	4	0.0007	0.0007	0.0002	0.47	0.760
Beetle size-class* Identity combination	6	0.0025	0.0021	0.0003	0.92	0.481
Larval size-class*Identity combination	6	0.0195	0.0197	0.0033	8.79	<0.001
Beetle size-class*Larval size-class*Identity combination	12	0.0037	0.0037	0.0003	0.84	0.611
Error	144	0.0537	0.0537	0.0004		
Total	181	0.2642				

The importance of beetle and larval identity in determining the significance of number of larvae killed is exemplified in additional one-way ANOVAs and *post-hoc* Tukey's (HSD) tests. These analyses also show the greater influence of larval size than beetle size in determining the number of prey items killed. In experiments using *C. xantholoma* and *R. sericeus* within each size-class of beetle significantly fewer medium and large larvae were killed than small larvae (Appendices A12, A13). In the case of large *R. sericeus* size-class, significantly more larvae from medium size clasess were killed than larvae in the large larval size-class (Appendix A13). Only large and small *C. variolosus* beetles killed significantly more small than large larvae (Appendix A14). In experiments involving *P. algarum* only within the small beetle size-class were more small larvae killed than medium or large larvae (Appendix A15). Across beetle size-classes the number of larvae killed within a certain larval size-class was dependent on experiment and larval size-class, and did not follow a consistent pattern. Significantly more small larvae were killed across large > medium > small beetle size-classes in experiments using *C. xantholoma*. Significantly more medium larvae were killed

between large > small beetle size-classes in *R. sericeus* experiments. In experiments using *P. algarum* only the mean number of large larvae killed increased with beetle size-class and here only between large and small beetles. In *C. variolosus* experiments there was no significant difference between numbers of individual larvae killed between beetle size-classes (within a larval size-class).

4.3.5 Predicted Number of Larvae Killed

The number of larvae killed was predicted using equations derived from metabolic scaling laws. This was only undertaken using experiments where there was a significant relationship between predator mass and prey mass loss. In all cases there was a significant difference between the observed and predicted number of individual larvae killed (Table 4.6 a, b). In all cases, predicted values based on metabolically predicted scaling exponents of 0.75 or 0.67, were much greater than those observed. In the case of *C. variolosus* & *C. frigida* experiments the mean number of predicted individual larvae eaten was 2554 and 3921 (based on exponents of 0.75 and 0.67 respectively) highlighting the sensitivity of this technique to outliers (table 4.6 a, b). Whilst there is no biological or *a priori* reason to exclude low values of prey mass loss from *C. variolosus* and *C. frigida* experiment (Figure 4.1) if they were not present the y intercept would be drastically reduced thus predicted values of prey mass loss and number of larvae killed would be considerably reduced and closer to those observed.

Table 4.6 Two sample t-test not assuming equal variances for observed and predicted number of individual larvae killed throughout the whole experiment. a) The number of individuals killed = ((C*predator dry mass g $^{0.75}$) * experimental duration)/ average dry prey mass and b) the number of individuals killed = ((C*predator dry mass g $^{0.67}$) * experimental duration)/ average dry prey mass. C is the y-intercept taken from the separate regressions in Figure 4.1.

a)

Factors	*n*	*Mean*	*Standard deviation*	*Standard error*	D.F.	*t*	P
All species combined Observed	182	2.54	1.64	0.12	188	-25.46	<0.001
All species combined Predicted	182	25	11.8	0.88			
Observed *P. algarum*	45	2.56	1.27	0.19	65	-7.20	<0.001
Predicted *P. algarum*	45	5.53	2.46	0.37			
Observed *C. variolosus*	45	3.84	1.59	0.24	44	-17.14	<0.001
Predicted *C. variolosus*	45	2554	998	149			

b)

Factors	*n*	*Mean*	*Standard deviation*	*Standard error*	D.F.	*t*	P
Observed All species combined	182	2.54	1.64	0.12	203	-18.96	<0.001
Predicted All species combined	182	13.13	6.63	0.49			
Observed *P. algarum*	45	2.56	1.27	0.19	52	-10.19	<0.001
Predicted *P. algarum*	45	8.96	4.02	0.60			
Observed *C. variolosus*	45	3.84	1.59	0.24	4	-17.13	<0.001
Predicted *C. variolosus*	45	3921	1533	229			

4.3.6 Kelp Mass Loss

The greatest mean *L. digitata* mass loss was observed in treatments containing *C. frigida* (Figure 4.3). Mean *L. digitata* mass loss g.h^{-1} appears to decrease from treatments of larva only > treatment of larvae and beetles > beetle only > control without beetles or larvae (Figure 4.3).

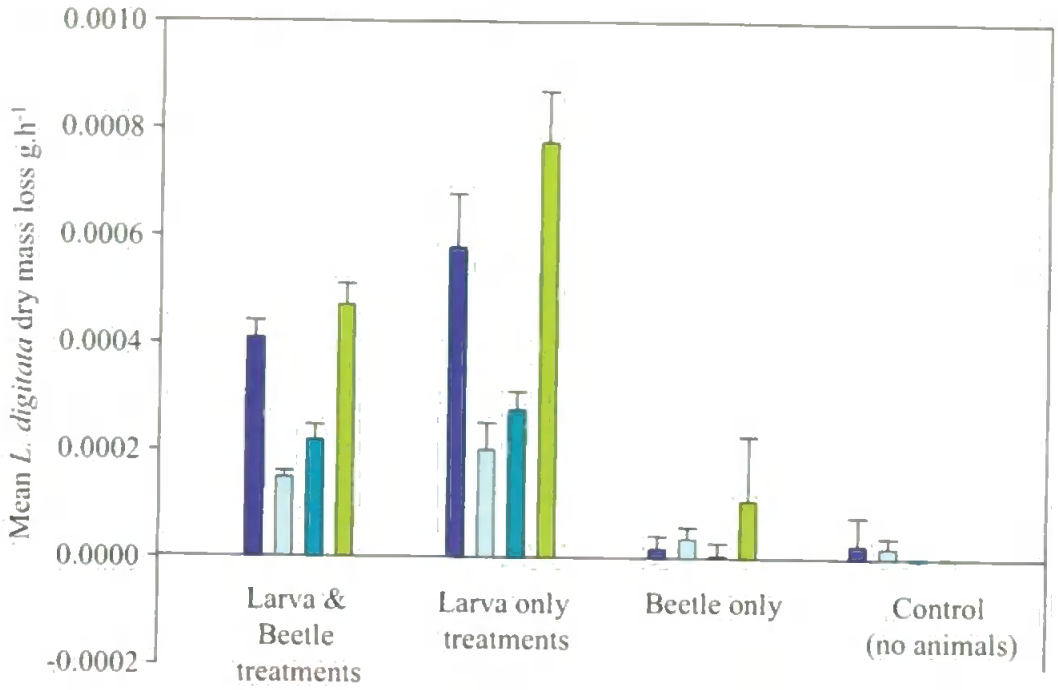

Figure 4.3 *L. digitata* dry mass loss $g.h^{-1}$ (mean ± s.e.) for each grouped treatment type. Blue = *C. xantholoma* & *C. frigida*, turquoise = *R. sericeus* & *C. pilipes*, teal = *P. algarum* & *D. anilis*, green = *C. variolosus* & *C. frigida*.

In each separate experiment one-way ANOVAs showed that grouped treatment type was significant in explaining the variability in *L. digitata* mass loss $g.h^{-1}$ (Appendix A16a-d). Tukey's (HSD) *post –hoc* test showed for each separate experiment, treatments without larvae, control and 'beetle only' treatments were significantly lower than treatments with larvae. However, the control treatments with and without beetles did not differ significantly from each other. Additionally, mean *L. digitata* mass loss $g.h^{-1}$ in treatments of larvae only were only significantly greater than treatments with the beetle and larvae in experiments involving *C. frigida* (*C. xantholoma* & *C. frigida* and *C. variolosus* & *C. frigida*), although it would be expected that in the absence of a predator, *L. digitata* mass loss $g.h^{-1}$ would be higher. This may be explained by the relatively lower consumption rates of *P. algarum* and *R. sericeus*. These predators consumed fewer larvae than *C. xantholoma* and *C. variolosus* (Figure 4.2a-d). Furthermore there were only nine replicates for each larval species in the absence of a

predator as opposed to 45 replicates of beetle and larval treatments. Thus the variability in *L. digitata* mass loss $g.h^{-1}$ in the absence of a predator would have been higher and small differences in *L. digitata* mass loss $g.h^{-1}$ between these two treatment groups may become not significant.

4.3.7 Final Prey Mass and Kelp Mass Loss

In all cases log(mean final prey mass/individual) and log(mean *L. digitata* mass loss $g.h^{-1}$/individual) were not normally distributed (test of the residuals at the 0.05 significance level) (Appendix A17). Non-parametric regressions were used to determine the relationship. There was a clear significant positive relationship between log(mean final prey mass/individual) and log(mean *L. digitata* mass loss $g.h^{-1}$/individual) when data from all experiments were combined and for each individual experiment, with the exception of *R. sericeus* & *C. pilipes* (Figure 4.4, Table 4.7).

When the results are segregated into separate predator and prey experiments there was variation in the value of the exponent depending on the predator and prey experiment (Figure 4.4).

Table 4.7 Kendall's rank correlation coefficient (on a two-sided continuity corrected z) and 95% confidence intervals of non-parametric line of best fit of predator dry mass *vs* prey mass loss $g.h^{-1}$.

Experiment	95% Confidence intervals	Kendall's rank correlation coefficient tau b	P
All experiments combined	0.6283 0.9082	0.3043	<0.001
C. xantholoma* & *C. frigida	0.0840 0.7063	0.2647	0.009
R. sericeus* & *C. pilipes	-0.3442 0.5678	0.0566	0.5905
P. algarum* & *D. anilis	0.1206 1.1217	0.2551	0.0141
C. variolosus* & *C. frigida	0.1042 0.7322	0.2617	0.0116

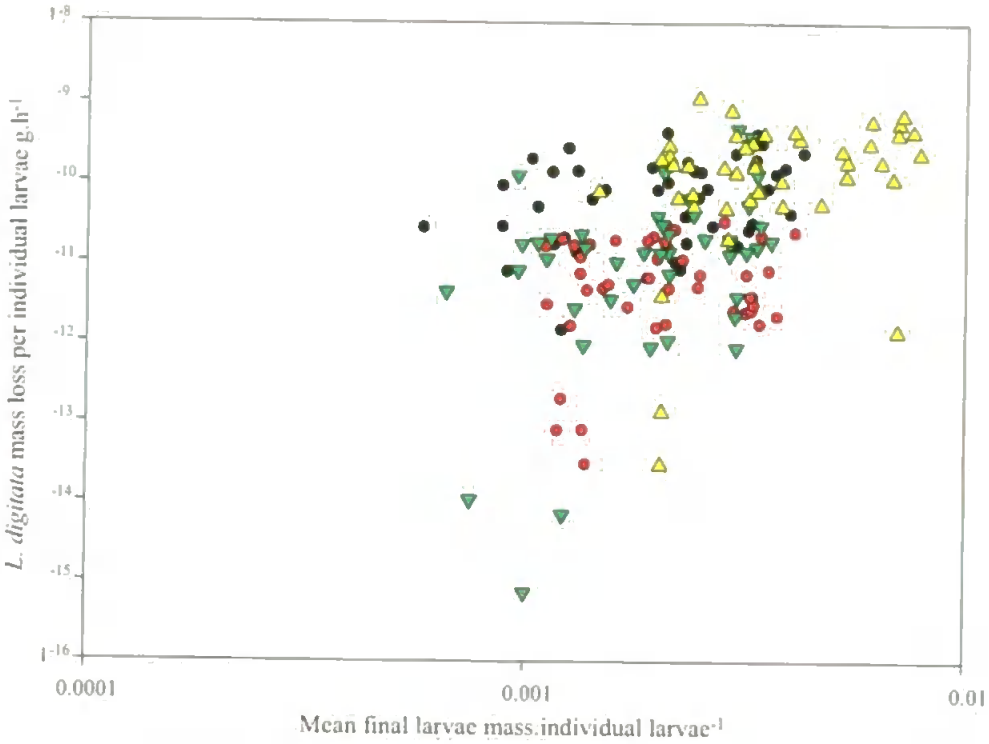

Figure 4.4 *L. digitata* mass loss per individual larvae $g.h^{-1}$ plotted against mean final dry prey mass.individual $larva^{-1}$, where the number of larvae is taken from the number remaining alive at the end of the experiment. Where s = significant relationship, n/s = no significant relationship see (Table 4.7). All experiments combined $Y=0.002549x^{0.7635}$ **(s),** Black circles = *C. xantholoma* & *C. frigida* $Y=0.000477x^{0.401}$ **(s)**, red circles = *R. sericeus* & *C. pilipes* $Y=0.0000202x^{0.106}$ **(n/s)**, green triangles = *P. algarum* & *D. anilis* $Y=0.000891x^{0.613}$ **(s)**, yellow triangles = *C. variolosus* and *C. frigida* $Y=0.000605x^{0.415}$ **(s)**. Where **s** = significant relationship, **n/s** = no significant relationship see (Table 4.7).

The size-class of predator and prey is not significant as a single or combined factor in explaining the variability in *L. digitata* mass loss $g.h^{-1}$ (Table 4.8). The results of a fully factorial ANOVA show that only the identity combination of predator and prey and beetle size-class * identity combination of predator and prey were significant in explaining the variability in kelp mass loss (Table 4.8).

Table 4.8 Fully factorial analysis of variance showing the effects of beetle size-class, larval size-class and beetle, larval identity combination on dry *L. digitata* mass loss $g.h^{-1}$ for all predator-prey body size experiments combined where initial beetle dry mass and initial larval dry mass are covariants.

Source of variation	Dry *L. digiata* mass loss g/ h*					
	D.F.	SS	Adjusted SS	Adjusted MS	*F*	P
Beetle dry mass	1	0.0000030	0.0000000	0.0000000	1.85	0.176
Larval dry mass	1	0.0000009	0.0000000	0.0000000	0.59	0.442
Beetle size-class	2	0.0000002	0.0000000	0.0000000	0.33	0.723
Larval size-class	2	0.0000003	0.0000001	0.0000001	2.27	0.107
Identity combination	3	0.0000004	0.0000002	0.0000001	3.03	0.031
Beetle size-class*Larval size-class	4	0.0000001	0.0000001	0.0000000	0.84	0.504
Beetle size-class* Identity combination	6	0.0000006	0.0000005	0.0000001	3.51	0.003
Larval size-class*Identity combination	6	0.0000002	0.0000003		1.64	0.139
Beetle size-class*Larval size-class*Identity combination	12	0.0000004	0.0000004	0.0000000	1.38	0.182
Error	144	0.0000037	0.0000037	0.0000000		
Total	181	0.0000098				

4.3.8 Predicted Kelp Mass Loss

When all species were combined log(kelp mass loss) scaled with log(final prey mass) to the exponent 0.763, which did not differ significantly from that predicted by metabolic theory of ecology (0.75) at the 10% significance level (Table 4.9 a).

The exponent describing the power regression between final prey mass/individual and kelp mass loss/individual in *P. algarum* & *D. anilis* experiments (0.613) did not differ significantly from that of 0.67 as predicted by metabolic scaling laws (Table 4.9 b). In all other predator- prey experiments where the regression between mean final prey mass and *L. digitata* mass loss/ individual was significant, observed values of dry kelp mass loss $g.h^{-1}$/individual larva differed significantly from those predicted by metabolic theory (Table 4.9a, b).

Table 4.9 Two sample t-test not assuming equal variances for observed and predicted *L. digitata* mass loss $g.h^{-1}$/individual larva. a) Predicted *L. digitata* mass loss $g.h^{-1}$/individual larva = ((C*mean final dry prey mass/individual $^{0.75}$) and b) predicted *L .digitata* mass loss $g.h^{-1}$/individual larva = ((C*mean final dry prey mass/individual $^{0.67}$). C is the y-intercept taken from the separate regression in Figure 4.3.

a)

Factors	*n*	*Mean*	*Standard deviation*	*Standard error*	D.F.	*t*	P
Observed All species combined	182	0.00003	0.00003	0.00002	303	2.02	0.044
Predicted All species combined	182	0.00003	0.00002	0.00000			
Observed *C. xantholoma*	47	0.00004	0.00002	0.00000	48	12.18	<0.001
Predicted *C. xantholoma*	47	0.00001	0.00003	0.00000			
Observed *P. algarum*	45	0.00002	0.00002	0.00000	49	4.37	<0.001
Predicted *P. algarum*	45	0.00001	0.00000	0.00000			
Observed *C. variolosus*	45	0.00006	0.00003	0.00000	49	9.73	<0.001
Predicted *C .variolosus*	45	0.00002	0.00001	0.00000			

b)

Factors	*n*	*Mean*	*Standard deviation*	*Standard error*	D.F.	*t*	P
Observed All species combined	182	0.00003	0.00003	0.00000	361	-5.05	<0.001
Predicted All species combined	182	0.00005	0.00003	0.00000			
Observed *C. xantholoma*	47	0.00004	0.00002	0.00000	54	9.69	<0.001
Predicted *C. xantholoma*	47	0.00001	0.00001	0.00000			
Observed *P. algarum*	45	0.00002	0.00002	0.00000	59	1.39	0.170
Predicted *P. algarum*	45	0.00002	0.00001	0.00000			
Observed *C. variolosus*	45	0.00006	0.00003	0.00000	61	6.47	<0.001
Predicted *C .variolosus*	45	0.00003	0.00001	0.00000			

As the predicted number of individual larvae killed for all experiments combined, or any single predator-prey experiment always included values of over 12 individual larvae, observed kelp mass loss was not compared to that predicted by metabolic theory using initial predator mass and prey mass as outlined in Section 4.2.7.3.

4.3.9 Preference Experiments

The number of larvae killed depends on the beetle species, the identity of the larvae and whether the larvae are presented to the predator together or in isolation (Figure 4.5a-d).

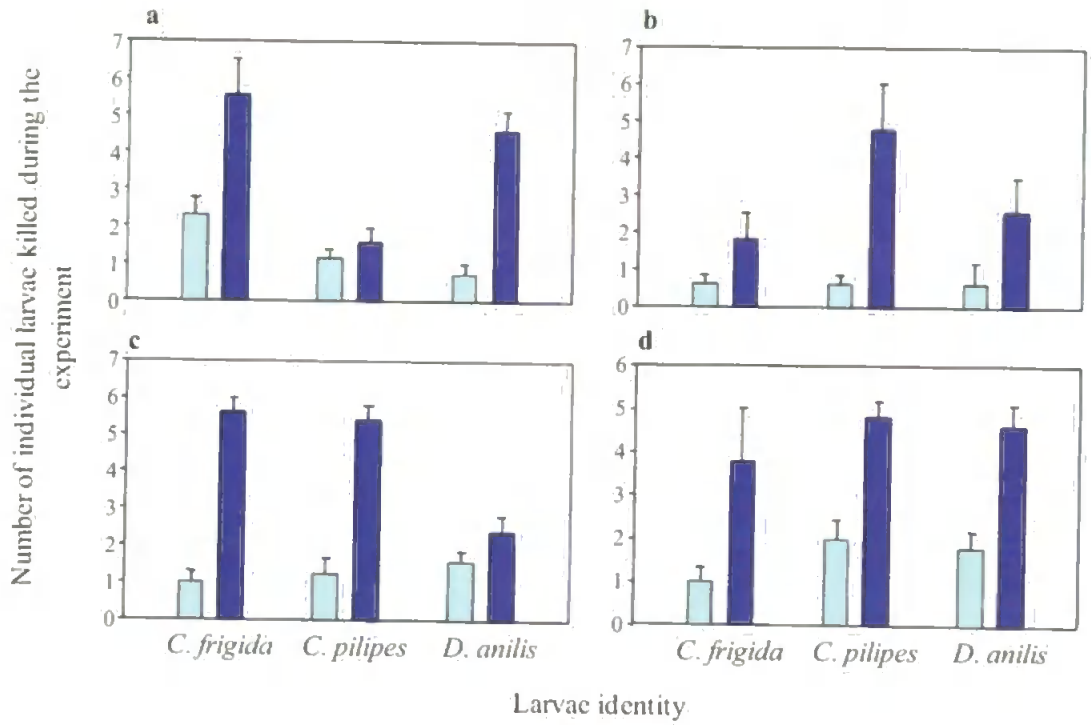

Figure 4.5 Number of individual larva killed throughout the experiment (mean ± s.e.). a) *C. xantholoma*, b) *R. sericeus*, c) *P. algarum*, d) *C. variolosus*. Turquoise = predator beetle species incubated with all three larva species together and blue = predator beetle species incubated each larva species separately (n = 12).

This observation is reflected in the separate fully factorial ANOVAs. When beetles were presented with each larval species separately the variation in the number of larvae killed depended upon the beetle and larval identity (Table 4.10 a). Prey size was also a significant covariable, however as prey size is not correlated with number of larvae killed/h (Pearson correlation -0.056, P = 0.653), prey size is not thought to affect the beetles' preference but rather reflects a difference in prey size between experiments as temporal changes in larval size-class in the strandline on collection days resulted in larval size differing between experiments (Table 4.2). When beetles were presented

with all larval species, only beetle identity was significant in explaining the variation in the number of larvae killed (Table 4.10b). Although beetle identity and larva identity as combined factors were not significant at the 5% significance level the p value of 0.055 suggests that these two factors combined may, as in the case when beetles were presented with each larval species separately, be important in determining the number of larvae killed.

When separate one-way ANOVAs were performed on the number of prey killed for each beetle species when prey were presented in isolation and combination, the number of prey killed did not differ significantly between prey species for the beetles *R. sericeus* and *C. variolosus* (Appendix A18 bi,ii, A18d,i,ii). When prey was presented to *P. algarum* separately there was a significantly lower number of *D. anilis* killed than the other two species of larva. However, when *P. algarum* was exposed to all three species of prey together there was not a significant difference in the number of larvae killed between larva species (Appendix A18c, i, ii). The results for *C. xantholoma* showed a discrepancy in the number of larvae of each species killed depending on whether *C. xantholoma* was exposed to individual larva species (significantly less *C. pilipes* were killed than *D. anilis* or *C. frigida)* or all three together (significantly less *D. anilis* were killed than *C. frigida*, the number of *C. pilipes* killed did not differed significantly from either species) (c.f. blue and turquoise bars Figure 4.3a, Appendix A18a, i, ii).

Table 4.10 Fully factorial ANOVA showing the effects of beetle identity and larval identity on the number of individual larvae killed throughout the experiment, for all predator-prey body size experiments combined where initial beetle dry mass and initial larval dry mass are covariants. a) Only one larval species was presented to the beetles in a given treatment and b) all three larvae were presented to the beetles.

a)

	Number of larvae killed					
Source	**D.F.**	**SS**	**Adjusted SS**	**Adjusted MS**	***F***	**P**
Beetle mass	1	0.010440	0.000318	0.000318	0.20	0.656
Larval mass	1	0.007067	0.010467	0.010467	6.60	0.013
Beetle identity	3	0.021787	0.013547	0.004516	2.85	0.046
Larva identity	2	0.029594	0.013250	0.006625	4.17	0.021
Beetle identity*larval identity	6	0.060486	0.0690486	0.010081	6.35	<0.001
Error	52	0.082526	0.082526	0.001587	2.827	
Total	65	0.211900	0.189157			

Leven's test of equal variance for larvae killed/h when presented to beetles separately; test statistic = -0.81, P = 0.629.

b)

	Number of larvae killed					
Source	**D.F.**	**SS**	**Adjusted SS**	**Adjusted MS**	***F***	**P**
Beetle mass	1	0.000555	0.0000319	0.0000319	0.06	0.801
Larval mass	1	0.001376	0.0004520	0.0004520	0.91	0.345
Beetle identity	3	0.007946	0.0076316	0.0025439	5.11	0.004
Larval identity	2	0.003512	0.0008771	0.0004385	0.88	0.420
Beetle identity*larval identity	6	0.006640	0.0066400	0.0011067	2.22	0.055
Error	52	0.025869	0.0258693	0.0004975	2.827	
Total	65	0.045898	0.0415019			

Leven's test of equal variance for larvae killed/h when presented to beetles together; test statistic = -0.44, P = 0.931.

4.4 Discussion

4.4.1 Results Summary

This study set out to investigate the validity of using body size and allometric scaling laws to predict predator-prey interactions and resource processing in the strandline ecosystem. In order for such an approach to be used a number of assumptions must be upheld (Section 4.1.2). Whilst this study showed the importance of size in determining predator-prey interactions and resource processing, predator and prey identity were also significant. Furthermore the assumptions behind the use of body size and allometric scaling laws to predict predator-prey interactions and resource processing were not always upheld. Overall interaction strength and decomposition could not be

predicted using the approach employed in this study. The inability of such an approach to accurately predict trophic interactions and ecosystem processes can be explained by the data failing to meet each assumption linking body size to interaction strength and ecosystem processes. The following sections discuss each of these assumptions in light of the results of the present findings and previous work.

4.4.2 Prey mass loss scales with predator mass 0.75 or 0.67

For body size to be used to predict trophic interactions between predators and prey there must be a consistent relationship between predator: prey body mass and energy flow. The mass of a predator must determine the amount of prey consumed. In this experiment prey mass loss was significantly correlated to predator mass. However, this was only significant when all experiments were combined and for two beetle-larva combinations, *P. algarum* & *D. anilis* and *C. variolosus* & *C. frigida*. Furthermore, even when significant, the relationship between predator mass and prey mass loss was not consistent between experiments. With *C. variolosus* & *C. frigida* the large exponent (1.96) relating prey consumption to predator mass is in part due to the exceptionally low values of prey mass loss in a few replicates with small predators. There is no *a priori* reason to exclude these individuals from the analysis but it does highlight the interspecific variation in consumption within this species.[22] Contrary to the results of this study, previous theoretical and experimental work, directly and indirectly suggest that there is a consistent relationship between predator size and prey consumption. According to metabolic theory the flux of mass from prey to predator should scale with predator mass $^{0.75 \text{ or } 0.67}$ on a log-log scale (Brown *et al.* 2004, Brown and Gillooly *et al.*

[22] Previous work on predatory strandline beetles has been limited to observations of their feeding (Backlund 1945, E. Mcaffe *pers. comm.*, see Section 2.7.3). There is no work that I am aware of that has empirically investigated feeding in strandline beetles with respect to predation rates or mechanisms. Furthermore, effects of predator body size on ingestion or consumption rates in these species remain wholly unexplored.

2003). However, in this experiment the exponent of the power relationship between $\log_{10}$ predator mass and $\log_{10}$ prey mass loss was significantly greater than that of 0.67 or 0.75 when all predator and prey combinations were combined, and for the two experiments *P. algarum* & *D. anilis*, and *C. variolosus* & *C. frigida*. Similarly the results of this study do not follow the theoretical arguments proposed by Emerson *et al.* (2005), relating energy flux from prey to predators, where the flux of energy from prey species to a predator is proportional to the mass of predator raised to ¾ / mass of prey raised to 1[23]. Following the allometric arguments proposed by Emerson *et al.* (2005) prey mass loss should have been directly proportional to predator mass $^{0.75}$ in this study[24]. Although empirical field measurements of energy transfer, predator: prey body size ratios and stomach content analysis from species in a stream food web supported various assumptions behind the energetic predictions made by Emerson *et al* (2005), empirical measurements of prey consumption by predators of different sizes was not made.

In contrast with the data presented here previous correlative approaches based on empirical measurements of bird and mammals have shown ingestion rate to scale with predator mass to the exponent 0.72 (Farlow 1979). This is remarkably similar to that of 0.75 or 0.67 as predicted by metabolic theory. Physiological differences between birds and mammals as investigated by Farlow (1979) and the invertebrates used in this

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[23] This is based on a series of energetic arguments. Firstly, metabolic rate scales with body mass $^{0.75}$ and species ingestion rate scales with metabolic rate $^{0.75}$ Thus ingestion of a single prey item by a predator = predators total ingestion rate subdivided among its prey species (calculated by the relative density of that prey item divided by the total density of all prey items). The second part of reasoning comes from inferring the density of prey species in a real food web based on allometric scaling principles. They assume (as found in freshwater and marine systems) that biomass*density is constant, i.e. biomass*abundance does not scale with mass and density scales with mass. In effect the energy flow from any single prey species to a predator is a function of the predator metabolic requirement / the relative density of that particular prey species relative to other prey species.

[24] In this experiment prey density was not altered. The interaction between a single predator and single prey item was measured, thus following the allometric arguments proposed by Emmerson *et al.* (2005). If these arguments held prey mass loss should have been directly proportional to predator mass $^{0.75}$. This was not the case.

present study may go some way to explaining the discrepancies between the results. The beetles and larvae used in this experiment are not endotherms and as such their metabolic rates may be more variable than those of birds and mammals. As found in this study there is evidence to suggest that the exponent relating predator mass to prey consumption is higher in heterotherms (Bartholomew and Tucker 1964). Bartholomew and Tucker (1964), investigating the ingestion rate of varanid lizards found in some species $\log_{10}$ predator mass scaled with $\log_{10}$ prey mass consumed $^{1.12}$. Unfortunately, few studies have empirically related predator body size and consumption and thus the generality of the exponent 0.75 to relate predator mass to prey consumed remains uncertain. However, the results of this study and that of Bartholomew *et al.* (1964) suggest that in the case of heterotherms exponent values may exceed that predicted by metabolic theory.

One of the few studies to calculate ingestion rate between invertebrate predators and prey found the average total ingestion rates of predators (as measured by total ingestion ÷the contribution of that prey tem to predator production) was negatively correlated with prey size, i.e. greater numbers of smaller prey were consumed (Woodward *et al.* 2005b). However, the exact scaling of this relationship and the effect of predator size on prey consumed was not calculated. In the present study there was only a significant relationship between predator mass and prey consumed in half of the predator-prey experiments, although, as found by Woodward *et al.* (2005b), in all cases the relationship was positive.

There is no empirically-tested mechanism or even rationale to explain why prey mass loss is not related to predator size in two of the predator-prey combinations investigated. This is especially interesting in light of the fact that prey mass loss scaled with predator mass in *C. variolosus* & *C. frigida* but not in experiments using *C.*

xantholoma & *C. frigida*. Both of these beetle species were incubated with the same prey species and the former beetle may be a variety of the latter.

The notion that predator consumption should scale consistently with predator body size is based on two assumptions, firstly that metabolic rates scales with body size and secondly that consumption rate is determined by the predator's metabolic rate. Thus the lack of a consistent and significant scaling relationship between body size and prey consumption found in this study suggest that the species investigated in this study do not meet either, or both, of these assumptions. There is an impressive amount of evidence to suggest that a consistent relationship exists between body size and metabolic rate from species differing in size by over 21 orders of magnitude (see Peters 1983, Calder 1984, Schmidt-Nelson 1984, Gillooly *et al.* 2001, 2002, Brown *et al.* 2004). However, there are also good counter-arguments suggesting that the widely documented scaling relationship between size and metabolic rate does not actually exist. If that was the case it is hardly surprising that no universal relationship between predator mass and prey mass loss was found in this study. The strongest argument against body size scaling relationships centres on the absence of a universally accepted mechanism to explain why metabolism should scale with body size; a number of theories have been proposed (McMahon 1975, West *et al.* 1997, 1999, Gillooly *et al.* 2001, Darveau *et al.* 2002, Hochachka *et al.* 2003, West and Brown 2005, Banavar *et al.* 1999, 2002, Bejan 1999, 2000) but nearly all of them have been heavily contested (see arguments in Bejan *et al.* 1999, 2002, Banavar *et al.* 2002, West *et al.* 2002, 2003, 2005, Darveau *et al.* 2003, Brown 2004).[25]

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[25] Proposed mechanism by which metabolism should scale with body size: multiple-causes of allometry linking cellular and whole animal metabolism (Darvaeu *et al.* 2002, Hochachka *et al.* 2003), elastic similarity (McMahon 1975), hierachical branching networks (West and Brown 2005) encompasses previously proposed theories; such as the fractal nature of energy distributing vascular networks in animals (West *et al.* 1997, Gilloly *et al.* 2001), resource distribution through hierachial branching networks in plants (West *et al.* 1999), geometry of nutrient supply networks (Banavar *et al.* 1999, 2002b, Bejan 2000) and four dimensional biology (West *et al.* 1999) Finally constructal law or theory, an old

Secondly, doubts have been raised concerning the interpretation of previous data sets. The previously demonstrated relationship between body size and metabolic rate may be an artifact of the statistical techniques used to fit the regression and investigate the significance of the relationship. Specifically the regression analysis used to derive the exponent (Ricker 1973). The choice of best line of fit may not have been appropriate (Harvey and Mace 1982, Martin and Barbour 1989, Riska 1991, Harvey and Pagel 1994). Type I regression analysis is commonly used and this assumes the independence and normal distribution of x and y variables, both of which are unlikely to be upheld when measurements of species body size and metabolic rate are made (Martin and Barbour 1989, Batterham *et al.* 1997, White and Seymour 2005, Nagy 2005). Furthermore, when a regression analysis is undertaken on double logged axis, as commonly used to define allometric relationships, the influence of outliers and large species will have a disproportionate effect in determining the overall relationship (Smith 1980). Finally, the significance of relationships is often undertaken using only the correlation coefficient and assuming its proximity to 0.75 or 0.67 without statistical comparisons (Smith 1980, Suarez and Darveau 2005). In order to overcome some of the statistical artifacts commonly encountered when analysing allometric relationships the present study used non-parametric regression techniques (which did not assume normality in error distribution or that error was only present in the y axis) to relate beetle size to prey mass loss and the regression compared to that of 0.75 and 0.67. If previous studies had applied such techniques a range of exponent values such as those found in this study may have been uncovered.

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concept that arguably holds many of the same assumptions as the theories proposed by West *et al.* (1997, 1999) and Bejan *et al.* (1999, 2000). Even the constructal law or hierarchical branching networks which forms the base of many of the mechanistic propositions laid down to explain the why metabolic rate should scale with body size has been questioned, in particular Makarieva *et al.* (2004) showed how the application of this approach resulted in violation of the energy conservation law.

If we accept that body size does scale with metabolic rate (notwithstanding poorly applied statistical techniques and the additional bias introduced in analyzing the relationship), the difference in the range of body sizes investigated between this and previous studies may explain why no universal relationship was found between predator mass and prey mass loss in each individual experiment. In this study there was no relationship between predator mass and prey mass loss in two of the experimental predator prey manipulations and the other two predator prey manipulations scaling relationships were higher than predicted based on metabolic scaling laws. Most studies investigating the relationship between body size and metabolic rate have used species covering a very wide range of body sizes (e.g. Peters 1983, Calder 1984, Schmid-Nelson 1984, Gillooly *et al.* 2001, 2002, Brown *et al.* 2004). This may bias results due to data aggregation effects (Torres *et al.* 2001, Savage 2004, and Cohen *et al.* 2005). Such data will yield an average and as such may not accurately reflect the relationship between body size and metabolic rate within species or groups. When the relationship between body mass and metabolism within, rather than across, species groups has been examined the widely documented scaling relationship of 0.75 or 0.67 is not observed (e.g. Boddington 1978, Hooper and Weibel 2005, for reviews, Birchard and Arendse 2001 on cockroaches, Darveau *et al.* 2002, on birds and Nespolo *et al.* 2003 on crickets). In fact, exponent values linking body size to metabolism ranging from 0.3 - 1 have been documented; 0.6 - 0.8 for mammals (Speakman 2005), 0.8 for some fish (Winberg 1960, Paloheimo and Dickie 1966), 0.3 for selected mammals (Dodds *et al.*2001), 0.69 for some birds (White and Seymour 2003) and 1.0 for trees (Reich *et al.* 2006). Thus a universal exponent linking body size to metabolism may not exist (vanBergen and Phillips 2005). Although this study did not explicitly measure metabolic rate, such data aggregation effects were seen. When the relationship between predator mass and prey mass loss from all predator-prey experiments was examined the

scaling exponent was significant, but did not reflect the scaling relationship of any single predator species and prey species combination. Furthermore for two of the predator-prey species combinations there was no significant relationship.

Perhaps the most convincing argument to explain the lack of a relationship between *C. xantholoma* and *R. sericeus* mass and prey consumption is that dry mass in these species is not a good proxy for metabolically active tissue. A significant relationship may exist between the metabolic rate and prey consumption of *C. xantholoma* and *R. sericeus*, but the measures made in this study (dry mass) did not accurately reflect metabolic rate. There are many cases in the literature where mammal or bird body size does not scale with metabolic rate, or at least not as convincingly as the size of specific organs (i.e. basal metabolic rate and the digestive and metabolically active tissues of mice, Konarzewski and Diamond (1995); maximal metabolic rate and skeletal muscles in house sparrows, Chappell *et al.* (1999); and male basal metabolic rate with the intestinal tract and lung mass of Turkeys, Hammond *et al.* (2000)). If larger beetle conspecifics contain a greater amount of metabolically inactive tissue, their dry mass would increase but smaller and larger individuals of the same species may have the same mass of metabolically active tissue and thus equivalent metabolic needs. This may translate to equal prey consumption between large and small beetles if metabolic requirements govern their ingestion rates. Lower mass-specific metabolic rates in larger invertebrates, compared with smaller conspecifics, have been attributed to the increase in non-metabolically active tissue in larger individuals of crabs (Weymouth *et al.* 1994) and freshwater amphipods (Glazier 1991). Furthermore, it has been previously suggested that, within a species, smaller individuals may have higher mass-specific rates of metabolism, than larger individuals, due to their stages of ontogeny stages. Young individuals (often smaller than older conspecifics) may be comprised of relatively fast-growing tissues whereas larger older individuals have lower metabolic

requirements for the maintenance of somatic growth and reproduction (Glazier 1991, Simcic and Brancelj 2003). There is little empirical evidence regarding how ontogeny may influence the scaling relationship between body mass and metabolic rate. However, Nespolo *et al.* (2004) found abdomen mass to be more closely related to metabolic rate in crickets than other size measurements, as head and thorax remain of a fixed size after maturity. Perhaps more convincingly, Simcic and Brancelj (2003) found evidence for the increase in non-metabolically active tissue in larger conspecifics of the amphipod *Gammarus fossarum* by investigating the electron transport system (EST) (as a proxy for O_2 uptake and thus metabolic rate) in the amphipod. The percentage of cytoplasm was greater in smaller than larger individuals, and there was a significant relationship between chitin mass and amphipod wet mass. However, both larval species wet and ln dry mass were significantly related to ln ETS. In this study the non-significant 'relationships' between prey mass loss and predator mass in treatments of *R. sericeus* and *C. xantholoma* may be explained if the mass of these species' chitinous structures increased with beetle size to a greater extent than in amphipods and crickets. If small individuals of *C. xantholoma* and *R. sericeus* had the same metabolic rate as larger individuals of the same species, it would follow that prey mass loss would not differ with size. However, this line of argument cannot explain the higher than metabolically predicted exponents of *P. algarum* and *C. variolosus* body mass to prey consumption.

Alternative explanations for the lack of difference in *C. xantholoma* and *R. sericeus* consumption with size come from postulated differences in feeding behaviour. Body size may scale with metabolic rate but factors other than metabolic rate may be determining consumption. Larger individuals of *C. xantholoma* and *R. sericeus* may have decreased their feeding rates, below that of their metabolic requirements if the larval prey were less nutritionally valuable to larger individuals of these two species; thus explaining the absence of a relationship between predator size and prey

consumption for these two beetle species and their prey. If larger individuals of *C. xantholoma* and *R. sericeus* have proportionally larger external chitinous structures than smaller conspecifics their nitrogen and phosphorus nutritional demands may be greater. The proportion of larvae in their natural diet relative to other prey items higher in N and P (such as amphipods) compared with those of smaller beetles may be smaller. As the experiment was undertaken on a short time scale, the larger and smaller beetles may still be consuming prey according rates in the field. Evidence to suggest that species alter their feeding rates in response to their nutrient demands is largely anecdotal, however, feeding rates have been shown to differ depending on the nitrogen content of the resource in caterpillar larvae (Slansky and Feeny 1977) and in *Daphnia* (DeMott *et al.* 1998). However, this does not explain why *C. variolosus* and *P. algarum* mass did scale with prey mass loss. Additionally, why larger *C. xantholoma* and *R. sericeus* individuals would have a greater nutrient demand relative to smaller conspecifics, but not larger *C. variolosus* or *P. algarum* beetles, is unclear.

Finally pre-exposure conditions may explain why there was no relationship between predator mass and prey mass loss in one half of the predator-prey experiments (*C. xantholoma* & *R. sericeus*) but not the other half (*C. variolosus* & *P. algarum*). If *C. xantholoma* and *R. sericeus* were ending a period of diapause it would seem logical to eat rapidly to compensate for mass loss during this period. If small and large *C. xantholoma* and *R. sericeus* have the same maximum rate of ingestion the amount of prey consumed/mass may have been equable between beetles irrespective of size. Following a period of food scarcity hyperphagia, or increased feeding, has been shown empirically in some invertebrates (see Calow 1975 for freshwater gastropods; Siekmann *et al.* 2001 for parasitic wasps). Additionally the ability to employ hyperphagia during periods of food abundance would be a logical behavioural and possibly physiological adaptation to survival in strandline environments where the deposition of wrack and

abundance of kelp fly larvae can be ephemeral (Section 2.5). However data on wrack and larval availability immediately preceding beetle collection are not available to support or refute this argument.

4.4.3 Interaction Strength

If metabolic rate scales with body size, and ingestion is directly proportional to metabolic rate, the trophic interaction between predator and prey should scale with body size. The results of this study throw serious doubt on the use of predator: prey body size as a means to predict interaction strength in the strandline. Although the number of larvae killed generally increased as larval size-class decreased (this being especially pronounced from large and medium size-classes to small larval size-classes) the effects of predator and prey identity were as important as predator and prey body size in determining interaction strength. The number of individual larvae killed was affected both by larval size-class * predator-prey identity combination. When each experiment was analysed separately the effects of beetle size-class on *per capita* prey consumption was not consistent for each predator-prey combination. For a particular larval size-class the number of individuals killed did not differ between every (*C. xantholoma, R. services* and *P. algarum*) or any (*C. variolosus*) beetle size-class[26].

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[26] Interestingly where the number of larvae killed (within an individual larvae size-class) was influenced to a large extent by beetle size (*C. xantholoma* and *R. sericeus* treatments) there was no significant relationship between prey mass loss and predator size. The apparent disparity between the effects of beetle size when analysed as number of individuals killed or prey mass loss in *R. sericeus* treatments may be attributable to pupation events. Although pupation rates were normally low, larvae pupation occurred in some treatments of *R. serviceus* and large larvae size-classes, resulting in overall prey mass loss despite little predation. There is no compelling evidence to suggest why the *per capita* predation of prey by *C. xanatholoma* appears to decrease with beetle size-class but prey mass loss does not decrease significantly with decreasing predator mass. One explanation may be the variability in prey mass within each larvae size-class. If large size-classes of beetles eat the smallest prey within the size-class and the reverse is true for smaller beetles, then, although the number of individuals killed decreases with beetle size-class prey mass loss may not. There is, however, no empirical evidence to support this.

Greater *per capita* consumption of smaller prey items, as found in this study has been found previously. Woodward *et al.* (2005b) found a negative correlation between prey size and interaction strength, (interaction strength was measured as annual ingestion/annual production), finding smaller species to suffer greater predation based on gut content analysis of animals from a stream food web. In field exclusion experiments, Ovadia and Schmitz (2002) found smaller grasshoppers suffered greater mortality than larger grasshoppers when presented to a predatory spider. Similarly Eklov and Werner (2000) showed that predation rates by both bluegill sunfish and odonate larval predators on bullfrog and greenfrog tadpoles decreased with increasing tadpole size. The greater *per capita* consumption of smaller larvae (than larger larvae) observed in this study is concurrent with predictions based on metabolic scaling laws. Each individual small larva will provide less energy than a larger conspecific, thus in order to fulfil metabolic energy requirements beetles will need to consume more larvae if they are small.

Contrary to the results of this study predator size has been shown to affect interaction strength (Woodward *et al.* 2005a, b, Woodward and Hildrew 2001, Sala and Graham 2001). Woodward and Hildrew (2001) found that the larger dragonfly nymphs had relatively higher *per capita* effects on their prey. Average interaction strengths between species and their prey were estimated using gut content analysis and *per capita* consumption of a predator on a specific prey item was determined by the proportion of that prey in the predator's diet. Similarly, in a study designed to investigate the community wide distribution of interaction strengths in giant kelp forests, Sala and Graham (2002) found a positive relationship between sea urchin (*Strongylocentrotus purpuratus*) body size and interaction strength (as defined by; (sporophyte density in aquaria with predators /sporophyte density without predators/)time/predator density). However, the relationship between herbivore size and *per capita* interaction strength

was limited in its applicability across all body sizes. The relationship between body size and interaction strength fitted a hypothetical Michaelis-Menten saturation curve reaching a plateau at high predator body sizes presumably, as suggested by the authors, because as predator: prey body size ratios increased the efficiency at which herbivores could remove sporophytes became limited. It is worth noting that sea urchins were separated into two size categories and small sea urchins removed fewer sporophytes than larger individuals of the same species (Sala and Graham 2002), a trend which was observed in some, but not all, predator-prey combinations in this study. Woodward *et al.* (2005c) found larger predators consumed larger prey, and smaller predators consumed smaller prey. This trend was not observed across all predator- prey combination experiments in the present study. However, the size range of predator and prey used by Woodward *et al.* (2005b) exceeded that of the present study. Woodward *et al.* (2005b) used small prey that were outside the large predator's diet breadth and *vice versa* for large prey and small predators. When the average number of larvae killed in each beetle size-class was considered the results of the present study agree well with previous investigations. Although, on average, larger beetles killed significantly more larvae than smaller conspecifics, owing to subtle differences in the number of larvae killed due to predator and prey identity and prey size, predator size was not a significant factor to affect interaction strength.

Measuring the relative body sizes of predators and prey has been advocated as method by which interaction strengths in an assemblage could be estimated. Theoretical arguments (Jonsson and Ebenman 1998, Emerson *et al.* 2005) and re-analysis of previous data (Wootton and Emerson 2005) suggest that there may be a relationship between predator: prey size ratios and interaction strength. This is based on the assumption that body size can encapsulate much of the biological information of a species (Brown *et al.* 2004). However simultaneous empirical measurements of both

predator and prey body sizes and interaction strength are rarely made. In all of the studies mentioned so far predator and prey body size have not been manipulated simultaneously (although there is evidence that separately both predator and prey size are important in determining interaction strength). However, only by measuring or manipulating either predator or prey size can subtle differences in interaction strength with predator or prey size, as found in this study, be discerned and the relative importance of species identity and non-direct interactions in affecting this relationship elucidated.

One of the few empirical investigations to manipulate the size and identity of both predator and prey species (Emerson and Raffaelli 2004) is often cited as evidence for the use of predator and prey body size as predictors of interaction strength. Using a design similar to that used in the present set of experiments Emerson and Raffaelli (2004) constructed mesocosm treatments were using four predator species: a crab, a shrimp and two fish. Each predator was segregated into three size-classes and every size-class of predator incubated separately with three distinct size-classes of mud-dwelling *Corophium volutator*. Additionally each predator size-class was incubated with three additional prey species (only one size-class was used). Predator prey body size ratios scaled significantly with interaction strength for the shrimp and crab predators. Emerson and Raffaelli (2004) stated that the power regression exponents between log(predator: prey body size) and log(interaction strength) were not significantly different from that predicted by metabolic theory (0.75). However interaction strength was calculated as a dynamic index (lnP/C*xt) where P is the density of prey with the predator and C is the density of prey in the absence of predator, x = density of predator and t = time. Thus as DI increases the number of prey consumed decreases. Therefore as shrimp and crab predators increase in size relative to prey, the number of prey they consume reduces. This is in contrast to what is predicted by

metabolic theory and what was observed in the current study experiment. Whether DI was inverted or the data transformed so that the reciprocal of DI was displayed is not known. Despite this, as in the present study, the body size-interaction strength relationships were dependent on the identity of the predator. There was no significant relationship between each fish species' predator: prey body size ratios and interaction strength. Additionally, although predator size and prey size were significant in explaining the distribution of interaction strengths, so too was predator identity (and the interactions between predator identity * predator size and predator identity * prey size). Thus the study of Emerson and Raffaelli (2004) provides conflicting evidence for the use of predator: prey body size relationships to predict interaction strength.

In the present study either beetle body size proved too be a poor surrogate measure of metabolic rate, or beetles were not feeding according to their metabolic requirements. The arguments presented in the previous section (Section 4.4.2) can apply here and may explain the discrepancies between the results of this study and those mentioned above. There is evidence that predation rates can be influenced by factors other than prey size. Eklov and Werner (2000) found that predation rates were affected by the non-lethal presence of another predator and were also dependent on prey identity. Although predator size and identity effects were not investigated by Eklov and Werner (2000), predation rates were influenced by strong behavioural responses of predators. Furthermore, metabolic requirements are not the only explanation for the greater *per capita* consumption of smaller prey items observed in the current study. A greater number of small larvae may have been consumed as they were easier to capture and subdue.[27]

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[27] During preliminary trials and the experiment when beetles initiated an attack on the larvae, the larvae increased movement markedly by massive posterior- anterior contractions. If the beetles initiated attack in the middle of the larvae they maintained a tight posterior-anterior contraction so that the posterior spiracles were touching the mouthparts and then repeatedly rolled dorsoventrally, in both cases the beetles were often lifted into the air violently and if they retained their hold were often thrown violently up and

Previous work, and the results of this study, provide evidence for the importance of predator and/or prey size in determining interaction strength. However, in the few instances where species identity effects have been segregated from those of species size, identity seems an equally important factor determining the distribution of interaction strengths. Additionally the scale at which the relationship between predator and prey body sizes and interaction strength are examined appears to affect the relationship. When average interaction strength for a single species of predator is related to average predator: prey size, there is a good correlation. In this study the average interaction strengths increased across beetle size-class. However interaction strengths were not distributed strictly adhering to every predator-prey size-class combination; this was especially noticeable across beetle size-classes.

4.4.4 Kelp Mass Loss

If, as predicted by metabolic theory, body size predicts metabolic rate and since ingestion is determined by metabolic rate then, the amount of a resource consumed (kelp mass loss) should be related to size of predators and prey. The size of the predator will determine the amount of prey it will consume, the amount and size of the remaining prey will determine kelp mass loss. This was clearly not the case for the species used in this experiment. As seen above size may not be a good surrogate measure for metabolic rate in general, or specifically with the species employed in this study. Alternatively ingestion rate may be controlled by factors other than body size. The arguments for and against the use of body size to predict metabolic rate are discussed in detail in Section

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down and from side to side. Presumably there is an energetic cost to subduing prey in this manner, supported by the observation in preliminary trails with different beetle density that often when prey were subdued by one beetle many other beetles started to feed on the larvae. The cost of subduing prey may be proportionately less per energy gain in smaller larvae where the beetles own body weight and size will enable easier handling.

4.4.2. Additional factors other than body size that may have affected kelp mass loss observed in this study are discussed below.

The identity of predator and prey was arguably more important in determining kelp mass loss than the size of the species in a treatment. Beetle size-class and larval size-class did not explain the variability in kelp mass loss either as single factors or as combined factors. The variability in kelp mass loss was explained by the interaction of beetle size-class * the identity of predator and prey, and the identity of predator and prey on its own. The importance of predator-prey identity in determining wrack processing rates is further reflected in the average larva's mass-specific values of kelp mass loss. Rates of kelp mass loss were greatest in incubations of *C. xantholoma* & *C. frigida* > *C. variolosus* & *C. frigida* > *P. algarum* & *C. pilipes* > *R. sericeus* & *D. anilis*. Kelp mass loss in *C. xantholoma* & *C. frigida* treatments was almost three times those observed in *R. sericeus* & *D. anilis* treatments. Additionally this experiment showed that the larvae have different processing rates suggesting that prey identity, rather than predator identity, is responsible for kelp mass processing rates. In the absence of predators kelp mass loss decreased in the sequence of *C. frigida* > *C. pilipes* > *D. anilis*. The importance of predator and prey identity rather than beetle size-class in affecting wrack processing rates is not surprising given that prey mass loss did not scale with predator mass for all predator-prey combinations (Section 4.3.2), and that the number of individual larvae killed did not increase consistently as predator size relative to prey size increased (Section 4.4.3).

Not only did prey and possibly predator identity affect kelp mass loss but there is evidence that kelp processing rates differ temporally. Discrepancies between the wrack processing rates within larval species suggest that wrack processing rates are not consistent. In this experiment when *C. frigida* was incubated on 05.07.06, the observed wrack processing rates were 0.665 mean $mg.h^{-1} \pm 0.133$(s.e) (control values from

experiments with *C. xantholoma*) and 0.777 mean $mg.h^{-1} \pm 0.093$ when it was incubated on 02.11.06 (control values from experiments with *C. variolosus*). The different wrack processing rates are most likely due to temporal variability in feeding rates. Although species were all incubated under identical conditions they were collected from the strandline at different times and thus their wrack processing rates may reflect conditions prior to laboratory incubation.[28] Despite variation in the rates of kelp mass loss the processing rates observed in this study were not outside the range of those previously reported. Wrack processing rates for *C. frigida* and *C. pilipes* were remarkably similar to those previously reported for these species (Griffiths *et al.* 1983, Chapter 3).[29] Furthermore, despite potential variation in processing rates larval identity has been seen to affect wrack processing rates previously (Chapter 3). Using the same density of larvae and mesocosm set up, *L. digitata* wet mass loss was calculated for each species of larva separately (Chapter 3). *C. frigida* consumed over twice that of *D. anilis* and *C. pilipes* although processing rates in single species treatments of *C. pilipes* and *D. anilis* were remarkably similar (Chapter 3).

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[28] *C. frigida* controls that displayed higher wrack processing rates were collected later in the year when temperatures were higher, thus these species may have been processing wrack at higher rates in the field. Why *C.frigida* collected later in the year would continue to process wrack at a higher rate than *C.frigida* collected later in the year when laboratory conditions were identical is unclear. One explanation may be that it takes time for the species collected earlier in the year to increase their consumption rates with an increase in temperature. Another explanation may be that individual *C. frigida* larvae produced when temperature and food supplies are low are physiologically different from those produced under optimal conditions, and as a result have lower metabolic requirements. This argument is seemingly sensible if heterotherms are produced in environments with food scarcity and colder temperatures a reduced metabolic demand would reduce the risk of starvation and possibly increase survival. It has been shown previously that the larvae of adult *C. frigida* and *C. pilipes* when reared in non- optimal conditions differ significantly in size, and as adults in wing size, and reproductive output (Philips *et al.* 1995, Dobson *et al.* 1974 , Leggett 1993).

[29] When *L. digitata* processing rates are calculated in terms of *L. digitata* loss g.g-1/h for the controls they range between 0.029 g.g-1/h (*C. variolosus* & *C. frigida* treatments) to 0.01 g.g-1/h (*R. serviceus* and *D. anilis* treatments). These rates are equitable to the processing rates previously reported for these species, using an identical mesocosm set up and incubating 12 individuals over 40 h, *C. frigida* 0.026 g.g-1/h, *D. anilis* 0.007 g.g-1/h (Chapter 3).

Contrary to predictions based on metabolic theory (Section 4.1.3), this experiment clearly shows that factors other than body size, specifically prey identity and possibly predator identity and temporal changes in feeding rates, determine wrack processing rates in the species and wrack employed in this study.

4.4.5 Prey Preference

If body size can be used to predict predator and prey interactions, the identity of species within a trophic level should not affect interaction strength. Using the species in this study predator and prey identity was important in affecting predator-prey interactions when each predator was incubated with different prey items. When the results of all experiments were combined, beetle identity determined *per capita* consumption of larva, whether beetles were incubated with a single larval species or all three larval species together. When beetles were incubated with a single larval species, larval identity as a single and combined factor with beetle identity was also significant in explaining the variability in *per capita* consumption of larvae. This is mostly likely due to differential *per capita* predation rates between beetle species. When each individual experiment was analysed separately a significant difference in the number of larvae killed between different species was seen only in experiments with *C. xantholoma* and *P. algarum*. *Cafius xantholoma* killed significantly less *C. pilipes* or *D. anilis* when incubated with a single larval species or multiple larval species respectively, *P. algarum* only killed significantly less *D. anilis* when larvae were incubated with the beetle separately.

Overall there appears to be very little preference for specific larvae species. Although larval identity may not affect interaction strength to a great extent, the assumption that interaction strength can be predicted by the size of a species irrespective of identity was not explicitly upheld.

4.4.6 The Use of Metabolic Scaling Principles to Determine Interaction Strength and Ecosystem Process.

The methodology presented in this chapter for determining interaction strength and ecosystem process is novel. Using the species and ecosystem process measured here it has been shown that we cannot accurately predict predator-prey interaction strengths or ecosystem processing from the body size distributions of predator and prey. Overall $\log_{10}$ predator mass scaled with $\log_{10}$ prey mass loss $^{1.08}$ for each individual predator-prey combination the relationship was either insignificant or scaled with a different exponent. Therefore predictions of the number of individuals killed could not be made for *C. xantholoma* and *R. sericeus*. Even where the number of individuals killed could be predicted,[30] observed values of number of individuals killed were significantly less than expected. When all species were combined predicted number of individuals killed were 5 - 10 times greater than observed, for *P. algarum* 2 - 4 times greater than observed and for *C. variolosus* a massive 665 - 1021 times greater than observed depending on the exponent used[31]. This technique, for predicting predator and prey interaction strength based on species body-size ratios is extremely sensitive to outliers. The degree that predicted values of the number of larvae killed overestimated observed values was directly related to the y intercept, which in turn was massively affected by the presence of low values of prey mass loss in some predator-prey manipulations[32]. As $\log_{10}$ prey mass loss was not related to $\log_{10}$ predator mass $^{0.75 \text{ or } 0.67}$ in any single predator-prey treatment it was not surprising that the predicted number of individuals

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[30] When the linear regression of $\log_{10}$ predator mass scaled with $\log_{10}$ prey mass loss was significant.
[31] The number of larvae killed was predicted using the equation ; (C*predator dry mass g $^{0.75}$)*experimental duration h)/prey mass g, and (C*predator dry mass g $^{0.67}$)*experimental duration h)/prey mass g, where C is the y intercept determined from the regression of predator mass and prey mass loss.
[32] Taking the predicted and observed number of individual larvae killed by *C. variolosus* as an example; owing to a few extremely low values of prey mass loss the y intercept of the relationship between $\log_{10}$ predator mass and $\log_{10}$ prey mass loss was 8.586. Incorporating this value into the equation [21] to calculate number of individuals killed resulted in the mean number of individuals killed by *C. variolosus* over the experimental time period to be 2554.

killed differed from those observed. As previously discussed the exponent of 0.75 or 0.67 is widely contested (Section 4.4.2), however, as there was no common exponent or intercept that related $\log_{10}$ prey mass loss to $\log_{10}$ predator mass the number of larvae killed in each predator- prey experiment could not have been predicted using any one single exponent value. Furthermore, as mentioned in the previous section, the effects of body-size, especially that of predatory beetles, were not consistent and were dependent on the identity of both predator and prey. In this system using predators from the same functional group and similar larva species from the same functional group the mass of prey consumed or interaction strength between predator and prey (as measured by *per capita* number of larvae killed) could not be predicted using body-size scaling exponents.

Larval mass specific rates of kelp mass loss could be significantly described by $\log_{10}$final prey mass $^{0.76}$ when results from all predator-prey experiments were combined. In this case larval size was a good surrogate of metabolic rate in accord with previously hypothesized scaling laws (Section 4.1.3) although it was only at the 10% significance level that the exponent of 0.76 did not differ significantly from the predicted exponent of 0.75. As larvae have little internal or external structures composed of non-metabolically active tissue, mass may be a good surrogate of metabolic rate for them. Owing to the temporal availability of wrack (Chapter 2) larvae would be expected to consume wrack at maximum rates in order to pupate and emerge before the next high tide potentially removes their habitat and food source, concurrent with the assumption that metabolic rate determines consumption rate. However, larval mass-specific rates of kelp mass loss differed between predator-prey experiments, highlighting the danger in using average relationships to predict or describe group-specific relationships. The individual exponent relating kelp mass loss to final prey mass resulted in values ranging from 0.613 (*P. algarum* & *D. anilis*), 0.415 (*C.*

variolosus & *C. frigida*), 0.401 (*C. xantholoma* & *C. frigida*) to 0.106 (*R. sericeus* & *C. pilipes*). All relationships, except the latter, were significant and only the exponent observed in *P. algarum* & *D. anilis* treatments did not significantly differ from that of 0.67 as predicted by allometric scaling principles. However, in the present study when treatments incorporating three trophic levels are considered, kelp mass loss was dependent on factors other than predator and prey size. The variability in kelp mass loss was explained by the interaction of beetle size-class * the identity of predator and prey, and the identity of predator and prey on its own. Owing to this disparity, kelp mass loss was not significantly related to larval mass in treatments containing *C. xantholoma*, *R. sericeus* and *C. variolosus*. Furthermore, ecosystem processes (kelp mass loss) could not be accurately predicted using only predator and prey body-size measurements. The predicted number of individual larvae killed for all experiments combined, or any single predator-prey experiment always included values of over 12 individual larvae; thus observed kelp mass loss could not be compared with that predicted based on the metabolic capacity of the larvae in a treatment after metabolically predicted predator consumption.

There are four main reasons why allometric scaling principles could not predict beetle feeding consumption and kelp mass loss from predator and prey body size in this system. These reasons are not mutually exclusive and they may be specific to this system: 1) body size in is not a good surrogate measure of metabolic rate, 2) metabolic rate does not scale with ingestion rate, 3) factors other than metabolic rate are governing interaction strength and energy flow and 4) the sensitivity of the approach used to infer predator and prey interactions and ecosystem processes from metabolically predicted relationship between body size and metabolic rate has limited predictive capability.

Despite the beetles being closely related and presumably fitting into the same feeding guild, certainly the same trophic level, and the same applying for their prey,

both the exponent and intercept values relating predator mass to prey mass loss differed to such an extent that one could not be substituted for the other. Similarly in half of the experiments the exponent relating predator mass to prey mass loss differed significantly forom that predicted by metabolic theory. Furthermore, kelp mass loss could not be predicted from initial predator and prey mass. Factors other than size, predator-prey identity and in the case of larva consumption possibly seasonality were as important as body-size in influencing predator-prey interactions and wrack processing.

Serious doubt is raised on the applicability of this method to predict interaction strengths between predator and prey and ecosystem process such as wrack processing based on predator and prey body sizes in species that are less similar unless species specific information on both the constant and exponent relating prey mass loss to predator mass is known. Obtaining such information is both time-consuming and labour-intensive and undermines the value of this method as a rapid and easy way of determining interaction strengths.

4.4.7 Conclusions and Limitations

Body size is clearly an important factor determining both predatory rates and decomposition in a marine strandline system using the beetle and larval species in this experiment. Although body size may influence interaction strength and processing rates, the importance of identity and lack of a general relationships between body size and predator-prey interactions and wrack processing in this system has implications for metabolic theory of ecology: a) as a general theory using allometric scaling principles to define interaction strengths and energy flow in food webs and b) to predict the effect of reduced species diversity on ecosystem processes.

Using only four predators and three consumers from the strandline this study does not attempt to actively dispute the validity of metabolic scaling principles, but it does show that in this ecosystem, it has a limitated predictive capacity.

This study also raises questions regarding the scale at which the relationship between body size and rates are examined. Certainly, relationships between body size and processing rates were found in this study. However they differed greatly according to species identity and presumably interactions. Studies examining the relationship between body size and rates should therefore consider the intraspecific variability of this relationship within species or groups either before allometric scaling principles are used in a predictive capacity, or body size is incorporated into models as a surrogate measure of biological rates.

As the species used in this study were some of the most commonly occurring species of predators and prey found in the strandline at Wembury beach (Chapter 2) this study has reveled the importance of the identity, interactions, and relative size of predator and prey, for the larval consumer population and wrack processing in the strandline, assuming the trophic interactions and processing rates measured in mesocosms can be extrapolated to rates in the field.

This study also has implications for future biodiversity and ecosystem process research. Although it did not explicitly examine the diversity ecosystem process relationship, the importance of predator and prey identity in determining processing rates and energy flow in this system using these species is clearly shown. There are few studies that have investigated the effects of diversity on ecosystem processes incorporating more than one trophic level, and this study clearly shows the importance of predators in affecting consumer processing rates. The relative importance of species interactions between and within trophic levels needs to be addressed in future BDEF

studies if the effects of reduced diversity on ecosystem processes are to be accurately determined.

CHAPTER 5: THE EFFECT OF LARVAL IDENTITY, DIVERSITY AND INTERACTIONS ON ECOSYSTEM PROCESSES IN THE PRESENCE OF A PREDATOR.

5.1 Introduction

This chapter investigates the difference between the effect of larval identity, diversity and interactions on ecosystem processes (decomposition) with and without a predator, using strandline larvae and a beetle predator and measuring kelp mass loss.

5.1.1 Rationale

Positive species interactions, where one or all species benefit from the presence of conspecifics, may be more prevalent than previously thought (Bruno *et al.* 2003). If, as suggested, (a) there is no universal trajectory that can describe diversity and ecosystem process (Chapter 1) and, (b) ecosystem process depends on species identity, and interactions (Chapters 1 and 3), then identifying positive species interactions, and factors which influence these interactions are of great importance, particularly when attempting to understand the effects of reduced diversity on ecosystem processes. How consumer-resource interactions are influenced by factors such as predation remains unknown, due to the fact that diversity across multiple trophic levels is rarely manipulated in BDEF studies.

5.1.2 Evidence for Positive Species Interactions

Identifying species interactions is important as the balance between negative and positive species interactions, combined with individual species effects, are likely to determine ecosystem processes and the diversity-ecosystem process relationship

(Section 3.4). Chapter 3 suggests that positive species interactions in strandline systems may be more prevalent than previously thought.

Few previous studies have been designed in a manner that allows the effects of species interactions on ecosystem process to be tested (Section 1.6). Even so, there are some examples of positive species interactions, e.g. within grassland systems (Loreau *et al.* 2001b), fungal assemblages (Tiunov and Scheu 2005), and decomposer assemblages (Cardinale *et al.* 2002, Cardinale and Palmer 2002, Jonsson and Malmqvist 2000, 2003a).

The presence of positive species interactions and the importance of these interactions for determining decomposition in the strandline were also highlighted in a laboratory mesocosm experiment (Marsh and Spicer *in prep.*). Three talitrid amphipods were incubated, maintaining equable biomass and density. Every possible single, two and three species combination were set up and the observed kelp mass loss quantified. Kelp mass loss in all two and three species treatments was significantly greater than any single species treatment and kelp mass loss was greatest when all three species were incubated together. Using a similar experimental design, every possible combination of three kelp fly larvae and a single talitrid amphipod were incubated with wrack material (Chapter 3). When observed decomposition in single species treatments was used to calculate expected decomposition in multi-species treatment (based on additive species effects) there was evidence of positive interactions between the kelp-fly larvae. In all but one of the two-species larval treatments, decomposition was greater than that expected, providing evidence that some larval species interact positively with each other to increase wrack processing. Overall diversity was not significant in explaining the variability in wrack mass loss and this was attributed to the negative amphipod-larval interactions that potentially masked the positive larval-larval interactions. This further highlights the importance of species interactions and provides evidence to support the

proposition that the unpredictability and idiosyncratic effect of diversity on ecosystem processes, found between and within earlier BDEF experiments, may lie in a failure to consider species interactions. In both cases, the observed increase in processing rates with talitrid and larval diversity was attributed to interspecific facilitation rather than niche differentiation or intraspecific competitive release (for further discussion see Section 3.4.4). In the BDEF literature, where a positive interaction has been found, the idiosyncratic effect of overall diversity on ecosystem processing rates suggests that competitive, negative interactions between species of the same trophic level can mitigate these positive species interactions. In one of the few studies to empirically investigate all species interactions, Jonsson and Malmqvist (2003a) provided evidence that competitive and additive species interactions within species of the same trophic level can ameliorate the overall positive diversity effect. If predictions regarding the effects of reduced diversity on ecosystem processes are to be made in real multi-trophic assemblages, then understanding the influence of factors such as predation on the direction and strength of non-trophic species interactions is of great importance.

5.1.3 Effect of Biotic and Abiotic Factors on Species Interactions

There are numerous biotic and abiotic processes that may influence positive interactions between species with respect to growth and population dynamics (see Bruno *et al.* 2003 for review).

Predation is a key biotic factor when considering the structure and function of energy flows in assemblages. The importance of predator-prey interactions for ecosystem processes has been shown experimentally (Mulder *et al.* 1999) and from analysis of a large data set (Duffy *et al.* 2003). Both studies provided evidence to suggest that trophic interactions may be more important than non-trophic diversity in determining ecosystem process. Mulder *et al.* (1999) found that removal of insects with

insecticide almost doubled plant biomass accumulation, and also removed the significant enhancement of plant biomass accumulation by plant species richness in unsprayed plots. Thus, the overall removal of insect herbivores had a stronger effect on biomass accumulation than a six-fold change in plant diversity. Duffy *et al.* (2003) also found that the overall standardised effect size of consumers on primary producer biomass was greater than that of primary producer diversity. Despite the potential importance of predator-prey interactions for ecosystem processes, how predators affect the connection between ecosystem processes and consumer identity, diversity and interactions remains somewhat speculative. There is a long-standing debate on whether food webs are top-down (predator) or bottom-up (resource) driven (see Raffaelli and Hall 1992), whether trophic interactions can affect prey populations, and whether predators themselves directly control specific ecosystem processes. A predator may indirectly impact upon resource processing by reducing the abundance of the consumer species. Additionally, if predators preferentially consume certain prey species, whether or not that prey species has a large or small impact on the ecosystem process of interest will determine the overall consequences for that ecosystem process (Paine 1992). Similarly, if predators preferentially consume prey species that interact positively with hetrospecifics belonging to the same trophic level, then not only will that species' contribution to the ecosystem processes be lost but also the "overyielding" or positive effect. Furthermore, by reducing prey populations a predator may ameliorate interspecific and/or intraspecific competition between consumer species. The balance of intraspecific and interspecific competition may determine the diversity-ecosystem processes connection (Jonsson and Malmqvist 2003b, Section 3.4.4). How predators may indirectly influence ecosystem processes through disruption of prey species and their interactions will be dependent upon the feeding behaviour of the predator and the interactions amongst prey species. With respect to ecosystem processes, if interspecific

competition is greater than intraspecific competition between consumer species then, in the absence of a predator, ecosystem functioning in diverse assemblages should be less than the sum of individual species effects. Conversely, if intraspecific competition is greater than interspecific competition, ecosystem process in diverse assemblages should be greater than the individual species' contributions when predators are absent. If a predator can reduce prey populations below that of the environment's carrying capacity then, competitive interactions with respect to the resource may be ameliorated. Thus, in the absence of facilitation between heterospecifics, species diversity should have an additive effect on ecosystem processes. Alternatively, predator species may alter prey behaviour; either increasing or decreasing time spent processing a resource or contributing to the ecosystem process of interest. By altering prey behaviour overall ecosystem process may decrease or increase in the presence of a predator. If only the behaviour of a specific species is altered then the response of an ecosystem process to species identity, diversity and interactions may change in the presence of a predator.

Despite the potential importance of predation for ecosystem processes, the effect of species identity, diversity and interactions on ecosystem processes in multi-trophic systems remains relatively understudied in BDEF research (Duffy 2002, Section 1.8). Therefore the effect of predators on the connection between ecosystem processes and consumer identity, diversity and interactions remains unknown. The logistics of manipulating and replicating multi-trophic level diversity and measuring ecosystem process, together with the daunting complexity of interpreting the effects of trophic interactions, has limited the number of experimental studies investigating multi-trophic level diversity and ecosystem process (e.g. Loreau *et al.* 2001, Raffaelli *et al.* 2001, Section 1.8).

Theoretical and modelling studies investigating the effects of species richness on ecosystem properties in multi-trophic systems suggest that responses of primary and

secondary productivity vary with species richness. The variability in the response ultimately depends on: the degree to which, (a) the system is closed to immigration, emigration, and allochthonous inputs, (b) top-down or bottom-up control determines assemblage structure and food web connectivity and, (c) the trophic level and functional characteristics of the species that are gained or lost (Strong 1992, Wardle *et al.* 1999, Duffy and Hay 2000, Hooper *et al.* 2000, Klironomos *et al.* 2000, Norberg 2000, Stephan *et al.* 2000, Johnson 1996, Loreau 2001b,c, Holt and Loreau 2002, Thebault and Loreau 2003, Duffy *et al.* 2003). Bruno and O'Connor (2005) gave an excellent example of how the feeding behaviour of predators can influence ecosystem processes and how predator diversity can indirectly influence these processes (algal biomass) by altering the consumer assemblage. They manipulated predator diversity in outdoor mesocosms and found algal biomass, composition and diversity was dependent upon the feeding strategy of the predator included. Obligate carnivorous predators reduced herbivore abundance and increased algal biomass and diversity. When all functional groups of predators were added to the mesocosm, algal abundance and diversity decreased due to the inclusion of an omnivorous predator which directly fed on the algae. However, the role of the predators in influencing herbivore identity, diversity and interactions with respect to algae processing was not investigated.

In the few studies that have investigated the BDEF relationship in multi-trophic assemblages the average process rates were seen to respond idiosyncratically to species diversity and identity. In microbial mesocosm experiments processing rates were seen to increase, decrease, stay the same, or follow more complex nonlinear patterns depending on community composition, trophic structure, and consumer diversity (e.g. Carpenter and Kitchell 1993, Naeem and Li 1998, Schindler *et al.* 1997, Cardinale *et al.* 2002, Mikola *et al.* 2002, Paine 2002, Raffaelli *et al.* 2002). However, the alteration of

positive, negative, or additive species interactions, with respect to ecosystem processing, in these multi-trophic assemblages was not explicitly examined.

The only previous work to explicitly test the effects of predator-prey interactions on diversity-ecosystem process relationships was undertaken using a model system (Fox 2004). Each plant species was modelled to use the resource in a different way (concurrent with complementary resource use mechanisms) and three simple mechanistic food-web models were constructed to predict total plant biomass (as the ecosystem process of interest) at different levels of plant diversity (Fox 2004). Excluding predators, multi-species plant systems outperformed any monoculture, as each plant species was assumed to use the resource in a different way. However, overyielding (a yield greater than predicted using single species additive yields) only occurred for a limited set of parameter values, when specialist herbivores mediated plant coexistence. Overyielding was not observed when generalist herbivores were modelled to mediate coexistence. However, the effect of predator-prey interactions on potential diversity-biomass enhancing mechanisms could not be discerned as the distributions of species traits (and thus interactions) were not kept constant across treatments, with and without predators. How predators may influence ecosystem processes by altering positive interactions between consumer species (with respect to resource processing) has not been empirically studied and, as yet, lacks an accepted mechanistic and/or theoretical basis.

Understanding the relative importance of non-trophic and trophic interactions for ecosystem process will add to the understanding of diversity -ecosystem process relationships in multi-trophic natural assemblages. Additionally, investigating the effects of trophic interactions on consumer-resource relationships is the first step in understanding the relevance of previous consumer-resource manipulations when determining the overall importance of species identity, diversity and interactions on

ecosystem processes in natural multi-trophic systems. Furthermore, investigating the response of ecosystem processes to changes in species identity, diversity and interactions, in the presence of a predator, will also contribute to elements of food-web ecology. Food-web ecological studies generally overlook non-trophic interactions. Where food webs have been modelled, non-trophic interactions are either omitted or have been allocated randomly between species, from a normal distribution of interaction strengths. Recent advances in food-web ecology (Cohen *et al.* 2003 Woodward *et al.* 2005b, Brown *et al.* 2004) incorporating principles from metabolic ecology (Brown *et al.* 2004, Emmerson *et al.* 2005) have resulted in attempts to quantify the links between the species in an assemblage. In quantifying these links measures of energy flow through an assemblage can be inferred. If species interactions can be accurately quantified and modeled, there is the potential to construct quantified food web models from which the consequences of reduced diversity on ecosystem process could be predicted. However, to enable accurate and useful predictions from quantified food webs, empirical experiments that assess the importance of non-trophic links with respect to ecosystem processes are essential.

5.1.4 Aims and Objectives of the Present Study

The primary aim of this chapter is to determine the effect of a predator, *C. xantholoma*, on the positive interactions between *Coelopa pilipes*, *Coelopa frigida* and *Dryomyza anilis* with respect to decomposition. This chapter will also investigate the overall effect of kelpfly larval diversity and identity combination on decomposition in the presence of a predator. These effects were investigated in a laboratory-based mesocosm study. Mesocosm treatments were constructed where the identity and diversity of kelpfly larvae were manipulated. Treatments of every possible single, two and three species combination were constructed. These treatments were replicated with

and without the predator, *C. xantholoma*. Previous experiments have shown that the kelpfly larva species interact in a positive manner with respect to wrack processing (Chapter 3). Thus, the effect of a predator on consumer species, and the subsequent implications for the connection between resource processing and consumer species diversity, identity and species interactions could be investigated.

If the response of ecosystem processes to species identity and diversity observed in previous consumer-diversity manipulations are applicable in real multi-trophic assemblages, the relationship between larval diversity, identity, interactions and decomposition should not change between treatments with and without the predator.

If current food-web models (which assume equal or random distribution of non-trophic interaction strengths) can be used to accurately predict energy flow and thus ecosystem processes in a system, then larval identity, diversity and interactions should not explain the variability in decomposition in the presence of the predator.

5.2 Material and Methods

5.2.1 Collection of Animal Material, Wrack and Sediment

Fly larvae, *Coelopa frigida*, *Coelopa pilipes*, *Dryomyza anilis*, and the beetle *Cafius xantholoma* were collected by hand from within and beneath the springtide strandline at the top of the shore, Wembury First Beach, Devon, UK (48.3°N, 50.4°E) during July 2006. At the same time, cast-up *L. digitata* and sediment from beneath the wrack bed were also collected. All material was transported immediately to the laboratory in large plastic bags. Once in the laboratory the animal material was separated according to species and size. The larvae were held in separate aquaria (vol. = 8 l). To mimic strandline conditions, each aquarium was filled (to a depth of 2 cm) with sand, overlain with two or three fronds of *L. digitata*. A paper towel soaked in distilled

water was placed under the aquarium lids to maintain a high relative humidity within. Both the lid and the towel also prevented the animals escaping. All aquaria were kept in a controlled temperature environment (T = 20°C ± 1 °C) for a maximum of 48 h before use in the experiments described below.

5.2.2 Species Selection and Mesocosm Construction

Species were selected due to their abundance, their ability to survive under laboratory conditions and their co-occurrence in the strandline. The fly larvae, specifically selected as heterospecifics, are suspected to interact positively with each other to enhance wrack decomposition (Section 3.3.2) in the absence of a predator. Mesocosms were constructed as described in Section 4.2.2. The experiment ran for 35 h[33].

5.2.3 Treatments and Predator Effects

Sixteen different treatments were constructed so that every possible combination of the three species of larvae was incubated with and without the predatory beetle, *C. xantholoma* (Table 5.1).

The number of pupated, dead, fully consumed and partially consumed larvae was quantified for each treatment at the end of the experiment. Larvae were carefully removed from each mesocosm and counted. As *C. xantholoma* does not consume the "husk" of the larva, 12 individual larvae, or their identifiable remains, were present at the end of the experiment. Where there was only a husk remaining that larva was classed as fully-consumed. If there was still material within the husk (i.e. larvae that had been killed and partially eaten), they were classed as partially consumed. Pupated and dead larvae are self explanatory.

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[33] This resulted in measurable *L. digitata* mass loss. The beetles ate but minimal larvae pupation and predator and prey mortality (in the latter case due to causes other than predator attack).

Table 5.1 Number and identity of species in each treatment. n = number of replicates, the numbers in brackets refer to the number of larvae of that species in a treatment.

Species and (density) in each treatment.	**n**
C. pilipes – (4), *C. frigida* - (4), *D. anilis*- (4), *C. xantholoma* – (1)	7
C. pilipes – (4), *C. frigida* - (4), *D. anilis*- (4)	7
C. pilipes – (12), *C. xantholoma* – (1)	7
C. pilipes – (12)	7
D. anilis – (12), *C. xantholoma* – (1)	7
D. anilis – (12)	7
C. frigida – (12), *C. xantholoma* – (1)	7
C. frigida – (12)	7
C. pilipes – (6), *D. anilis* – (6), *C. xantholoma* – (1)	5
C. pilipes - (6), *D. anilis* - (6)	5
C. pilipes - (6), *C. frigida* - (6), *C. xantholoma* – (1)	5
C. pilipes - (6), *C. frigida* - (6)	5
C. frigida - (6), *D. anilis* - (6), *C. xantholoma* – (1)	5
C. frigida - (6), *D. anilis* - (6)	5
Control, *C. xantholoma* – (1)	7
Control, no species	7

5.2.4 Kelp Mass Loss

Actual kelp mass loss was determined as wet *L. digitata* mass loss $g.h^{-1}$. Each disc was blotted and wet weighed before and after the experiment [34] (Mettler Toledo AT201 ± 0.01mg). The total mass in a treatment may have differed throughout the course of the experiment due to *C. xantholoma* consumption. Therefore, *L. digitata* mass loss was also calculated per initial, final and mean larval mass. Initial larval mass was quantified by blotting dry each larva in a treatment and taking their collective mass. Final larval mass was determined for each treatment by using initial mean larval mass divided by the number of larvae in the treatment and multiplying this figure by the number of larvae remaining at the end of the experiment. Mean larval mass for each replica was the mean of initial and final larval mass.

[34] See Section 3.2.2 and Appendix A1

5.2.5 Statistical Analyses

All statistical analyses were carried out using MINITAB (Version 13.32, MINITAB Inc, State College PA). Where ANOVA analysis was used, Levene's test for equal variance was used to ensure the assumption of homogeneity of variance was maintained. Where ANOVA analysis detected a significant difference Tukey's *post-hoc* (HSD) test was used to determine which treatments differed significantly from each other ($P < 0.05$).

5.2.5.1 Predator Consumption

The significance of any difference in the total number of larvae killed by *C. xantholoma* between different larval identity combination treatments was determined using a one-way ANOVA. The significance of any difference in predator consumption depending on different prey species was determined using separate one-way ANOVAs for each treatment, where the number of larvae killed was the response variable and larval identity the factor.

5.2.5.2 Pupation

The significance of any differences in the number of individual larvae pupating in different treatments with and without *C. xantholoma* was analysed using a one-way ANOVA by treatment.

5.2.5.3 Actual Kelp Mass Loss

A one-way ANOVA was used to determine the significance of any effect of identity combination on actual *L. digitata* mass loss. Bonferroni-corrected Student's t-tests were used for each larval identity combination treatment to assess the difference in *L. digitata* with and without *C. xantholoma.*

5.2.5.4 Species Diversity and Identity Combination

A fully-nested Type III ANOVA was used to test for significant effects of species diversity and prey species identity combination. Species identity combination (treatment) was a factor nested within species diversity. The dependent variables were *L. digitata* mass loss ($g.h^{-1}$), calculated per initial, final and also mean larval mass (g). This analysis was undertaken separately for treatments with and without *C. xantholoma* (identity combination refers to treatment and species diversity the number of different larval species in a treatment).

5.2.5.5 Species Interaction

For all treatments, positive, negative and additive species interactions were determined by comparing the mean observed *L. digitata* mass loss ($g.h^{-1}$) per initial larval mass (g) with mean expected rates of *L. digitata* mass loss ($g.h^{-1}$) per initial larval mass for all two and three species combinations. These comparisons used Bonferroni corrected t-tests (Box 5.1). Fourteen tests were carried out so a P value of 0.001786 was used (0.025/14). This relates to 2.91 standard deviations.

Box 5.1

Expected decomposition

Two species treatments: $We_1(X_1/W_1) + We_2(X_2/W_2)$.

Three species treatments: $We_1(X_1/W_1) + We_2(X_2/W_2) + We_3(X_3/W_3)$

Where X = global means of; *L. digitata* mass loss in single species treatments,
W = mass of individuals in the single species treatment,
We = mass of individual species in the mixed species treatments.

Standard deviation for observed decomposition

= variance/ ($\sqrt{}$ n).

Standard deviation for expected decomposition

Two species treatment = error MS/$\sqrt{n}$ * $\sqrt{(We_1/W_1)^2 + (We_2/W_2)^2}$

Three species treatment = error MS/$\sqrt{n}$ * $\sqrt{(We_1/W_1)^2 + (We_2/W_2)^2 + (We_3/W_3)^2}$

Standard deviation for observed-expected decomposition

Two species treatment = (Standard deviation for observed decomposition)*($\sqrt{(1+((We_1/W_1)^2 + (We_2/W_2)^2)}$

Three species treatment = (Standard deviation for observed decomposition)*($\sqrt{(1+((We_1/W_1)^2 + (We_2/W_2)^2 + (We_3/W_3)^2)}$

Where 5 = the number of replicates, and variance was taken from the $\sqrt{}$error MS.
Where error MS = within group adjusted means squares.
Where n= the number of replicates.

Comparing observed and expected rates of *L. digitata* mass loss in multi-species treatments when *L. digitata* mass loss was calculated per initial, mean and final larval mass would require a large number of individual tests. When performing multiple analyses, the probability of falsely rejecting the null hypothesis, due to chance alone increases (Type I error). To account for this, the level of probability needed to demonstrate significance can be increased using the Bonferroni correction. However, the problem then arises that any decrease in the P value also increases the likelihood that the null hypothesis could be falsely rejected and that real differences may be missed (Type II error). This is especially likely if all observed and expected rates of *L. digitata* mass loss per initial, final and mean larval mass in multi-species treatments were

compared owing to the extreme nature of the Bonferroni correction (B. Clarke *pers. comm.*) and the large number of tests.

5.3 Results

5.3.1 Standardising Initial Conditions

5.3.1.1 Larval Size

All larvae were collected from Wembury beach at the same time (to ensure continuity and comparability of results). However at the time of collection, the three species differed in their size distributions. Despite efforts to minimise mass differences between treatments, the time necessary to remove enough large *D. anilis* and small *C. frigida* from strandline samples in order to achieve equable biomass between treatments, made this logistically impossible, especially as after five or more days in the laboratory the rate of larval pupation increased dramatically. Consequently, the larvae used in this experiment differed in mass (values are means with range in parentheses for each species' wet mass: *C. frigida,* 0.013099 g (0.008625 g - 0.016967 g); *C. pilipes,* 0.015666 g (0.007000 g - 0.028117 g); *D. anilis,* 0.008747 g (0.006300 g - 0.01205 g)). There was a significant difference in initial larval mass by treatment (Table 5.2). However, Tukey's (HSD) *post-hoc* test showed that for each separate larval identity combination treatment, initial larval mass with and without *C. xantholoma* did not differ significantly from each other (Appendix A19). Furthermore, efforts were made in mixed larval treatments to use larvae of equitable mass.

Table 5.2 One-way ANOVA of the variability in total initial larval wet mass g by treatment.

Source	D.F.	SS	MS	*F*	P
Identity combination	13	0.102848	0.007911	8.51	<0.001
Error	72	0.019977	0.000277		
Total	85	0.122825			

Levene's Test for equal variances was not significant for initial larval mass by treatment test statistic = 1.74, P = 0.070.

5.3.1.2 Initial Kelp Mass

Although efforts were taken to standardize initial kelp mass in all replicate. Initial *L. digitata* wet mass g ranged between 0.5415-1.7269g, μ 0.982, (median 0.971 ± 0.0167 s.e). However, initial kelp mass was not correlated with actual observed *L. digitata* mass loss (Pearson correlation = -0.058, P = 0.564) and as such is not considered further.

5.3.1.3 Mortality

There was no *C. xantholoma* mortality in any treatment/replicate. Larval non-predatory mortality was also very low.

5.3.2 Effect of *C. xantholoma* on Larvae

Prey diversity had little effect on prey consumption, as measured by total consumption of larvae by *C. xantholoma* (Figure 5.1). Although the total number of larvae killed was different depending on treatment (Figure 5.1) *C. xantholoma* did not show a consistent preference for one species of larva over another. The greatest number of larvae killed was observed in treatments containing *C. frigida* and *D. anilis* (single species treatments of *C. frigida* μ 5.57 ± 0.92 s.e., closely followed by treatments of *C. frigida* & *D. anilis* μ 5.4 ± 057 s.e., and single species treatments of *D. anilis* μ 4.57 ± 0.53s.e.). Single and two species treatments containing *C. pilipes* had the lowest

observed number of larvae killed (single species treatments of *C. pilipes* μ 1.57 ± 0.37s.e. < *C. pilipes* & *C. frigida* μ 2.4 ± 0.69s.e. < *C. pilipes* & *D. anilis* μ 2.6± 0.69 s.e.). When all three species were incubated together the number of larvae killed was intermediate (μ 4.14 ± 0.46 s.e.).

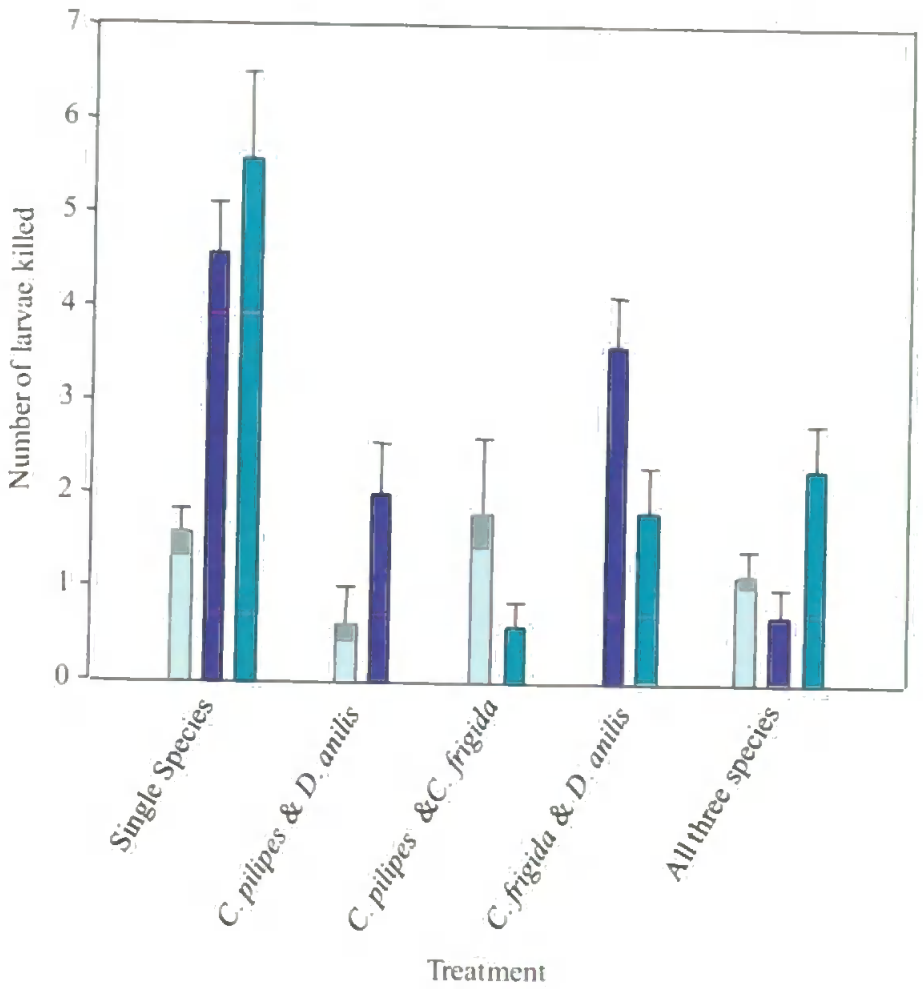

Figure 5.1 Number of larvae killed for each treatment (mean ± s.e.). Light blue = *C. pilipes*, dark blue = *D. anilis*, Teal = *C. frigida*, hatched areas represent the number of larvae partially consumed by *C. xantholoma*.

Significant differences between the numbers of larvae killed by *C. xantholoma* were found between species incubated separately. More *C. frigida* were killed > *D. anilis* > *C. pilipes* (Figure 5.1). Also in two species treatments more individual *D. anilis*

than *C. frigida* or *C. pilipes* were killed, and more *C. pilipes* than *C. frigida* were killed (Figure 5.1). When all three species were incubated together the number of individual larvae killed decreased from *C. frigida* > *C. pilipes* > *D. anilis* (Figure 5.1). The consumption of larvae by *C. xantholoma* was significantly different depending on treatment (larval identity combination) (Table 5.3a A20). However, the number of larvae killed of each species only differed significantly between, single species treatments, two species treatments of *C. frigida* & *D. anilis* and when all three species were combined (Tables 5.3b-f).

Table 5.3 One-way ANOVA showing the variability in the total number of individual larvae killed, a) in each treatment, b) in single species treatments only, c) of *C. pilipes* and *D. anilis* in treatments of *C. pilipes* & *D. anilis*, d) of *C. pilipes* and *C. frigida* in treatments of *C. pilipes* & *C. frigida*, e) *C. frigida* and *D. anilis* killed in treatments of *C. frigida* & *D. anilis*, f) of *C. frigida*, *C. pilipes* and *D. anilis* killed in treatments of *C. frigida*, *C. pilipes* & *D. anilis*.

a)[35]

Source	D.F.	SS	MS	*F*	P
Larval identity	6	91.52	15.25	5.63	<0.001
Error	36	97.60	2.71		
Total	42	189.12			

b)[36]

Source	D.F.	SS	MS	*F*	P
Larval identity	2	60.67	30.33	10.27	0.001
Error	18	53.14	2.95		
Total	20	113.81			

c)[37]

Source	D.F.	SS	MS	*F*	P
Larval identity	1	4.90	4.90	4.26	0.073
Error	8	9.20	1.15		
Total	9	14.10			

[35] Levene's test for equal variances was not significant for total larvae killed in each treatment; Test statistic = 0.48, P = 0.820.
[36] Levene's Test for equal variances was not significant for number of larvae killed between single species treatments Test statistic = 0.86, P = 0.440.
[37] Levene's Test for equal variances was not significant for number of larvae killed between species Test statistic = 0.13, P = 0.724.

d)[38]

Source	D.F.	SS	MS	*F*	P
Larval identity	1	3.60	3.60	2.06	0.189
Error	8	14.00	1.75		
Total	9	17.60			

e)[39]

Source	D.F.	SS	MS	*F*	P
Larval identity	1	8.10	8.10	6.48	0.034
Error	8	10.00	1.25		
Total	9	18.10			

f)[40]

Source	D.F.	SS	MS	*F*	P
Larval identity	2	9.238	4.619	5.29	0.016
Error	18	15.714	0.873		
Total	20	24.952			

5.3.3 Pupation

5.3.3.1 Treatments with C. xantholoma

Pupation varied between treatments containing *C. xantholoma*, depending on treatment (Figure 5.2).

The importance of species identity in determining overall pupation in treatments was seen when the pupation events of individual larva species in each treatment were examined (Figure 5.2a). The highest rates of pupation occurred in treatments containing, *C. pilipes*, in isolation or when incubated with *C. frigida* or *D. anilis* (Figure 5.2). This was mostly likely due to *C. pilipes* which accounted for 100 %, 86.7 % and 93.3 % of the pupation events in these treatments respectively (Figure 5.2a). Lowest levels of

[38] Levene's Test for equal variances was not significant for number of larvae killed between species Test statistic = 4.55, P = 0.066.

[39] Levene's Test for equal variances was insignificant for number of larvae killed between species Test statistic = 0.00, P = 1.000.

[40] Levene's Test for equal variances was insignificant for number of larvae killed between species Test statistic = 0.20, P = 0.821.

pupation were encountered in treatments containing *C. frigida* in isolation, or when combined with *D. anilis* and when all three species were combined (Figure 5.2a). In treatments where *C. frigida* did pupate, the number of individuals pupating was lower than in other fly species.

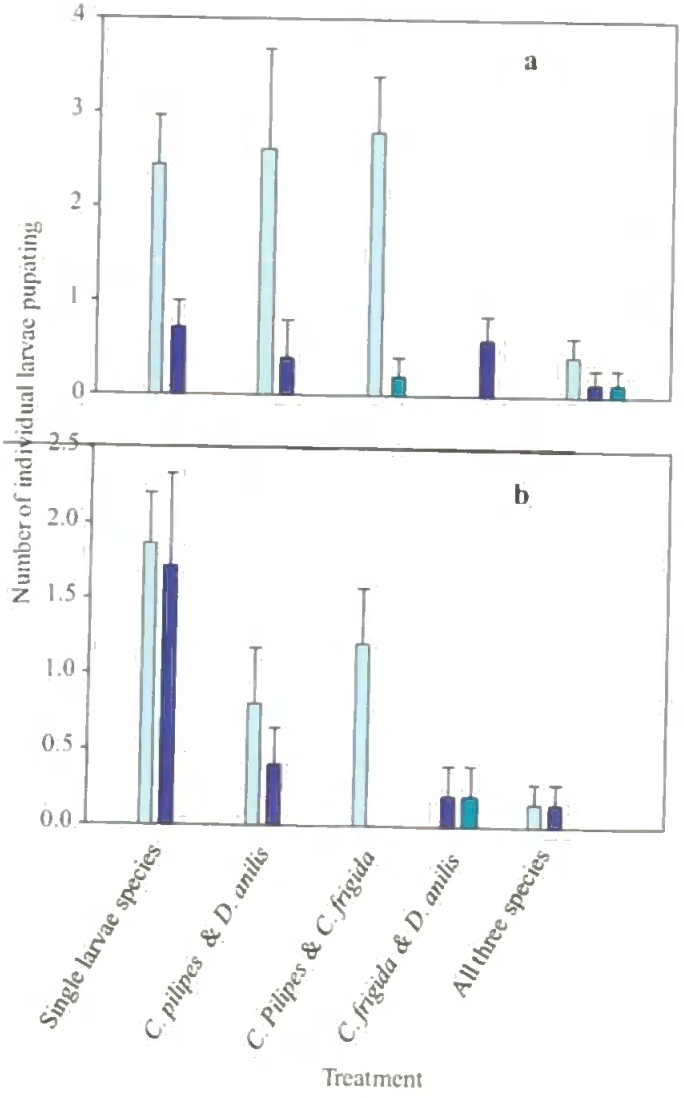

Figure 5.2 Number of individual larvae pupating throughout the entire experimental duration (mean ± s.e.) for each treatment. a = treatments with *C. xantholoma* and b = treatments without *C. xantholoma*. Light blue = *C. pilipes*, dark blue = *D. anilis*, Teal = *C. frigida*.

Total pupation differed significantly between treatments (Table 5.4). This is most likely due to the high rates of *C. pilipes* pupation. Pupation in single species treatments of *C. pilipes* was significantly higher than pupation in single species treatments of *C. frigida* and pupation in any two species treatment containing *C. pilipes* was significantly higher than every other treatment except single species *C. pilipes* ($P < 0.05$) (Appendix A21).

Total pupation for treatments containing *C. xantholoma* was not correlated with *L. digitata* mass loss $g.h^{-1}$ when it was expressed in terms of initial, (Pearson correlation = -0.112, p = 0.473), final (Pearson correlation = 0.245, P = 0.113) or mean (Pearson correlation = -0.034, P = 0.829) larval mass.

Table 5.4 Results of one-way ANOVA showing the variability in the total number of individual larvae pupated by treatment, a) with *C. xantholoma* and b) without *C. xantholoma*.

a)[41]

Source	*F*	SS	MS	*F*	P
Treatment	6	56.51	9.42	0.10	<0.001
Error	36	47.77	1.33		
Total	42	104.28			

b)[42]

Source	*F*	SS	MS	*F*	P
Treatment	6	46.81	7.80	0.35	0.010
Error	36	83.89	2.33		
Total	42	130.70			

5.3.3.2 Treatments without C. xantholoma

As seen in treatments with *C. xantholoma*, total pupation events differed between treatments containing different larval identity in the absence of *C. xantholoma*, (Figure 5.2 b). Total pupation was generally greater in treatments containing *C. pilipes*

[41] Levene's test for equal variances was not significant for total larvae pupation by treatment; Test statistic = 2.15, P = 0.072.
[42] Levene's test for equal variances was not significant for total larvae pupation by treatment; Test statistic = 1.65, P = 0.161.

than those containing *C. frigida*, with the exception of the three species treatment (relatively low levels of total pupation) and when *C. pilipes* and *C. frigida* were incubated together (relatively high levels of pupation) (Figure 5.2b).

A similar pattern of species-specific pupation was observed for treatments with *C. xantholoma* as for those without *C. xantholoma*. Again *C. frigida* had the lowest mean rates of pupation and individuals of this species did not pupate in every treatment. However, without *C. xantholoma, C. frigida* individuals did pupate in treatments with *D. anilis* (Figure 5.2 a, b). More *C. pilipes* individuals than *D. anilis* individuals pupated when the two species were incubated together (Figure 5.2 b). As observed in treatments with *C. xantholoma,* when all three species were incubated together, there was little difference between the different larva species in terms of the number of individuals pupating in treatments without *C. xantholoma.*

The difference in total pupation was only significant at the 0.05 significance level between treatments containing only *C. pilipes* and only *C. frigida* (Table 5.4b Appendix A22).

Total pupation in treatments without *C. xantholoma* was not correlated with *L. digitata* mass loss when it was calculated in terms of initial (Pearson correlation = -0.172, P = 0.269), final (Pearson correlation = -0.283, P = 0.066) or mean (Pearson correlation = -0.251, P = 0.105) larval mass.

Additionally there was no significant difference in the total number of larvae pupating with or without *C. xantholoma* for any single treatment (larva combination) (Table 5.5).

Table 5.5 Separate Students t-test for treatments (larval identity combinations) with and without *C. xantholoma.*

Treatment (larva combination)	D.F.	t	P
C. pilipes	11	-0.37	0.719
D. anilis	6	-1.43	0.203
C. frigida		Identical	
C. pilipes & D. anilis	5	1.30	0.250
C. pilipes & C. frigida	7	0.41	0.695
C. frigida & D. anilis	6	0.43	0.685
All three species	11	0.00	1.000

5.3.4 Kelp Mass Loss

5.3.4.1 Actual L. digitata mass loss

L. digitata mass loss varied between treatments. The greatest loss was observed in treatments including all three species of larva without C. *xantholoma* (Figure 5.3). The lowest loss was observed in control treatments without *C. xantholoma* (Figure 5.3). The lowest actual *L. digitata* mass loss in treatments (excluding the controls) was found in single species treatments of *D. anilis* with *C. xantholoma* (Figure 5.3).

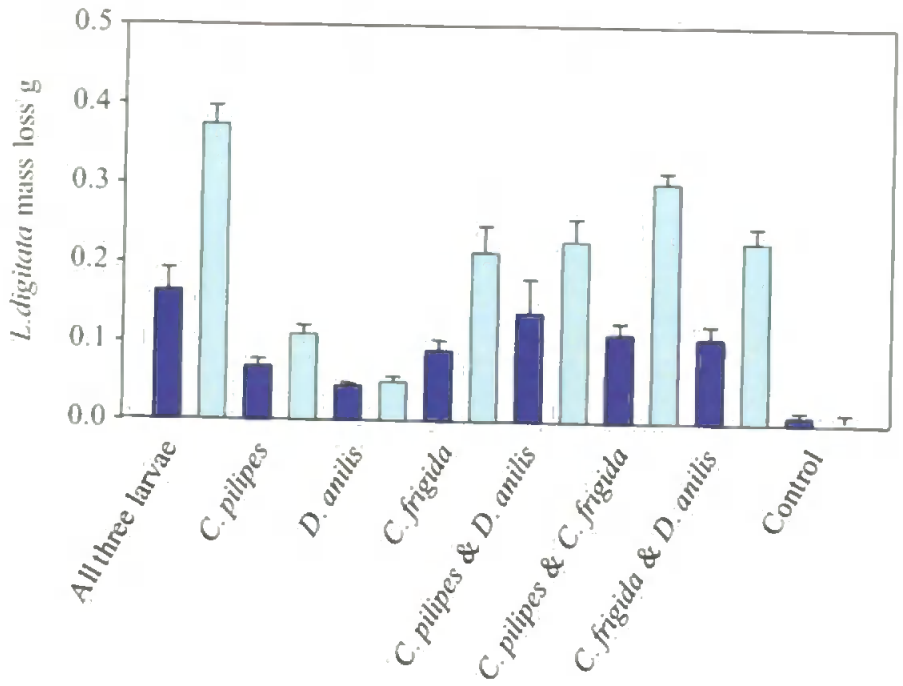

Figure 5.3 Actual *L. digitata* wet mass loss g (mean ± s.e.) for each treatment, Dark blue bars = treatments with *C. xantholoma*, light blue bars = treatments without *C. xantholoma.*

The variation in actual *L. digitata* mass loss between treatments was significant (Table 5.6). As total biomass in each larva treatment varied (Table 5.6), direct comparisons between larva treatments that do not account for differences in larval mass are not made here. It is important to note that *L. digitata* mass loss in the control treatment (without larvae or *C. xantholoma*) and the predator control (with *C. xantholoma*) were not significantly different from *D. anilis* single species treatments with or without *C. xantholoma* (Appendix A23). Observed *L. digitata* mass loss is lower in larval treatments with *C. xantholoma* than those without (Figure 5.3). This difference was only significant ($P < 0.05$) between treatments with and without *C. xantholoma* for larval combinations including, *C. frigida; C. frigida* in isolation, *C. pilipes* & *C. frigida, C. frigida* & *D. anilis* and all three larva species (Appendix A23).

Table 5.6 One-way analysis of variance showing the variability in the actual log (1÷(log *L. digitata* mass loss by treatment+1)).

Source	*F*	SS	MS	*F*	P
Treatment	5	0.373408	0.024894	29.91	<0.001
Error	4	0.069923	0.000832		
Total	9	0.443330			

Levene's test for equal variances was significant for actual *L. digitata* mass loss g by treatment; test statistic = 1.90, P = 0.034 so data were transformed, log((log *L. digitata* mass loss g+1)+1) by treatment; test statistic = 1.62, P = 0.086.

5.3.4.2 L. digitata mass loss in the absence of C. xantholoma

In the absence of *C. xantholoma*, increased larval species diversity increased *L. digitata* mass loss. This was seen for all measures of larval mass; initial, mean or final larval mass (Figure 5.4, turquoise bars).

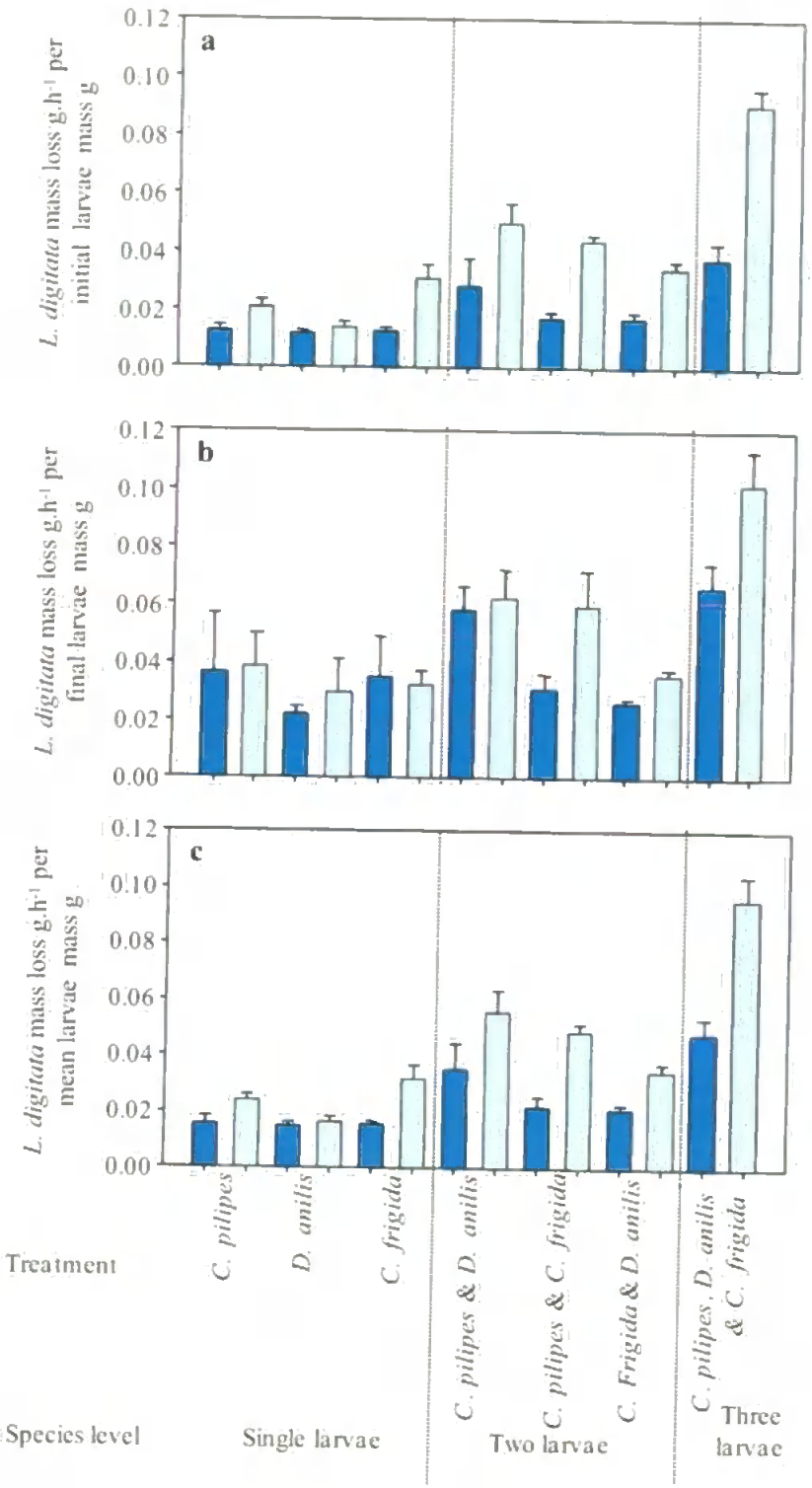

Figure 5.4 *L. digitata* mass loss g (mean ± s.e.) for each treatment (larva combination). Turquoise bars = treatment without *C. xantholoma*. Dark blue = treatments with *C. xantholoma*. a) *L. digitata* mass loss $g.h^{-1}$ per initial larval mass g, b) *L. digitata* mass loss $g.h^{-1}$ per final larval mass g, c) *L. digitata* mass loss $g.h^{-1}$ per mean larval mass g.

The variability in *L. digitata* mass loss was significantly different depending on the number of different species in a treatment (Species level), when the variability in *L. digitata* mass loss per initial, final or mean larval mass was analysed using a Type III nested ANOVA (treatment was nested within species level) (Tables 5.7 a-c).

Table 5.7 General Linear Model (GLM) showing the effects of identity combination nested within species level and species level on, **a)** ***L. digitata*** mass loss $g.h^{-1}$ per initial larval mass g , **b)** *L. digitata* mass loss $g.h^{-1}$ per final larval mass g, **c)** *L. digitata* mass loss $g.h^{-1}$ per mean larval mass g. All without beetle predator.

a)

Source	*F*	Sequential SS	Adjusted SS	Adjusted MS	*F*	P
Identity combination (Species level)	4	0.0017113	0.0017113	0.0004278	3.86	0.010
Species level	2	0.0247952	0.0247952	0.0123976	111.75	<0.001
Error	36	0.0039938	0.0039938	0.0001109		
Total	42	0.0305003				

Levene's Test for equal variances was not significant for *L. digitata mass* loss $g.h^{-1}$ per initial larval mass g by species level statistic = 0.02, P = 0.982, and by species identity combination; test statistic = 1.25, P = 0.305.

Post-hoc Tukey's; *L. digitata mass* loss $g.h^{-1}$ per initial larval mass g by species level (See Appendix A24a); 3>2>1.

Post-hoc Tukey's; *L. digitata mass* loss $g.h^{-1}$ per initial larval mass g by larval identity combination (See Appendix A24b);
All three species> any treatment.
All singles species treatment equable.
C. pilipes < all two species treatments except *C. frigida* & *D. anilis.*
D. anilis < all two species treatments.
C. frigida not significantly difference from any two species treatment.

b)

Source	*F*	Sequential SS	Adjusted SS	Adjusted MS	*F*	P
Identity combination (Species level)	4	0.0025369	0.0025369	0.0006342	0.96	0.439
Species level	2	0.0248282	0.0248282	0.1241410	188.75	<0.001
Error	36	0.0236759	0.0236759	0.0006577		
Total	42	0.0510409				

Levene's Test for equal variances was not significant for *L. digitata mass* loss $g.h^{-1}$ per final larval mass g by species level statistic 0.01, P = 0.991, and by species identity combination; test statistic 0.22, P = 0.969.

Post-hoc Tukey's; *L. digitata mass* loss $g.h^{-1}$ per final larval mass g g by species level (See Appendix A25); 3>2=1.

c)

Source	*F*	Sequential SS	Adjusted SS	Adjusted MS	*F*	P
Identity combination (Species level)	4	0.0019580	0.0019580	0.0004895	3.05	0.029
Species level	2	0.0272627	0.0272627	0.0136314	84.87	<0.001
Error	36	0.0057819	0.0057819	0.0001606		
Total	42	0.0350026				

Levene's Test for equal variances was not significant for mean larval mass by species level
statistic = 0.44, P = 0.648, and by species identity combination, test statistic = 1.15, P = 0.352.

Post-hoc Tukey's; *L. digitata* mass loss $g.h^{-1}$ per mean larval mass g by species level (See Appendix A26a); 3>2>1.

Post-hoc Tukey's; *L. digitata* mass loss $g.h^{-1}$ per mean larval mass g by larval identity combination (See Appendix A26b);
All three species> any treatment.
All singles species treatment equable.
C. pilipes < all two species treatments except *C. frigida* & *D. anilis.*
D. anilis < all two species treatments except *C. frigida* & *D. anilis.*
C. frigida < *C. pilipes* & *D. anilis.*

Using separate one-way ANOVAs and Tukey's (HSD) *post-hoc* tests, *L. digitata* mass loss in treatments containing all three larval species was always significantly higher than that observed in two and single species treatments combined. However, *L. digitata* mass loss only increased significantly between single and two species treatments when it was calculated per initial or mean larval mass (Tables 5.7a-c).

L. digitata mass loss when calculated per initial larval mass or mean larval mass varied significantly between treatments (species identity combination) (Table 5.7a,c) but not when *L. digitata* mass loss was calculated per final larval mass using a Type III nested ANOVA (Table 5.7b).

Using separate one-way ANOVAs and Tukey's (HSD) *post-hoc* tests *L. digitata* mass loss in treatments containing all three larva species was significantly higher than any two or single larva species treatment regardless of how *L. digitata* mass loss was calculated.(Tables 5.7a-c). Where *L. digitata* mass loss was calculated per initial larval mass; *L. digitata* mass loss in treatments of *D. anilis* alone was significantly lower than *L. digitata* mass loss in any treatments containing two larva species (Table 5.7a). Single treatments of *C. pilipes* were only significantly lower than two species larva treatments containing *C. pilipes* (Table 5.7a). Also, single species treatments of *C. frigida* were not significantly different from any two larva treatment (Table 5.7a). Where *L. digitata* mass loss was calculated per mean larval mass, the two species treatment of *C. pilipes* & *D. anilis* was significantly higher than any single species larva treatment (Table 5.7a). The two lowest single species larvae treatments (*C. pilipes* and *D. anilis*) were also significantly lower than the two species treatment of *C. pilipes* & *C. frigida* (Table 5.7c).

5.3.4.3 L. digitata mass loss in the presence of C. xantholoma

The effects of larval species diversity and identity on *L. digitata* mass loss in treatments containing *C. xantholoma* were similar to those observed in treatments without *C. xantholoma.* Again, increased larval species diversity increased *L. digitata* mass loss. (Figure 6.4, dark blue bars). Also the variability in *L. digitata* mass loss per initial, final or mean larval mass (analysed using a type III nested ANOVA), differed significantly between species levels (Tables 5.8 a-c). Again the increase in kelp mass loss with diversity was not consistent between each species level and depended on whether *L. digitata* mass loss was calculated in terms of initial, final or mean larval mass (Tables 5.8a-c). *L. digitata* mass loss in treatments containing all three larval species was always significantly higher than those in two and single species treatments

(Table 5.8a-c). However, *L. digitata* mass loss only increased significantly between single and two species treatments when it was calculated per initial or mean larval mass (Table 5.8a-c).

Unlike the results for kelp mass loss without a predator, species identity combination was not a significant factor affecting kelp mass loss, when calculated per initial, mean or final larval mass (Table 5.8a-c).

Table 5.8 General Linear Model (GLM) showing the effects of identity combination nested within species level and species level on, a) transformed $\log_{10}$ *L. digitata* mass loss g/initial larval mass, b) *L. digitata* mass loss g/final larval mass loss g, c) $\log_{10}$*L. digitata* mass loss g/mean larval mass. All with *C. xantholoma*.

a)

Source	D.F.	Sequential SS	Adjusted SS	Adjusted MS	*F*	P
Identity combination (Species level)	4	0.2636	0.2636	0.0659	0.34	0.848
Species level	2	6.9413	6.9413	3.4707	17.99	<0.001
Error	36	6.9452	6.9452	0.1929		
Total	42	14.1502				

Levene's Test for equal variances was not significant for *L. digitata* mass loss g/initial larval mass g in the absence of a predator for identity combination Test statistic = 3.09, P = 0.015, data were transformed, $\log_{10}$ *L. digitata* mass loss g/initial larval mass $g.h^{-1}$ in the absence of a predator for species level Test statistic = 0.48, P = 0.624, and species identity combination test statistic = 1.69, P = 0.152.
Post-hoc Tukey's; $\log_{10}$ *L. digitata* mass loss g /initial larval mass g by species level 3>2>1 (See Appendix A27).

b)

Source	D.F.	Sequential SS	Adjusted SS	Adjusted MS	*F*	P
Identity combination (Species level)	4	0.0038210	0.0038210	0.0009552	0.10	0.371
Species level	2	0.0066110	0.0066110	0.0033055	3.81	0.032
Error	36	0.0312558	0.0312558	0.0008682		
Total	42	0.0416878				

Levene's Test for equal variances was not significant for *L. digitata* mass loss g/ final larval mass by species level statistic = 0.06, P = 0.939, and by species identity combination; test statistic = 0.54, P =0.776.
Post-hoc Tukey's; *L. digitata* mass loss g /final larval mass g by species level 3 <1=2 (See Appendix A28).

c)

Source	*F*	Sequential SS	Adjusted SS	Adjusted MS	*F*	P
Identity combination (Species level)	4	0.5319	0.5319	0.1330	0.85	0.503
Species level	2	7.2280	7.2280	3.6170	23.11	<0.001
Error	36	5.6295	5.6295	0.1564		
Total	42	13.3894				

Levene's Test for equal variances was not significant for *L. digitata* mass loss g/mean larval mass g in the absence of a predator for species identity combination (Test statistic = 3.79, P = 0.0005, so data were transformed); *L. digitata* mass loss g/mean larval mass g species level Test statistic = 0.26, P = 0.770, and species identity combination test statistic =1.90, P = 0.108.

Post-hoc Tukey's; *L. digitata* mass loss g /mean larval mass g by species level 1 <2 <3 (See Appendix A29).

5.3.4.4 Species interactions.

When observed values of *L. digitata* mass loss per initial larval mass were compared with expected values, based on *L. digitata* mass loss in single species treatments, the results were similar for treatments with and without *C. xantholoma*. In all multi-species treatments without *C. xantholoma* observed values of *L. digitata* mass loss were significantly higher than expected (Table 5.9). In all multi-species treatments, in the presence of *C. xantholoma*, expected values of *L. digitata* mass loss were significantly higher than expected except in the two species treatment of *C. frigida* & *D. anilis* (Table 5.9). When *C. frigida* & *D. anilis* were combined in a treatment and incubated with *C. xantholoma* observed values of *L. digitata* mass loss were not significantly different than expected (both with and without applying the Bonferroni corrected significance level) (Table 5.9).

Table 5.9 95% and Bonferroni corrected confidence intervals for observed-expected *L. digitata* mass loss g per initial mass g.

Treatment		95% confidence intervals		Bonferroni corrected confidence intervals	
With *C. xantholoma*	*C. pilipes* & *D. anilis*	0.0011	0.0007	0.0012	0.0006
	C. pilipes & *C. frigida*	0.0016	0.0012	0.0017	0.0012
	C. frigida & *D. anilis*	0.0000	-0.0003	0.0001	-0.0004
	C. pilipes, D. anilis & *C. frigida*	0.0624	0.0622	0.0624	0.00621
Without *C. xantholoma*	*C. pilipes* & *D. anilis*	0.0020	0.0019	0.0021	0.0018
	C. pilipes & *C. frigida*	0.0816	0.0814	0.0816	0.0813
	C. frigida & *D. anilis*	0.0019	0.0017	0.0019	0.0017
	C. pilipes, D. anilis & *C. frigida*	0.0775	0.0774	0.0776	0.0774

5.4 Discussion

5.4.1 Main Findings

As the first study to empirically test the effect of a predator on consumer-resource interactions, there was little evidence to suggest that *C. xantholoma* changes the effect of larval identity, combination, or diversity on the decomposition of kelp. Increasing larval diversity increased *L. digitata* mass loss with or without the presence of *C. xantholoma*. Greater than expected rates of decomposition in multi-larval treatments were apparent both with and without the presence of *C. xantholoma*. However, there were subtle differences in larva-resource interactions with and without *C. xantholoma*. Larval identity combination was only a significant factor to explain the variability in *L. digitata* mass loss when *C. xantholoma* was not present. Additionally,

greater than expected decomposition in treatments containing *C. frigida* & *D. anilis* was not observed when these species were incubated with the predator.

Furthermore, despite direct consumption of larvae and possibly indirect effects of *C. xantholoma* on larval feeding, not all treatments containing the predator displayed significantly lower wrack processing rates than those without.

The consumption of larvae by *Cafius xantholoma* was different for different larval species and depended on the combination of larvae in a treatment. Larval pupation was also dependent on larval species and similar trends were observed with and without *C. xantholoma*.

5.4.2 Larval Identity, Diversity and Interactions in the Absence of *C. xantholoma*

As expected, based on the results obtained in Chapter 3, the current experiment has demonstrated that decomposition (*L. digitata* mass loss) increases as the diversity of larva in a treatment increases. In multi-species treatments, wrack loss exceeded that expected based on single species additive effects. Overall processing rates in the current study were lower than those previously reported (Chapter 3), possibly due to the lower pre-experiment temperatures in the strandline. In the current study, decomposition in all multi-species treatments was significantly higher than expected. In contrast, Chapter 3 showed that *L. digitata* loss in treatments of *C. frigida* & *D. anilis* combined was not significantly higher than expected. This discrepancy between results may indicate that positive interspecific larval interactions only occur in the presence of *C. pilipes* with the other two larval species (Chapter 3). Whilst there is no sound explanation for the discrepancy between these two identical experiments, it may have been due to the different times in which the experiments were undertaken, highlighting the potential importance of pre-exposure environmental conditions for species interactions.

Similar to the results of Chapter 3, decomposition increased significantly in treatments containing greater larval diversity (whether *L. digitata* mass loss was calculated per initial, mean, or final larval mass). Irrespective of how *L. digitata* mass loss was calculated, all three species larval treatments were significantly higher than any two or single species treatment, although subtle differences in decomposition between treatments containing different larval identities were observed. The identity combination of the larvae also significantly affected decomposition in both the current (this chapter) and previous (Chapter 3) studies. However, in the current study this only occurred when *L. digitata* mass loss was calculated per initial or mean larval mass. The implications of positive larval interactions for ecosystem processes and BDEF research are discussed in depth in Chapter 3. The mechanisms behind the observed increased processing rates in multi-larval treatments are discussed in Section 3.4.5 and are applicable here. As in Chapter 3 (Section 3.4.5) and Marsh and Spicer (*in prep.*), it is proposed that the increase in wrack processing in these heterospecific assemblages is indicative of interspecific facilitation. A mechanism of microbial facilitation was proposed to explain the increase in wrack mass loss with larval diversity (Section 3.4.5, Marsh and Spicer *in prep.*). Evidence for this hypothesis is at best anecdotal and a more complete reasoning can be found in Section 3.4.5. It should be reiterated that using the replacement design employed in this study (where larval total density was maintained but the relative density of each species decreased as the number of larval species (diversity) increased), does not allow the mechanisms behind positive species interactions to be discerned explicitly (Underwood 1984, 1986, Benedetti-Cecchi 2004). However, the positive effect of heterospecific larval treatments on wrack processing, despite the reduction of larval density due to *C. xantholoma* consumption, adds weight to the previously proposed interspecific facilitation hypothesis used to explain the greater than expected processing rates in multi-larva treatments. Competitive

interactions should be reduced at lower densities. Thus the effects of mechanisms such as intraspecific competitive release, that could also explain the higher than expected processing rates in multi-larva treatments, should be less at lower larval densities (i.e. in treatments with *C. xantholoma*). Whether the positive effect of larva species diversity on *L. digitata* mass loss was due to intraspecific competitive release or interspecific facilitation cannot be conclusively discerned. However, reducing the diversity of larva species will result in reduced ecosystem processes, whether this occurs through increased intraspecific competitive interactions or the loss of positive interspecific interactions (for more in-depth discussions see Sections 3.1.3 and 3.4.5).

5.4.3 The Effect of *C. xantholoma* on Larval Populations

The consumption of larvae differed depending on larval identity and the identity combination of larvae in a treatment. There is no unequivocal explanation for why a predator's preference for a particular larva species should change when the predator is presented with different combinations of prey species. However, differential pupation by larval species may in part explain the observed results. The consumption of pupae by *C. xantholoma* has never been documented, and was not observed in this experiment. In treatments where larval pupation rates were relatively high, according to optimal foraging theory, the reduced density of available prey would have increased search time (MacArthur and Pianka 1966), therefore time spent actually consuming prey would have been reduced. Preliminary experiments have shown that consumption of larvae by *C. xantholoma* was either reduced or deceased when larval density was low. This would suggest that *C. xantholoma* will only eat when it encounters prey by chance, rather than actively searching for prey. The number of individual larvae consumed by *C. xantholoma* when incubated with a single larval species follows the direct inverse pattern of the number of pupation events in single species treatments *C. frigida* < *D.*

anilis < *C. pilipes*. Similarly, in the two species treatment of *C. pilipes* & *D. anilis*, less *C. pilipes* were consumed and this species displayed a higher number of pupation events. Also, in the two species treatment of *C. frigida* & *D. anilis*, significantly more *C. frigida* were consumed than *D. anilis* pupated. However, why this trend was not observed for the other multi-larva treatments is as yet unclear.

5.4.4 Larval Identity, Diversity and Interactions in the Presence of *C. xantholoma*

Despite the fact that direct removal of larvae through consumption and the differential consumption of larvae was shown to depend on both the larval identity and the identity combination of larvae in a treatment, the effect of larval diversity and larval interactions with respect to *L. digitata* mass loss was not greatly affected by the presence of *C. xantholoma*. Additionally, the apparent positive interactions between larval species, with respect to processing rates, seen in the absence of a predator are generally maintained in treatments with *C. xantholoma*. *L. digitata* mass loss in all multi-larval treatments, with the exception of *C. frigida* & *D. anilis* were greater than predicted based on additive single species processing rates. The equable processing rates between observed and expected decomposition in the *C. frigida* & *D. anilis* treatment can be explained by the high consumption of larvae in this treatment (Figure 5.1). More total larvae were killed in the *C. frigida* & *D. anilis* treatment than any other multi-species larval treatment. Calculating expected processing rates based on single-species treatments may have resulted in an overestimation of expected processing rates because rates were corrected by the initial mass in multi-species treatments (Box 5.1). However, the absence of a diversity effect in this treatment could also be due to *C. xantholoma* interrupting the positive effect of these two species with regards to wrack processing, as observed in treatments without the predator.

Despite the possible errors in calculating mass-specific rates of wrack loss in the presence of a predator, wrack processing in all other multi-species treatments was higher than expected, based on single-species processing rates. This suggests that the positive interactions in heterospecific larval assemblages are not affected by *C. xantholoma*. Interestingly, in Chapter 3, processing rates in treatments of *C. frigida* & *D. anilis* were not significantly higher than expected without a predator. There appears to be no sound explanation for this discrepancy (Section 5.4.2). Whether the positive effects of *C. frigida* & *D. anilis* on wrack processing were interrupted in the presence of *C. xantholoma*, vary generally or are dependent on factors not considered in this and previous (Chapter 3) studies is unclear. Although the diversity effect and, in general, the positive effect of larval interactions[43] on wrack processing, were unchanged in the presence of *C. xantholoma*, subtle differences in processing rates with respect to larval identity were uncovered. The effect of larval identity combination was not significant in determining processing rates when larvae were incubated with *C. xantholoma*. This was in contrast to the results from treatments where *C. xantholoma* was absent. This may be due to the difference in kelp mass loss observed in single-species treatments of *C. frigida* with and without the predator. *L. digitata* mass loss in single-species treatments of *C. frigida* was reduced in the presence of *C. xantholoma*. *C. frigida* had the highest single species processing rates, and in treatments without *C. xantholoma* this single-species treatment was not significantly different from all two-species larval treatments.

There are no previous experimental studies which have explicitly compared the effect of positive interactions (within a trophic group) on ecosystem processes with and without a predator. However, a number of modelling studies have attempted to ascertain the effects of multiple-trophic level diversity on ecosystem processes. Contrary to the results of this study, in theoretical assemblages, predators have been shown to greatly

[43] Whether through intraspecific competitive release or interspecific facilitation (see Section 5.4.2)

influence ecosystem processes. Thebault and Loreau (2003) found that the relationship between diversity and ecosystem function (measured as plant and herbivore biomass) was dependent on the predator's mode of feeding and the distribution of plant traits[44]. However direct comparisons between the present study and that of Thebault and Loreau (2003) are difficult as the feeding mode of the predator remained constant in this study, and in their study plant species did not interact positively with respect to ecosystem processes in the modelled assemblage. Similarly, Thebault *et al.* (2007) used food web models that differed in diversity and incorporated four trophic levels and found that ecosystem process (biomass) at each trophic level depended massively on which trophic level the removed species belonged to[45]. However, ecosystem processes were also affected by initial diversity and the presence of intraspecific and interspecific competition. In addition to this, trophic level was never manipulated and species were allowed to go extinct. Therefore, the exact effects of higher predator interactions on intraspecific and interspecific competition amongst prey and the consequence of this for ecosystem processes cannot be discerned. Similarly, using model simulations, Fox (2004) showed how the presence of herbivores can affect the diversity ecosystem process relationship in plants. Positive species interactions (overyielding) were found for a wide range of parameter values without predators but only for a limited set of parameter values with a specialist predator and not at all with generalist predators. This is in contrast to the results of the current study where positive species interactions (greater wrack mass loss than expected based on single-species processing rates) were observed both with and without a predator. However, the positive interactions (overyielding) between plant species in the study by Fox (2004) was based on

[44] This was based on a mechanistic model of plants, herbivores, and carnivores where plants were nutrient limited and differed in their productivity (biomass) and herbivores and carnivores could be generalists or specialists.

[45] Models had different amount of connectance, intra and interspecific variation and predator prey interaction strength (all drown randomly and normally distributed).

differential resource use. As previously discussed this mechanism is unlikely to explain the positive species interactions observed in this study (Section 5.4.3). Thus, transgressive overyielding with specialist herbivores required that the inferior competitor takes up resources at a higher per-unit rate than the superior competitor. Furthermore, as the trait distributions between plant species, with and without, herbivores was altered (Fox 2004) the effects of diversity and positive interactions on ecosystem processes with and without a secondary trophic level, could not be discerned.

Previous studies provide mixed evidence for the effects of predators on consumer-resource interactions. Contrary to the results of the current study, ecosystem processeses have been affected by predatory interactions to a greater extent than non-trophic interactions. Duffy *et al.* (2003) used data from previous studies of plant diversity and consumer removal experiments in terrestrial and aquatic systems to assess and compare the overall effect size of plant diversity and consumers on plant biomass accumulation[46]. These limited experimental data suggested that removal of carnivore species often has impacts on total plant biomass comparable with, or greater than, those of removing a large fraction of plant species. Although the current study did not explicitly compare the effect size of diversity and compare it with the effect size of predators on an ecosystem proces, larval diversity arguably had a larger effect than predators on wrack mass loss. *Laminaria digitata* mass loss increased from the single to three species level, both with and without predators, whereas the difference in *L. digitata* mass loss with and without *C. xantholoma* was not significant for every treatment. The contrasting results of the current study and that of Duffy *et al.* (2003) may be explained by the differing methods of data collection. In the study by Duffy *et al.* (2003), the diversity-biomass accumulation data were taken mainly from terrestrial

[46] Effect size was standardised using the log ratio of the plant biomass accumulation in the presence vs. absence of altered diversity. The impacts of predator reductions on plant biomass were standardized from the meta-analysis of trophic cascade experiments by Shurin *et al.* (2002).

grassland studies, whereas the effect of predator removal for ecosystem processes was taken from aquatic ecosystem studies. If the comparison is restricted to terrestrial systems, plant diversity reduction yielded a mean effect whereas terrestrial predator removal effects did not differ significantly from zero. Either predator removal had weak effects on land, consistent with the argument that community-wide trophic cascades are rare on land (e.g. Strong 1992, Polis 1999) or, intuitively the comparison between studies of consumer removal in aquatic and diversity effects in terrestrial ecosystems is invalid. Similarly, Mulder *et al.* (1999) provides evidence that trophic interactions can have a greater effect on ecosystem process than within trophic level diversity. In outdoor mesocosms an increase in plant species richness increased productivity as measured by biomass accumulation in the absence of herbivores (plots were sprayed with pesticide, although not all herbivores were excluded). However the inclusion of herbivores (unsprayed plots) resulted in a doubling of plant biomass (Mulder *et al.* 1999). In terms of effect size, predators increased plant productivity over six times more than did species richness (Duffy *et al.* 2003). However, species diversity was comprised of randomly drawn species identities, and biomass accumulation in monocultures without herbivores was not tested. Thus, the interactions between species, and any positive diversity effects for biomass accumulation with herbivores could not be ascertained. Furthermore, although the overall effect of herbivores on productivity cannot be disputed, it was more likely due to the alteration in plant species evenness and diversity in unsprayed plots rather than a direct or indirect effect on positive species interactions. Naeem *et al.* (2000), using aquatic microcosms containing three trophic levels of bacteria, showed how the positive effect of algal species richness on algal biomass was eliminated in the presence of bacteria. Bacterial consumers fed on bacteria instead of algae thus reducing grazing pressure on algal. Whilst demonstrating the importance of trophic cascades for primary producer biomass, the mechanisms behind

the positive diversity biomass effect were not explicitly demonstrated and how this mechanism was affected by increased trophic levels was not determined.

As suggested by the results of the current study, there is tentative evidence that ecosystem processes are as reliant on non-trophic interactions as on trophic interaction. The conclusions reached by Setala *et al.* (1998), based on a review of current literature, on energy flow and material cycles in soil food webs agree, in part, with the results of the current study. Within-functional group interactions were deemed important to energy processing and some groups of predator were found to have little effect on energy processing. However, not all non-trophic interactions were significant in affecting ecosystem processes and there were many other variables, such as litter quality that had as large an effect as species diversity. Furthermore, some predator groups (mesostigmatid predators) affected ecosystem process. As these conclusions came from different studies, none of which had experimentally assessed the effects of predators on the interactive affects within a trophic level with respect to ecosystem processes, the relative impact of between-trophic level interactions and within-trophic level interactions in determining ecosystem process cannot be discerned.

In all of these examples the effect of predators on consumer-resource interactions was not measured or estimated empirically, making inferences on the effect of predators on positive non-trophic interactions difficult and limiting further comparison with the current study. There is some evidence from other systems to suggest that, as found in the present study, predators have little effect on consumer-resource interactions (Downing 2005, Duffy 2005). As part of a much wider experiment examining the effects of species richness on ecosystem processes in ponds, Downing (2005) measured macrophyte biomass in treatments containing identical numbers but different species compositions of grazer and macroalgae species with and without predators. Macrophyte biomass did not differ significantly with and without predators

despite the predatory influence on grazer biomass. However, as species identity was not consistent in treatments with and without predators, the effect of predator and grazer species identity on resource biomass cannot be discerned, e.g. if less efficient grazers were included in treatments without predators than those with, macrophyte biomass may have been similar in both treatments despite the reduced grazer biomass (due to predation) in the latter. However, as in the current study, within-treatment variability in processing rates, owing to interspecific differences, may have masked the relatively smaller indirect effects of predators on processing rates due to consumer removal. Similarly, Duffy (2005) found some strikingly similar trends to those observed in the current study despite the fundamental differences in the system and the species involved. Duffy (2005) manipulated species grazer diversity in seagrass mesocosms resulting in four single-species treatments and one treatment including all four species, and measured plant community biomass and composition. These treatments were replicated with generalist predators (three individuals of the same juvenile crab species). As in the current study, a positive effect of species number on ecosystem processes in the presence of predators was observed. Although, all multi-species interactions with respect to resource use were not discerned, and the effect of multi-species treatments compared to that expected based on single-species additive effects, as in this study the positive effect of species number on ecosystem processes in the presence of predators was observed. An increase in diversity from one to four species decreased sediment microalgal and macroalgal biomass, a trend that was maintained both with and without predators. However, there are important differences between the results of the current study and that of Duffy (2005). The current study suggests that positive diversity effects are not altered by predators. In contrast, Duffy (2005) suggested that positive diversity ecosystem process relationships are maintained by alteration of the consumer assemblage by the predator. With predators, epiphyte biomass decreased with grazer

species richness and eelgrass biomass decreased. This positive diversity effect was not apparent in the absence of predators. Furthermore, the mechanisms behind the positive diversity ecosystem process effects were not due to positive interactions as suggested in the current study[47] but instead, were due to differences in resource use between grazer species, density compensation among competing prey species and trade-offs between competitive ability and resistance to predation. In the current study there was only one food source for the consumer, whereas Duffy (2005) provided eelgrass, macroalgae and epiphytes. Different consumer species altered the biomass of the primary producers to different degrees. This combined with the different susceptibility of consumer species to predation, and the fact that species density compensation was allowed, resulted in a reduction of the most inefficient grazer and an increase in the most efficient grazers in the presence of predators.

5.4.5 The Effect of *C. xantholoma* on Kelp Mass Loss

L. digitata mass loss in single species treatments of *C. pilipes* and *D. anilis*, and these two species combined was not significantly lower than treatments without the predator, despite consumption of larvae by *C. xantholoma*. This can be explained, in part, by *C. xantholoma* consumption and larval pupation. When *C. xantholoma* was presented with a single larval species the predator consumed fewer *C. pilipes* and *D. anilis*, than *C. frigida* (although the difference was only significant between *C. frigida* and *C. pilipes*). Additionally, reduced larval density through pupation may have had greater impact on *L. digitata* mass loss in single species treatments than reduction in density due to *C. xantholoma* consumption. In single-species treatments, *C. frigida* did not pupate whereas single species treatments of *C. pilipes* and *D. anilis* with and

[47] Whether through intraspecific competitive release or interspecific facilitation (see Section 5.4.2)

without *C. xantholoma* showed high incidences of pupation. If larvae reduce their *L. digitata* processing prior to pupating then the combined effects of reduced processing followed by a reduction in larval density may mask the smaller effect due to larval removal through direct consumption. Variable processing rates between replicates within a treatment, due to differential species-specific pupation may have made differences in processing rates due to single or two species removal by *C. xantholoma* non-significant. Furthermore, once a single larval species pupates, the other species in the treatment quickly pupate in succession (*pers. obs.*). This is perhaps not unexpected as larval life-cycles have been observed to coincide with each other (Hodge and Arthur 1997, Blanche 1992), presumably as an adaptation to the tidal cycle which supplies wrack material, their food source (Section 2.5.2). *Ergo*, owing to the short time scale of this experiment, if larvae reduce processing rates prior to pupation and some species in a treatment pupated, the remaining species may have been close to pupating themselves and already be displaying reduced processing rates. However, until feeding rates throughout the life cycle of larvae are measured the influence of pupation and pre-pupation periods on wrack processing cannot be determined.

5.4.6 Wider Significance and Conclusions

This current study provides some of the first empirical evidence for the effects of trophic interactions on positive non-trophic interactions with respect to ecosystem processes. Although *C. xantholoma* consumed a considerable amount of fly larvae, the presence of *C. xantholoma* did not affect the positive effect of larval diversity on wrack processing, or in general, the positive interactions amongst kelpfly larvae. Additionally, the presence of *C. xantholoma* did not significantly reduce wrack processing rates in all larval treatments. The current study also provides support for the previously proposed

mechanisms of interspecific facilitation used to explain the greater than expected processing rates in multi-larval species treatments.

Whilst caution should be urged in extrapolating the results of this study to other systems, the current study does suggest that the effect of consumer diversity on ecosystem processes, as found in previous BDEF studies, may be valid in multi-trophic systems. The importance of positive species interactions within trophic groups on ecosystem processing is clear from the current study. In marine strandline systems, appreciating the role of species interactions is particularly relevant as ecological processes within such systems are relatively underrepresented in the BDEF literature. In addition decomposition has large implications for the associated species and assemblages in strandline systems (Section 2.6). Furthermore, ecosystem processes in coastal transition zones have implications for adjacent systems as they link terrestrial and marine environments (McGwynne *et al.* 1988, Snelgrove *et al.* 1997, Levin *et al.* 2001). The implications of positive species interactions, as found between the larval species in the current study, for future BDEF studies, conservation and predictions of system functioning is discussed in Section 3.4.6. The current study also raises concerns over the validity and predictive capacity of food-web models that only consider trophic interaction strengths in determining energy flow in food webs. Additionally, consumption of prey by *C. xantholoma* depended upon the prey combination with which the predator was presented. Although only the feeding of a single predator at equal prey densities was investigated this does highlight the limitation of the assumption made in many food-web models that predator consumption is assumed to correlate with prey abundance/density. Before food-web models are used to predict the effect of predators on prey, and consequently ecosystem processes, it is imperative that the assumptions underlying these models are tested empirically. Although no definitive conclusion on the usefulness of metabolic theory as a unifying theory of ecology can be

drawn from the results of the current study, at least in the system investigated here, several limitations are revealed in the use of metabolic theory in predicting ecosystem process using a methodology that ignores non-trophic interactions, and species identity within a trophic level.

CHAPTER 6: GENERAL DISCUSSION

6.1 Introduction and Outline

In the current climate of biodiversity loss, how species diversity and ecosystem process are linked is, arguably, one of the most pressing issues and greatest challenges currently facing the scientific community (Section 1.2). And yet there is no universally accepted trajectory either between diversity and ecosystem process, or the form of the relationship being reliant on species identity and their interactions (Sections 1.4, 1.5). Despite this the role of species interactions is rarely considered (Section 1.6).

Chapters 3-5 experimentally examined some of the assumptions underpinning predictions of species identity, diversity, trophic and non-trophic interactions with respect to ecosystem processes, using the marine strandline as a model system. Consequently what follows is an overall discussion of that experimental work (Chapters 3, 4 & 5) presented both in the context of the natural history of the specific system investigated (Chapter 2) and a desire to understand the role species identity, diversity and interactions play in the relationship between biodiversity and ecosystem processes (Chapter 1). The wider implications of the studies in this thesis for biodiversity research and ecological theory are discussed.

6.2 The Importance of Non-trophic Interactions for Ecosystem Processes

Non-trophic species interactions are clearly important in determining ecosystem processes. This was demonstrated when the effects of strandline detritivore species identity, diversity and interactions on wrack decomposition were investigated (Sections 3.3.4, 3.4.3). These findings have important implications for both conservation and future biodiversity ecosystem process research. Despite different single species processing rates, it was the balance of positive and negative species interactions that led

to the overall non significant effect of diversity on ecosystem processes (Section 3.4.3). The species used were all from the same functional group, where redundancy, the ability to compensate for species loss in terms of processing rates, is predicted to be greatest. Not only did each single species exhibit different processing rates (Section 3.4.1) but, processing rates in multi-species assemblages could not be accurately predicted from single species additive effects (Section 3.4.3). If accurate predictions of the effects of reduced diversity on ecosystem processes are to be made, and conservation efforts prioritised accordingly, it is imperative that the manner in which species interact is taken into consideration. Furthermore, this study adds to a growing body of evidence suggesting that some detritivores may interact positively with each other in respect to ecosystem processes (Section 3.4.3). Multi-species larval combinations were greater than expected based on single species processing rates (Sections 3.4.3, 5.4.2). If positive species interactions with respect to ecosystem processes are common occurrence, and species extinction rates continue at current or projected rates, ecosystem processes on which we rely may be drastically and irreversible reduced.

6.3 The Prediction of Trophic Interactions and Ecosystem Process Using Body Size Scaling Relationships

The methodology for determining interaction strength and ecosystem process presented in this thesis is novel (Section 4.2.7). No single universal relationship was found between size and interaction strength and ecosystem processes that could be used to predict the effect of trophic interactions on ecosystem processes (Sections 4.3.2, 4.3.3, 4.3.5, 4.3.7, 4.3.8). Using the particular species and ecosystem process measured in this thesis, neither predator and prey body size nor metabolic scaling principles proved good predictors of predator and prey interactions and ecosystem processes

(Section 4.4.6). The results presented in this thesis have important implications for the use of allometric scaling laws in a predictive capacity. The widely documented scaling laws that link body size with metabolic rate (Section 4.1.3) may not be as prevalent or applicable as previously thought, or may only apply over larger scales, such that they cannot be used to predict species-specific relationships between size and energy flow (interaction strength and decomposition) between the strandline species studied in this thesis (Section 4.4.6). Alternatively, size and metabolic rate may be intrinsically linked but factors other than metabolic rate may determine species interactions both between predator and prey and consumer and resource on smaller scales. At least in the strandline system, using species size as a surrogate measure for interaction strength, will lead to incorrect predictions of the consequence of reduced species diversity for energy flow through these assemblages. This thesis also emphasises the importance of considering species size in biodiversity ecosystem process studies before the effects of reduced diversity on ecosystem process in real assemblages is inferred. In this thesis, predator size and larval size influenced both predator-prey interactions and decomposition to some degree (Section 4.4.7). In real assemblages, species can vary both interspecifically and intraspecifically. Unless previously observed effects of species identity, diversity and interaction on ecosystem process are shown to be size-independent, inferring the effects of reduced diversity on ecosystem process from previous studies to real assemblages, has limited validity. Furthermore, the use of previous diversity-ecosystem process research, which has only manipulated diversity within a trophic level, to predict the effect of reduced species diversity on ecosystem processes in real multi-trophic assemblages may also be of limited utility.

6.4 Importance of Trophic and Non-trophic Interactions

This thesis has shown that the effect of diversity on ecosystem processes can remain the same in the presence of a predator. Furthermore, positive interactions, between larval heterospecifics with respect to wrack processing were observed both with and without the predators (Sections 5.4.2, 5.4.4). Although predators generally depressed wrack decomposition this was not significant for all dipteran larval combinations. Additionally, as wrack processing in multi-species larval treatments at lower densities (due to predator removal) was greater than expected, the results of Chapter 5 provided some evidence in support of the previously proposed mechanisms of interspecific facilitation rather than intraspecific competitive release as an explanation of the greater wrack processing at higher larval diversities. From these conclusions it could be suggested that previous BDEF studies which have not incorporated multiple trophic levels may still have use in predicting the general trends associated with reduced diversity on ecosystem processes, even if the values of ecosystem processes at different diversity levels change in the presence of multiple trophic levels. Furthermore, in the strandline system used in this thesis, positive species interactions with respect to ecosystem processes appear to be resilient to the presence of a predator (Section 5.4.4). This again highlights the threat posed by species loss for ecosystem processes. The loss of a single species in real assemblages, *via* loss of positive species interactions, may result in a greater decrease in ecosystem processes than that attributable to the contribution of the removed species. The results presented in this thesis also have implications for the modelling of food webs. Current approaches to food web modelling are beginning to quantify the links between species to make predictions of the energy flow through a system. However, unless non-trophic interactions are accurately defined, these models are at risk of inaccurately predicting energy flows. Similarly caution should be exercised when using food web models to make predictions of ecosystem

process, under different environmental conditions or at different levels of diversity. At the scale investigated in this thesis it is clear that non-trophic interactions should not automatically be assumed to be either constant or follow that of a normal distribution of interaction strengths.

6.5 Implications for Our Understanding of Strandlines

The background to the experimental chapters, i.e. the ecology of the strandline used to supply species for experiments, turned out to be more difficult to study than was apparent from the literature (Chapter 2). It was difficult to achieve any temporal and spatial resolution due mainly to the temporal and ephemeral nature of the wrack cover on Wembury beach (Section 2.2.2). As in previous studies, the strandline assemblage was dominated by a handful of eucoenic species (Section 2.3.2). Contrary to previous studies species distributions in the strandline at Wembury did not appear to follow temporal succession and were controlled by factors other than the chemical and physical properties of the wrack measured (Section 2.3.2). The strandline at Wembury may be unique, or factors other than the chemical and physical propertied of the wrack may determine the distribution of strandline species in other strandline systems. Unless the factors determining strandline species distributions are identified, inferring species distributions based on wrack properties alone may lead to incorrect conclusions of the strandline assemblage and thus incorrect conclusions on decomposition and energy flow through these systems. Future studies investigating the strandline may benefit from employing a range of sampling methods. In this thesis the sampling technique appeared to be critical in characterising the fauna of the strandline at Wembury. A higher diversity and abundance of beetle species were collected using pitfall trapping compared with box cores (Section 2.3.2.). By using a range of sampling methods the strandline assemblage, may be more accurately quantified.

6.6 The Value of Macroecology

Understanding and describing patterns and processes, and the mechanisms that produce them, is the essence of science and the key to development of principles for management (Levin 1992). Macroecology;

> *"the subfield of ecology which deals with the study of relationships between organisms and their environment at large spatial scales to characterise and explain statistical patterns of abundance, distribution and diversity"*
>
> - (Brown and Maurer 1989)

has the potential to help progress science and prioritise environmental management. Understanding the complexity and variability of the patterns and process in the environment is a daunting task. Elucidating and describing patterns of species distribution and links between species and their environment by unifying underlying mechanisms is an extremely attractive means of approaching, and working with, this complexity (Levin 1992). However attractive and tractable macroecological theory may be, its use in a predictive capacity is both limited, and arguably fraught with problems, unless the assumptions underlying the theory are explicitly upheld, and the scale at which predictions are made carefully considered.

This thesis highlights the limitations of some macroecological theories in their use for predicting the effects of reduced diversity on both ecosystem processes, and species interactions at the small scale investigated in this study. No previously proposed single mechanistic relationship accurately described the relationship between diversity within a single species level and decomposition (Section 3.4.4). Decomposition was dependent on species interactions, and thus the identity combination of species (Section 3.4.3). Even accepting the tentatively proposed hypothesis of microbial facilitation and inhibition to explain the generally positive interactions between larvae and negative interactions between larvae and amphipod (Section 3.4.4), larvae did not always interact positively with each other and not dipteran all larval-amphipod interactions were

negative (Section 3.3.4). Furthermore, the positive effect of *C. frigida* and *D. anilis* larvae on wrack processing was variable both between and within studies (Chapter 3, 5).

As seen when comparing previous BDEF studies, there does not appear to be a single mechanistic explanation that can adequately explain the relationship between diversity and ecosystem processes. As suggested in Chapter 3 many mechanisms may operate simultaneously to collectively determine this relationship. Even if a universal mechanism could describe the relationship between diversity and ecosystem processes, the discrepancy in observed values of decomposition in larval treatments between Chapter 3 and Chapter 5 highlights the temporal variability in processing rates and limits the quantification of processing rate reduction due to diversity loss.

Allometric scaling laws based on the relationship between body size and metabolic rate could not be used to accurately predict interaction strength or decomposition using the species in Chapter 4. Accepting that allometric scaling relationships do exist, the present study illustrates how general allometric scaling relationships may differ on small scales between species, thus limiting their use in a predictive capacity. Factors such as beetle feeding behaviour, pre-exposure conditions and larval pupation, may have been more significant in determining interaction strength and ecosystem processes measured at this scale of observation than when interaction strength and ecosystem processes are measured at larger scales (Sections 4.4.2, 5.4.3).

Although the overall effect of diversity on decomposition did not change in the presence of a predator, smaller species-specific trends were mitigated (Section 5.4.4). Larval identity combination became a significant factor to describe the variability in decomposition when *Cafius xantholoma* was present (Section 5.3.4.3). In addition, the positive interaction between *C. frigida* & *D. anilis* disappeared in the presence of *C. xantholoma*. Subtle differences in the relationships between species and ecosystem process in the presence of a predator are not considered in previous mechanistic

explanations in the BDEF literature. Species-specific, non-trophic interactions currently are not considered in theories of metabolic scaling relationships. Food-web ecology has yet to provide any theoretical and /or mechanistic explanations for the distribution of non-trophic interaction strengths. At the scale investigated in this thesis the use of macroecology theory to correctly predict ecosystem processes in real assemblages, let alone under conditions of reduced diversity and assemblage identity change, would appear to be limited.

In this thesis understanding the role of microbes in dipteran larvae and amphipod feeding and identifying the microbial community associated with these species could have allowed the prediction of consumer-resource interactions and thus the effects of reduced diversity decomposition to be better predicted and understood (Section 3.4.4). Species-specific information on the beetle's and larvae's metabolically active tissue, feeding behaviour and on larval pupation and the role of environmental factors and ontogeny in influencing species interactions and species-resource interactions may have enabled accurate predictions of specific predator-prey interactions and larva-kelp interactions and ultimately the overall rates of decomposition. Whilst natural history information and species specific information may help to make predictions on the interaction between species and species and ecosystem process and how both of these interactions vary temporally, these predictions will be limited in their applicability to other systems and species. The predictive capacity of such research in terms of informing our understanding of the effects of reduced diversity for ecosystem process will be limited in its generality. The scale at which patterns and process are considered and the approach that we take in trying to elucidate and generalise them is an age old debate (Levin 1992). Whilst large-scale, mechanistic explanations or laws behind ecological phenomena may set the boundaries in which small-scale patterns and process operate, without consideration of the process behind

small scale interactions, (e.g. species specific natural history information such as species interactions, behaviour and ontogeny and how these interact with the environment), predictions of the consequence of reduced diversity for energy flow and ecosystem process within a system will be severely limited.

The results of the studies presented in this thesis highlight the importance of rigorously testing the assumptions behind macroecological theory (and allowing key natural history observations to inform experimental design and interpretation) before the proposed relationships and mechanisms are accepted and used for the prediction of small-scale patterns and process. This particularly applies to the links between species interactions and ecosystem processes.

In using only one system, and then only a few species from that system, making inferences about the effect of species identity, diversity and interactions on ecosystem process across systems and species is illegitimate. Likewise deducing the suitability of macroecological theory to make predictions of the relationship between species identity, diversity and interactions on ecosystem process is system and species constrained. That said, this thesis represents one of only a few studies to investigate the influence of non-trophic interactions on ecosystem process, and the role of predators in affecting these interactions and is the first study I know of that has explicitly tested the use of body size as a surrogate measure of interaction strength and ecosystem processes.

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APPENDICES

A 1 Mass of a single *L. digitata* disc, repeated measurements were taken using either the water saturation method; mass of the disc was taken after being submerged in distilled water, or the blotting method; mass of the disc was taken after being rinsed in distilled water and blotted dry using blue roll.

	Water saturation method	Blotting method
Mass 1	0.3381 g	0.3898 g
Mass 2	0.4591 g	0.3881 g
Mass 3	0.3728 g	0.3899 g
Mass 4	0.4439 g	0.3882 g
Mass 5		0.3878 g
Mean	0.4035 g	0.3887 g
S.D	0.5757 g	0.0010 g
Maximum measure	0.4591 g	0.3899 g
Minimum measure	0.3381 g	0.3878 g
Difference between minimum and maximum measure	0.1210 g	0.0021 g

A2 One-way ANOVA of $\log_{10}$(total initial animal mass g) by treatment and Tukey's (HSD) *post-hoc* test for initial larvae mass in each treatment. 1= all three species with beetle, 2= all three species without beetle, 3= *C. pilipes* with beetle, 4= *C. pilipes* without beetle, 5= *D. anilis* with beetle, 6= *D. anilis* without beetle, 7= *C. frigida* with beetle, 8= *C. frigida* without beetle, 9= *C. pilipes & D. anilis* with beetle, 10= *C. pilipes & D. anilis* without beetle, 11= *C. pilipes & C. frigida* with beetle, 12= *C. pilipes & C. frigida* without beetle, 13= *C. frigida & D. anilis* with beetle, 14=*C. frigida & D. anilis* with beetle.

Source	D.F.	SS	MS	F	P
Treatment	14	1.90637	0.13617	28.05	0.000
Error	60	0.29129	0.00485		
Total	74	2.19767			

Levene's Test for equal variances was significant for total initial animal mass by treatment test statistic = 2.11, P = 0.024. Levene's Test for equal variances was not significant for $\log_{10}$total initial animal mass by treatment test statistic = 1.594, P = 1.07

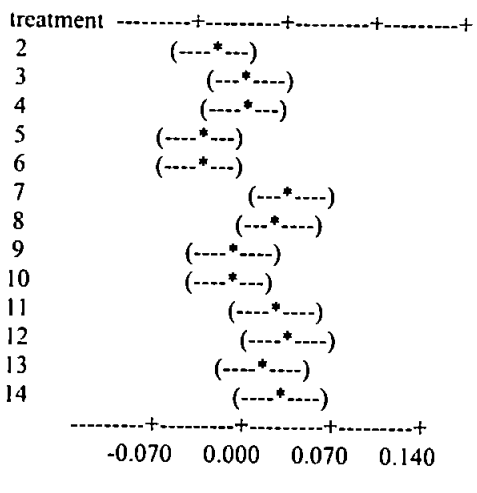
Individual 95% CIs for mean based on pooled StDev

```
Level  N    Mean   StDev ---+---------+---------+---------+------
1      7 0.12126 0.01968    (---*--)
2      7 0.11811 0.00372    (---*--)
3      7 0.15763 0.02064             (---*---)
4      7 0.15373 0.01536             (---*---)
5      7 0.10636 0.00647 (--*---)
6      7 0.10617 0.00825 (--*---)
7      7 0.20641 0.00808                       (---*---)
8      7 0.19197 0.02417                     (---*--)
9      5 0.14050 0.00652          (---*---)
10     5 0.13186 0.00591          (----*---)
11     5 0.18426 0.02211                  (----*---)
12     5 0.19808 0.02812                    (----*---)
13     5 0.16792 0.02953               (---*---)
14     5 0.18982 0.00562                    (---*---)
                ---+---------+---------+---------+------
                  0.105     0.140     0.175     0.210
Pooled StDev = 0.01666
```

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of larvae treatment
Individual confidence level = 99.91%

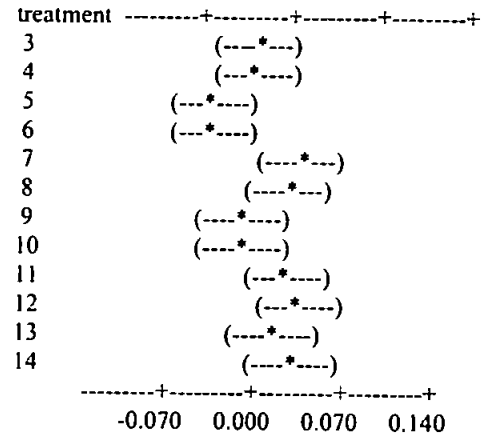
Larvae treatment = 1 subtracted from:

Larvae treatment	Lower	Center	Upper
2	-0.03405	-0.00314	0.02777
3	0.00546	0.03637	0.06728
4	0.00156	0.03247	0.06338
5	-0.04581	-0.01490	0.01601
6	-0.04600	-0.01509	0.01583
7	0.05425	0.08516	0.11607
8	0.03980	0.07071	0.10163
9	-0.01462	0.01924	0.05311
10	-0.02326	0.01060	0.04447
11	0.02914	0.06300	0.09687
12	0.04296	0.07682	0.11069
13	0.01280	0.04666	0.08053
14	0.03470	0.06856	0.10243



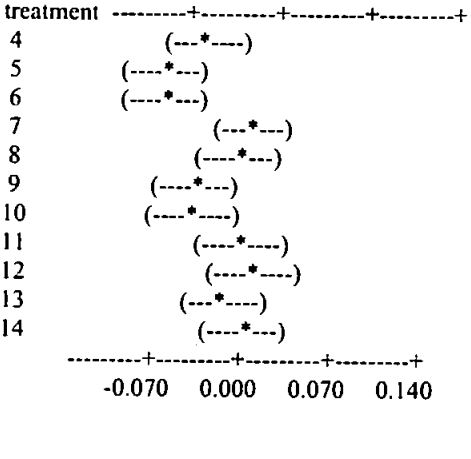
Larvae treatment = 2 subtracted from:

treatment	Lower	Center	Upper
3	0.00860	0.03951	0.07043
4	0.00470	0.03561	0.06653
5	-0.04267	-0.01176	0.01915
6	-0.04285	-0.01194	0.01897
7	0.05739	0.08830	0.11921
8	0.04295	0.07386	0.10477
9	-0.01148	0.02239	0.05625
10	-0.02012	0.01375	0.04761
11	0.03228	0.06615	0.10001
12	0.04610	0.07997	0.11383
13	0.01594	0.04981	0.08367
14	0.03784	0.07171	0.10557



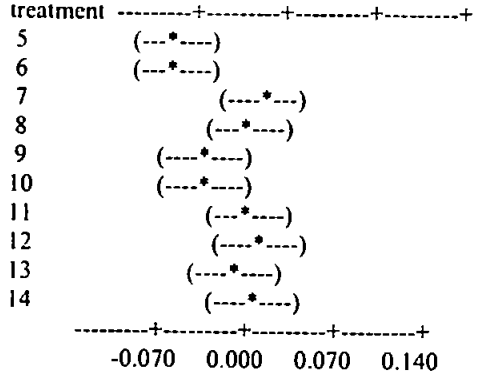
Larvae treatment = 3 subtracted from:

treatment	Lower	Center	Upper
4	-0.03481	-0.00390	0.02701
5	-0.08218	-0.05127	-0.02036
6	-0.08237	-0.05146	-0.02055
7	0.01787	0.04879	0.07970
8	0.00343	0.03434	0.06525
9	-0.05099	-0.01713	0.01673
10	-0.05963	-0.02577	0.00809
11	-0.00723	0.02663	0.06049
12	0.00659	0.04045	0.07431
13	-0.02357	0.01029	0.04415
14	-0.00167	0.03219	0.06605



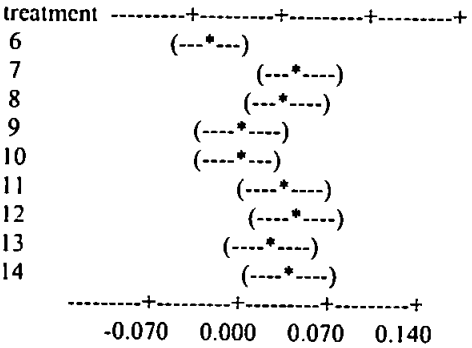
Larvae treatment = 4 subtracted from:

treatment	Lower	Center	Upper
5	-0.07828	-0.04737	-0.01646
6	-0.07847	-0.04756	-0.01665
7	0.02177	0.05269	0.08360
8	0.00733	0.03824	0.06915
9	-0.04709	-0.01323	0.02063
10	-0.05573	-0.02187	0.01199
11	-0.00333	0.03053	0.06439
12	0.01049	0.04435	0.07821
13	-0.01967	0.01419	0.04805
14	0.00223	0.03609	0.06995



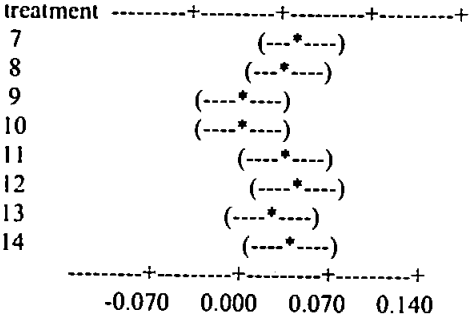
Larvae treatment = 5 subtracted from:

treatment	Lower	Center	Upper
6	-0.03110	-0.00019	0.03073
7	0.06915	0.10006	0.13097
8	0.05470	0.08561	0.11653
9	0.00028	0.03414	0.06801
10	-0.00836	0.02550	0.05937
11	0.04404	0.07790	0.11177
12	0.05786	0.09172	0.12559
13	0.02770	0.06156	0.09543
14	0.04960	0.08346	0.11733



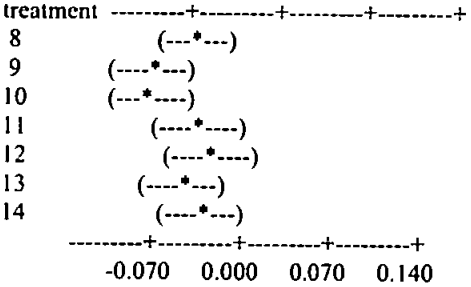
Larvae treatment = 6 subtracted from:

treatment	Lower	Center	Upper
7	0.06933	0.10024	0.13115
8	0.05489	0.08580	0.11671
9	0.00047	0.03433	0.06819
10	-0.00817	0.02569	0.05955
11	0.04423	0.07809	0.11195
12	0.05805	0.09191	0.12577
13	0.02789	0.06175	0.09561
14	0.04979	0.08365	0.11751



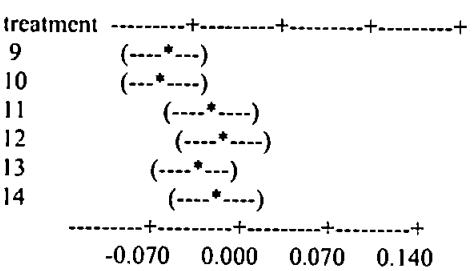
Larvae treatment = 7 subtracted from:

treatment	Lower	Center	Upper
8	-0.04535	-0.01444	0.01647
9	-0.09978	-0.06591	-0.03205
10	-0.10842	-0.07455	-0.04069
11	-0.05602	-0.02215	0.01171
12	-0.04220	-0.00833	0.02553
13	-0.07236	-0.03849	-0.00463
14	-0.05046	-0.01659	0.01727



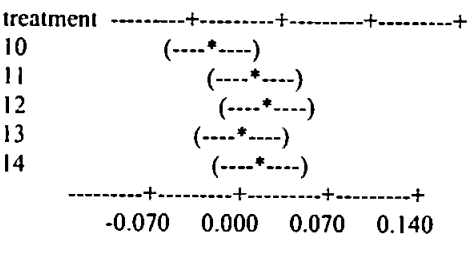
Larvae treatment = 8 subtracted from:

treatment	Lower	Center	Upper
9	-0.08533	-0.05147	-0.01761
10	-0.09397	-0.06011	-0.02625
11	-0.04157	-0.00771	0.02615
12	-0.02775	0.00611	0.03997
13	-0.05791	-0.02405	0.00981
14	-0.03601	-0.00215	0.03171



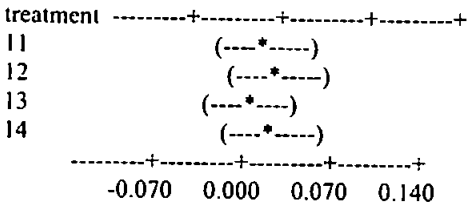
Larvae treatment = 9 subtracted from:

treatment	Lower	Center	Upper
10	-0.04522	-0.00864	0.02794
11	0.00718	0.04376	0.08034
12	0.02100	0.05758	0.09416
13	-0.00916	0.02742	0.06400
14	0.01274	0.04932	0.08590



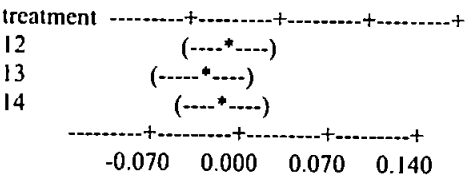
Larvae treatment = 10 subtracted from:

treatment	Lower	Center	Upper
11	0.01582	0.05240	0.08898
12	0.02964	0.06622	0.10280
13	-0.00052	0.03606	0.07264
14	0.02138	0.05796	0.09454



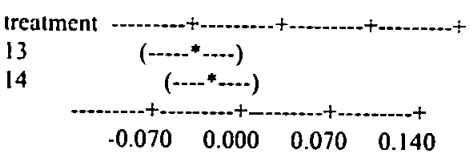
Larvae treatment = 11 subtracted from:

treatment	Lower	Center	Upper
12	-0.02276	0.01382	0.05040
13	-0.05292	-0.01634	0.02024
14	-0.03102	0.00556	0.04214



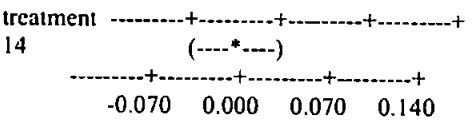
Larvae treatment = 12 subtracted from:

treatment	Lower	Center	Upper
13	-0.06674	-0.03016	0.00642
14	-0.04484	-0.00826	0.02832



Larvae treatment = 13 subtracted from:

treatment	Lower	Center	Upper
14	-0.01468	0.02190	0.05848



A3 Kruskal-Wallis test of initial animal mass by species level and Tukey's (HSD) *post-hoc* test between the total number of larvae killed by *C. xantholoma* in each treatment type: 1 = All three species together, 3= *C. pilipes*, 5= *D. anilis* 7= *C. frigida*, 9= *C. frigida* & *C. pilies*, 11= *C. frigida* & *D. anilis*, 13= *C. pilipes* & *D. anilis* .

H = 24, D.F. = -3, P = 0.000(adjusted for ties)
Levene's Test for equal variances was significant for total initial animal mass by species level test statistic = 7.66, p = 0.000. Levene's Test for equal variances was significant for total initial animal mass by species level test statistic = 4.37, P = 0.007.

A4 Kruskal-Wallis test of % larvae pupation by treatment.

H = 56.95, D.F. = -13, P = 0.000 (adjusted for ties)
Levene's Test for equal variances was significant for % larvae pupation by treatment Levene's Test statistic = 2.23, P = 0.020. Levene's Test for equal variances was significant for log % larvae pupation by treatment Levene's Test statistic = 2.41, P = 0.012.

A5 Kruskal-Wallis test of % larvae pupation by species level.

H = 14.16, D.F. = -3, P = 0.003 (adjusted for ties)
Levene's Test for equal variances was significant for % larvae pupation by species level Levene's Test statistic = 4.69, P = 0.005. Levene's Test for equal variances was significant for log % larvae pupation by treatment Levene`s Test statistic = 10.98, P <0.001.

A6 One-way ANOVA of talitrid mortality by treatment.

Source	D.F.	SS	MS	F	P
Treatment	7	345.5	49.4	4.74	0.001
Error	32	333.3	10.4		
Total	39	678.8			

Levene's Test for equal variances was significant for talitrid mortality by treatment test statistic = 1.26,P = 0.303.

A7 One-way ANOVA of talitrid mortality by species level.

Source	D.F.	SS	MS	F	P
Treatment	3	111.7	37.2	2.36	0.087
Error	36	567.1	15.8		
Total	39	678.8			

Levene's Test for equal variances was not significant for talitrid mortality by species level test statistic 2.19, P = 0.106.

A8 One-way ANOVA and Tukey's (HSD) *post-hoc* test of *L. digitata* mass loss g.g-1 between single species treatments.

Source	D.F.	SS	MS	F	P
Treatment	3	1.9537	0.6512	8.96	0.001
Error	16	1.1629	0.0727		
Total	19	3.1167			

Levene's Test for equal variances was not significant for *L. digitata* mass loss g.g-1 between single species treatments test statistic = 1.37, P = 0.287.

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of spp. single

Individual confidence level = 98.87%

Spp. single = 1 subtracted from:

```
Spp.
single   Lower  Center  Upper --------+---------+---------+---------+-
2      -0.0905 0.3978 0.8861            (------*------)
3      -0.4611 0.0272 0.5155          (------*------)
4       0.2773 0.7656 1.2539                (------*------)
                    --------+---------+---------+---------+-
                          -0.70     0.00     0.70     1.40
```

Spp. single = 2 subtracted from:

```
Spp.
single   Lower  Center  Upper --------+---------+---------+---------+-
3      -0.8589 -0.3706 0.1177      (------*------)
4      -0.1205 0.3678  0.8561            (------*------)
                    --------+---------+---------+---------+-
                          -0.70     0.00     0.70     1.40
```

Spp. single = 3 subtracted from:

```
Spp.
single   Lower  Center  Upper --------+---------+---------+---------+-
4      0.2501  0.7384  1.2267              (------*------)
                    --------+---------+---------+---------+-
                          -0.70     0.00     0.70     1.40
```

A9 Tukey's (HSD) *post-hoc* test of *L. digitata* mass loss g.g-1 between larvae diversity treatments.

Tukey 95% Simultaneous Confidence Intervals
All Pairwise Comparisons among Levels of larvae species level
Individual confidence level = 98.06%

larvae species level = 1 subtracted from:

species level	Lower	Center	Upper	---+---------+---------+---------+------
2	0.1496	0.4289	0.7081	(-----*----)
3	0.2715	0.6664	1.0613	(-------*-------)
				---+---------+---------+---------+------
				-0.50 0.00 0.50 1.00

larvae species level = 2 subtracted from:

species level	Lower	Center	Upper	---+---------+---------+---------+------
3	-0.1573	0.2375	0.6324	(-------*-------)
				---+---------+---------+---------+------
				-0.50 0.00 0.50 1.00

A10 Individual equations relating wet mass to dry mass for each species. In each case equations are based on 50 measurements of species wet mass and dry mass where X= wet mass.

Species	Equation	R^2
C. frigida	X*0.2247-0.0015	0.9934
C. pilipes	X*0.1306+0.0245	0.9024
D. anilis	X*0.219-0.0008	0.8641
L. digitata in *C. Xantholoma* & *C. Frigida* experiemtns	X*0.1415+0.0141	0.9814
L. digitata in *R. serviceus*& *C. pilipes* experiemtns	X*0.065+0.0423	0.7901
L. digitata in *P. algarum* & *D. anilis* experiemtns	X*0.1192+0.0321	0.7117
L. digitata in *C. verilosus* & *C. frigida* experiemtns	X*0.1362+0.0263	0.8992

A11 Anderson-Darling normal distribution test of the residuals for regressions of predator dry mass (g) vs prey dry mass loss ($g.h^{-1}$).

Experiment	N	A-D	P
All experiments combined	182	1.791	<0.005
C. xantholoma & *C. frigida*	47	1.877	<0.005
R. serviceus & *C. pilipes*	45	0.741	<0.005
P. algarum & *D. anilis*	45	3.470	<0.005
C. verilosus & *C. frigida*	45	1.667	<0.005

A12 One-way ANOVA and Tukey's (HSD) *post-hoc* tests, of the effect of *C. xantoloma***C. frigida* size-class on the number of individual larvae killed throughout the entire experimental duration. 33= large beetle, large larvae, 32=large beetle, medium larvae, 31=large beetle, small larvae, 23= medium beetle , large larvae, 22= medium beetle, medium larvae, 21= medium beetle, small larvae, 13= small beetle, large larvae, 12= small beetle, medium larvae, 11= small beetle, small larvae.

Source	D.F.	SS	MS	F	P
Beetle*Larvae size-class	8	80.923	10.115	17.03	<0.001
Error	38	22.567	0.594		
Total	46	103.489			

Levene's Test for equal variances was not significant for the number of larvae killed by *C. xantholoma* in each size-class combination; test statistic = 0.76, P = 0.581.

Individual 95% CIs For mean based on pooled StDev

Level	N	Mean	StDev	----------+---------+---------+---------+--
11	5	3.4000	0.8944	(----*---)
12	6	1.6667	0.8165	(---*---)
13	6	1.1667	0.4082	(---*---)
21	5	4.2000	0.8367	(----*----)
22	5	1.6000	0.5477	(----*---)
23	5	1.2000	0.4472	(----*----)
31	5	5.0000	1.0000	(---*----)
32	5	2.4000	0.8944	(----*----)
33	5	1.6000	0.8944	(----*---)

----------+---------+---------+---------+--
1.5 3.0 4.5 6.0

Pooled StDev = 0.7706

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of beetle and larvae size-class
Individual confidence level = 99.78%

Beetle and larvae size-class = 11 subtracted from:

size class	Lower	Center	Upper	----------+---------+---------+---------+-
12	-3.2677	-1.7333	-0.1990	(----*----)
13	-3.7677	-2.2333	-0.6990	(-----*----)
21	-0.8025	0.8000	2.4025	(-----*----)
22	-3.4025	-1.8000	-0.1975	(----*----)
23	-3.8025	-2.2000	-0.5975	(-----*----)
31	-0.0025	1.6000	3.2025	(----*-----)
32	-2.6025	-1.0000	0.6025	(-----*----)
33	-3.4025	-1.8000	-0.1975	(----*----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 12 subtracted from:

size class	Lower	Center	Upper	----------+---------+---------+---------+-
13	-1.9629	-0.5000	0.9629	(----*----)
21	0.9990	2.5333	4.0677	(----*-----)
22	-1.6010	-0.0667	1.4677	(----*----)
23	-2.0010	-0.4667	1.0677	(----*-----)
31	1.7990	3.3333	4.8677	(----*----)
32	-0.8010	0.7333	2.2677	(----*-----)
33	-1.6010	-0.0667	1.4677	(----*----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 13 subtracted from:

size-class	Lower	Center	Upper	----------+---------+---------+---------+-
21	1.4990	3.0333	4.5677	(----*----)
22	-1.1010	0.4333	1.9677	(----*-----)
23	-1.5010	0.0333	1.5677	(----*----)
31	2.2990	3.8333	5.3677	(----*----)
32	-0.3010	1.2333	2.7677	(----*----)
33	-1.1010	0.4333	1.9677	(----*-----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 21 subtracted from:

size class	Lower	Center	Upper	----------+---------+---------+---------+-
22	-4.2025	-2.6000	-0.9975	(----*-----)
23	-4.6025	-3.0000	-1.3975	(----*----)
31	-0.8025	0.8000	2.4025	(-----*----)
32	-3.4025	-1.8000	-0.1975	(----*----)
33	-4.2025	-2.6000	-0.9975	(----*-----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 22 subtracted from:

size-class	Lower	Center	Upper	----------+---------+---------+---------+-
23	-2.0025	-0.4000	1.2025	(-----*----)
31	1.7975	3.4000	5.0025	(----*-----)
32	-0.8025	0.8000	2.4025	(-----*----)
33	-1.6025	0.0000	1.6025	(----*----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 23 subtracted from:

size-class	Lower	Center	Upper	----------+---------+---------+---------+-
31	2.1975	3.8000	5.4025	(----*----)
32	-0.4025	1.2000	2.8025	(----*----)
33	-1.2025	0.4000	2.0025	(----*-----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 31 subtracted from:

size-class	Lower	Center	Upper	----------+---------+---------+---------+-
32	-4.2025	-2.6000	-0.9975	(----*-----)
33	-5.0025	-3.4000	-1.7975	(-----*----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

Beetle and larvae size-class = 32 subtracted from:

size-class	Lower	Center	Upper	----------+---------+---------+---------+-
33	-2.4025	-0.8000	0.8025	(----*-----)

----------+---------+---------+---------+-
-3.0 0.0 3.0 6.0

A13 One-way ANOVA and Tukey's (HSD) *post-hoc* tests of the effect of *R. serviceus*C .pilipes* size-class on the number of individual larvae killed throughout the entire experimental duration. 33= large beetle, large larvae, 32= large beetle, medium larvae, 31= large beetle, small larvae, 23= medium beetle , large larvae, 22= medium beetle, medium larvae, 21= medium beetle, small larvae, 13= small beetle, large larvae, 12= small beetle, medium larvae, 11= small beetle, small larvae.

Source	D.F.	SS	MS	F	P
Beetle*Larvae size-class	8	80.923	10.115	17.03	<0.001
Error	38	22.567	0.594		
Total	46	103.489			

Levene's Test for equal variances was not significant for the number of larvae killed by *R. serviceus* in each size-class combination; test statistic = 0.50, P = 0.848

```
                Individual 95% CIs for mean based on pooled StDev
Level  N   Mean  StDev ---+---------+---------+---------+------
11     5 2.4000 0.5477                  (----*----)
12     5 0.6000 0.5477     (----*----)
13     5 0.2000 0.4472 (----*----)
21     5 2.4000 0.5477                  (----*----)
22     5 1.0000 0.0000        (----*----)
23     5 0.2000 0.4472 (----*----)
31     5 3.0000 0.7071                       (----*----)
32     5 1.8000 0.8367             (----*----)
33     5 0.4000 0.8944   (----*----)
                 ---+---------+---------+---------+------
                  0.0       1.0       2.0       3.0
Pooled StDev = 0.6055
```

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of beetle and larvae size-class
Individual confidence level = 99.78%

Beetle and larvae size-class_1 = 11 subtracted from:

Beetle and larvae size-class_1	Lower	Center	Upper
12	-3.0619	-1.8000	-0.5381
13	-3.4619	-2.2000	-0.9381
21	-1.2619	0.0000	1.2619
22	-2.6619	-1.4000	-0.1381
23	-3.4619	-2.2000	-0.9381
31	-0.6619	0.6000	1.8619
32	-1.8619	-0.6000	0.6619
33	-3.2619	-2.0000	-0.7381

```
Beetle and larvae size-class_1
    ------+---------+---------+---------+---
12          (----*----)
13        (----*----)
21              (----*----)
22          (----*----)
23        (----*----)
31              (----*----)
32            (----*----)
33        (----*----)
       ------+---------+---------+---------+---
          -2.5       0.0       2.5       5.0
```

Beetle and larvae size-class_1 = 12 subtracted from:

Beetle and larvae size-class_1	Lower	Center	Upper
13	-1.6619	-0.4000	0.8619
21	0.5381	1.8000	3.0619
22	-0.8619	0.4000	1.6619
23	-1.6619	-0.4000	0.8619
31	1.1381	2.4000	3.6619
32	-0.0619	1.2000	2.4619
33	-1.4619	-0.2000	1.0619

```
                      ------+---------+---------+---------+---
                           -2.5       0.0       2.5       5.0
```

Beetle and larvae size-class_1 = 13 subtracted from:

Beetle and larvae size-class_1

	Lower	Center	Upper	------+---------+---------+---------+---
21	0.9381	2.2000	3.4619	(----*----)
22	-0.4619	0.8000	2.0619	(----*----)
23	-1.2619	0.0000	1.2619	(----*----)
31	1.5381	2.8000	4.0619	(----*----)
32	0.3381	1.6000	2.8619	(----*----)
33	-1.0619	0.2000	1.4619	(----*----)

------+---------+---------+---------+---
-2.5 0.0 2.5 5.0

Beetle and larvae size-class_1 = 21 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper
22	-2.6619	-1.4000	-0.1381
23	-3.4619	-2.2000	-0.9381
31	-0.6619	0.6000	1.8619
32	-1.8619	-0.6000	0.6619
33	-3.2619	-2.0000	-0.7381

Beetle and larvae sizeclass_1

------+---------+---------+---------+---
22 (----*----)
23 (----*----)
31 (----*----)
32 (----*----)
33 (----*----)
------+---------+---------+---------+---
-2.5 0.0 2.5 5.0

Beetle and larvae size-class_1 = 22 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	------+---------+---------+---------+---
23	-2.0619	-0.8000	0.4619	(----*----)
31	0.7381	2.0000	3.2619	(----*----)
32	-0.4619	0.8000	2.0619	(----*----)
33	-1.8619	-0.6000	0.6619	(----*----)

------+---------+---------+---------+---
-2.5 0.0 2.5 5.0

Beetle and larvae size-class_1 = 23 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	------+---------+---------+---------+---
31	1.5381	2.8000	4.0619	(----*----)
32	0.3381	1.6000	2.8619	(----*----)
33	-1.0619	0.2000	1.4619	(----*----)

------+---------+---------+---------+---
-2.5 0.0 2.5 5.0

Beetle and larvae size-class_1 = 31 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper
32	-2.4619	-1.2000	0.0619
33	-3.8619	-2.6000	-1.3381

Beetle and larvae size-class_1

------+---------+---------+---------+---
32 (----*----)
33 (----*----)
------+---------+---------+---------+---
-2.5 0.0 2.5 5.0

Beetle and larvae size-class_1 = 32 subtracted from:
Beetle and larvae size-class_1
Lower Center Upper
33 -2.6619 -1.4000 -0.1381

Beetle and larvae size-class_1
33 (----*----)
-2.5 0.0 2.5 5.0

A14 One-way ANOVA and Tukey's (HSD) *post-hoc* tests, of the effect of *C. verilosus***C. frigida* size-class on the number of individual larvae killed throughout the entire experimental duration. 33= large beetle, large larvae, 32= large beetle, medium larvae, 31= large beetle, small larvae, 23= medium beetle, large larvae, 22= medium beetle, medium larvae, 21= medium beetle, small larvae, 13= small beetle, large larvae, 12= small beetle, medium larvae, 11= small beetle, small larvae.

Source	D.F.	SS	MS	F	P
Beetle*Larvae size-class	8	64.71	8.09	6.17	<0.001
Error	36	47.20	1.31		
Total	44	111.91			

Levene's Test for equal variances was not significant for the number of larvae killed by *C. verilosus* for each size-class combination; test statistic = 64, P = 0.738

Individual 95% CIs for mean based on pooled StDev
Level N Mean StDev
11 5 4.600 0.894 (------*------)
12 5 2.400 0.894 (------*------)
13 5 1.800 0.837 (------*------)
21 5 4.800 0.837 (------*------)
22 5 4.000 1.225 (------*------)
23 5 3.400 1.517 (------*------)
31 5 6.000 0.000 (------*------)
32 5 4.200 1.924 (------*------)
33 5 3.400 1.140 (------*------)
1.6 3.2 4.8 6.4
Pooled StDev = 1.145

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of beetle and larvae size-class_1
Individual confidence level = 99.78%
Beetle and larvae size-class_1 = 11 subtracted from:

Beetle and larvae size-class_1
Lower Center Upper
12 -4.586 -2.200 0.186 (------*------)
13 -5.186 -2.800 -0.414 (------*------)
21 -2.186 0.200 2.586 (------*------)
22 -2.986 -0.600 1.786 (------*------)
23 -3.586 -1.200 1.186 (------*------)
31 -0.986 1.400 3.786 (------*------)
32 -2.786 -0.400 1.986 (------*------)
33 -3.586 -1.200 1.186 (------*------)
-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 12 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
13	-2.986	-0.600	1.786	(------*------)
21	0.014	2.400	4.786	(------*------)
22	-0.786	1.600	3.986	(------*------)
23	-1.386	1.000	3.386	(------*------)
31	1.214	3.600	5.986	(------*------)
32	-0.586	1.800	4.186	(------*------)
33	-1.386	1.000	3.386	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 13 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
21	0.614	3.000	5.386	(------*------)
22	-0.186	2.200	4.586	(------*------)
23	-0.786	1.600	3.986	(------*------)
31	1.814	4.200	6.586	(------*------)
32	0.014	2.400	4.786	(------*------)
33	-0.786	1.600	3.986	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 21 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
22	-3.186	-0.800	1.586	(------*------)
23	-3.786	-1.400	0.986	(------*------)
31	-1.186	1.200	3.586	(------*------)
32	-2.986	-0.600	1.786	(------*------)
33	-3.786	-1.400	0.986	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 22 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
23	-2.986	-0.600	1.786	(------*------)
31	-0.386	2.000	4.386	(------*------)
32	-2.186	0.200	2.586	(------*------)
33	-2.986	-0.600	1.786	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 23 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
31	0.214	2.600	4.986	(------*------)
32	-1.586	0.800	3.186	(------*------)
33	-2.386	0.000	2.386	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 31 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
32	-4.186	-1.800	0.586	(------*------)
33	-4.986	-2.600	-0.214	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

Beetle and larvae size-class_1 = 32 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	---------+---------+---------+---------+
33	-3.186	-0.800	1.586	(------*------)
				---------+---------+---------+---------+
				-3.5 0.0 3.5 7.0

A15 One-way ANOVA and Tukey's (HSD) *post-hoc* tests, of the effect of *P. algarum***D. anilis* size-class on the number of individual larvae killed throughout the entire experimental duration. 33= large beetle, large larvae, 32= large beetle, medium larvae, 31= large beetle, small larvae, 23= medium beetle, large larvae, 22= medium beetle, medium larvae, 21= medium beetle, small larvae, 13= small beetle, large larvae, 12= small beetle, medium larvae, 11= small beetle, small larvae.

Source	D.F.	SS	MS	*F*	P
Beetle*Larvae size-class	8	41.511	5.189	6.31	<0.001
Error	36	29.600	0.822		
Total	44	71.111			

Levene's Test for equal variances was not significant for the number of larvae killed by *P. algarum* for each size-class combination; test statistic = 0.81, P= 0.602

Individual 95% CIs for mean based on pooled StDev

Level	N	Mean	StDev	+---------+---------+---------+---------
11	5	2.8000	0.8367	(-----*----)
12	5	1.6000	0.5477	(-----*----)
13	5	0.8000	0.4472	(----*-----)
21	5	3.4000	0.5477	(-----*----)
22	5	2.0000	1.0000	(----*-----)
23	5	2.2000	0.8367	(-----*----)
31	5	4.2000	1.4832	(----*----)
32	5	3.0000	1.2247	(----*----)
33	5	3.0000	0.7071	(----*----)
				+---------+---------+---------+---------
				0.0 1.5 3.0 4.5

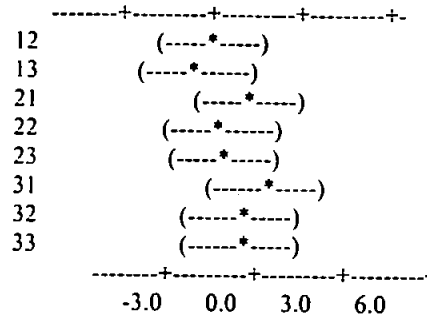
Pooled StDev = 0.9068

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of beetle and larvae size-class_1
Individual confidence level = 99.78%

Beetle and larvae size-class_1 = 11 subtracted from:
Beetle and larvae size-class_1

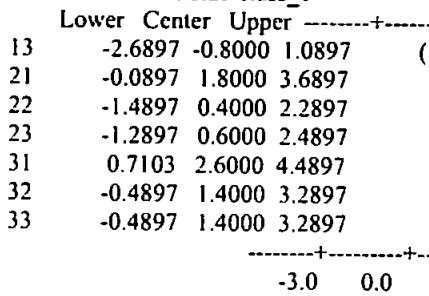
	Lower	Center	Upper
12	-3.0897	-1.2000	0.6897
13	-3.8897	-2.0000	-0.1103
21	-1.2897	0.6000	2.4897
22	-2.6897	-0.8000	1.0897
23	-2.4897	-0.6000	1.2897
31	-0.4897	1.4000	3.2897
32	-1.6897	0.2000	2.0897
33	-1.6897	0.2000	2.0897

Beetle and larvae size-class_1



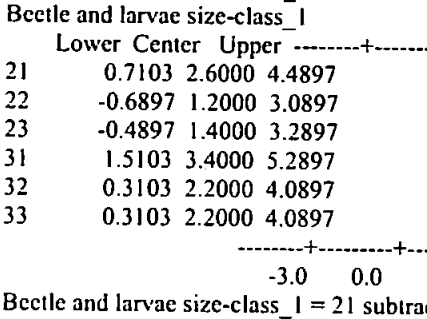
Beetle and larvae size-class_1 = 12 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper
13	-2.6897	-0.8000	1.0897
21	-0.0897	1.8000	3.6897
22	-1.4897	0.4000	2.2897
23	-1.2897	0.6000	2.4897
31	0.7103	2.6000	4.4897
32	-0.4897	1.4000	3.2897
33	-0.4897	1.4000	3.2897



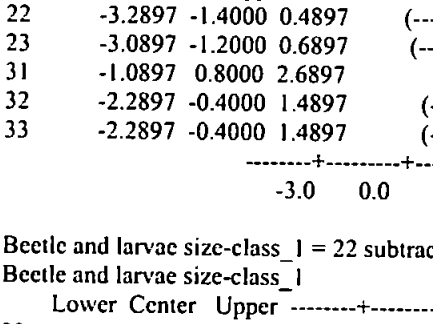
Beetle and larvae size-class_1 = 13 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper
21	0.7103	2.6000	4.4897
22	-0.6897	1.2000	3.0897
23	-0.4897	1.4000	3.2897
31	1.5103	3.4000	5.2897
32	0.3103	2.2000	4.0897
33	0.3103	2.2000	4.0897



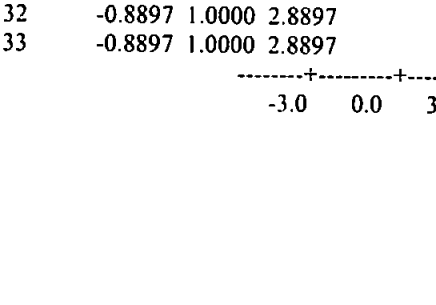
Beetle and larvae size-class_1 = 21 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper
22	-3.2897	-1.4000	0.4897
23	-3.0897	-1.2000	0.6897
31	-1.0897	0.8000	2.6897
32	-2.2897	-0.4000	1.4897
33	-2.2897	-0.4000	1.4897



Beetle and larvae size-class_1 = 22 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper
23	-1.6897	0.2000	2.0897
31	0.3103	2.2000	4.0897
32	-0.8897	1.0000	2.8897
33	-0.8897	1.0000	2.8897



Beetle and larvae size-class_1 = 23 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	--------+---------+---------+---------+-
31	0.1103	2.0000	3.8897	(------*-----)
32	-1.0897	0.8000	2.6897	(------*-----)
33	-1.0897	0.8000	2.6897	(------*-----)
				--------+---------+---------+---------+-
				-3.0 0.0 3.0 6.0

Beetle and larvae size-class_1 = 31 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	--------+---------+---------+---------+-
32	-3.0897	-1.2000	0.6897	(-----*-----)
33	-3.0897	-1.2000	0.6897	(-----*-----)
				--------+---------+---------+---------+-
				-3.0 0.0 3.0 6.0

Beetle and larvae size-class_1 = 32 subtracted from:
Beetle and larvae size-class_1

	Lower	Center	Upper	--------+---------+---------+---------+-
33	-1.8897	0.0000	1.8897	(-----*-----)
				--------+---------+---------+---------+-
				-3.0 0.0 3.0 6.0

Table A16a One-way ANOVA and Tukey's (HSD) *post-hoc* tests results, showing the effect of *C. xantholoma* & *C. frigida* grouped treatment type on the variability in *L. digitata* mass loss $g.h^{-1}$.

Source	D.F.	SS	MS	*F*	P
Grouped treatment type	3	0.0000036	0.0000012	27.54	0.000
Error	68	0.0000030	0.0000000		
Total	71	0.0000066			

Levene's Test for equal variances was not significant for the variability in *L. digitata* mass loss g.h-1 by each grouped treatment type; Test statistic = 2.70, P = 0.054.
Tukey's (N HSD) *post-hoc* test showed control treatments without larvae (no *C. xantholomas* or *C. frigida* and *C. xantholoma* only) to be significantly lower than treatments with larvae (*C. xantholomas* and *C. frigida* treatments and *C. frigida* only treatment). Also *C. frigida* only treatments were significantly higher than *C. frigida* and *C. xantholoma* treatments.

TableA16b One-way ANOVA and Tukey's (HSD) *post-hoc* tests results, showing the effect of *R. serviceus* and *C. pilipes* grouped treatment type on the variability in *L. digitata* mass loss $g.h^{-1}$.

Source	D.F.	SS	MS	*F*	P
Grouped treatment type	3	0.0000002	0.000001	7.70	0.000
Error	60	0.0000004	0.0000000		
Total	63	0.0000006			

Levene's Test for equal variances was not significant for the variability in *L. digitata* mass loss g.h-1 by each grouped treatment type; test statistic = 0.98, P = 0.409
Tukey's (N HSD) *post hoc* test showed control treatments without larvae (no *C. frigida* or *C. xantholoma* and *C. xantholoma* only) to be significantly lower than treatments with larvae (*C. xantholoma* and *C. frigida* treatments and *C. frigida* only treatment).

TableA16c One-way ANOVA and Tukey's (HSD) *post-hoc* tests results, showing the effect of *P. algarum* and *D. anilis* grouped treatment type on the variability in *L. digitata* mass loss $g.h^{-1}$.

Source	D.F.	SS	MS	*F*	P
Grouped treatment type	3	0.0000005	0.000002	6.21	0.001
Error	60	0.0000016	0.0000000		
Total	63	0.0000021			

Levene's Test for equal variances was not significant for the variability in *L. digitata* mass loss $g.h^{-1}$ by each grouped treatment type; Test statistic = 1.50, P= 0.225.
Tukey's (HSD) *post hoc* test showed control treatments without larvae (no *P. algarum* or *D. anilis* and *P. algarum* only) to be significantly lower than treatments with larvae (*P. alagrum* and *D. anilis* treatments and *D. anilis* only treatment).

TableA16d One-way ANOVA and Tukey's (HSD) *post-hoc* tests results, showing the effect of *C .verilosus* and *C. frigida* grouped treatment type on the variability in *L. digitata* mass loss $g.h^{-1}$.

Source	D.F.	SS	MS	*F*	P
Grouped treatment type	3	0.0000026	0.000009	13.76	0.000
Error	60	0.0000037	0.0000001		
Total	63	0.0000063			

Levene's Test for equal variances was not significant for the variability in *L. digitata* mass loss $g.h^{-1}$ by each grouped treatment type; test statistic = 2.70, P = 0.054

Tukey's (HSD) *post-hoc* test showed control treatments without larvae (no *C. verilosus* or *C. frigida* and *C. verilosus* only) to be significantly lower than treatments with larvae (*C. verilosus* and *C. frigida* treatments and *C. frigida* only treatment). Also *C. frigida* only treatment were significantly higher than *C. frigida* and *C. verilosus* treatments.

A17 Anderson-Darling normal distribution test of the residuals for regressions of mean final prey dry mass g/individual vs mean *L. digitata* mass loss $g.h^{-1}$/individual (where no individuals = no alive at the end of the experiment).

Experiment	n	A-D	P
C. xantholoma* & *C. frigida	47	0.903	0.020
R. serviceus* & *C. pilipes	45	1.197	<0.005
P. algarum* & *D. anilis	45	1.205	<0.005
C. verilosus* & *C. frigida	45	3.359	<0.005

A 18 One-way ANOVA and Tukey's (HSD) *post-hoc* test of i) the number of larvae killed of each species when they were incubated with the beetle separately, and ii) the number of larvae killed of each species when they were incubated with the beetle in combination. Where level related to larvae species; 1= *C. frigida*, 2= *C. pilipes* 3= *D. anilis* and a) *C. xatholoma*, b) *R. serviceus*, c) *P. algarum* and d) *C. verilosus*.

A18ai

Source	D.F.	SS	MS	*F*	P
Larvae species	2	60.67	30.33	10.27	0.001
Error	18	53.14	2.95		
Total	20	113.81			

```
                Individual 95% CIs for mean based on pooled StDev
Level N  Mean StDev ---------+---------+---------+---------+
1     7 5.571 2.440              (------*------)
2     7 1.571 0.976 (------*------)
3     7 4.571 1.397           (------*------)
              ---------+---------+---------+---------+
                     2.0     4.0     6.0     8.0
Pooled StDev = 1.718

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of c.x prey id
Individual confidence level = 98.00%

c.x prey id = 1 subtracted from:
c.x preyid
    Lower  Center  Upper  -+---------+---------+---------+--------
2  -6.344 -4.000 -1.656  (-------*------)
3  -3.344 -1.000  1.344          (-------*------)
                  -+---------+---------+---------+--------
                -6.0     -3.0     0.0     3.0
```

c.x prey id = 2 subtracted from:
c.x prey id
Lower Center Upper -+---------+---------+---------+--------
3 0.656 3.000 5.344 (-------*-------)
-+---------+---------+---------+--------
-6.0 -3.0 0.0 3.0

A18aii

Source	D.F.	SS	MS	*F*	P
Larvae species	2	9.238	4.619	5.29	0.016
Error	18	15.714	0.873		
Total	20	24.952			

Individual 95% CIs for mean based on pooled StDev
Level N Mean StDev +---------+---------+---------+---------
1 7 2.2857 1.2536 (---------*---------)
2 7 1.1429 0.6901 (---------*---------)
3 7 0.7143 0.7559 (---------*---------)
+---------+---------+---------+---------
0.00 0.80 1.60 2.40
Pooled StDev = 0.9344

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of c.x prey id
Individual confidence level = 98.00%

c.x prey id = 1 subtracted from:
c.x prey id
Lower Center Upper ----+---------+---------+---------+-----
2 -2.4177 -1.1429 0.1320 (----------*----------)
3 -2.8463 -1.5714 -0.2965 (----------*----------)
----+---------+---------+---------+-----
-2.4 -1.2 0.0 1.2

c.x prey id = 2 subtracted from:
c.x
prey
id Lower Center Upper ----+---------+---------+---------+-----
3 -1.7035 -0.4286 0.8463 (----------*----------)
----+---------+---------+---------+-----
-2.4 -1.2 0.0 1.2

A18bi

Source	D.F.	SS	MS	*F*	P
Larvae species	2	24.13	12.07	2.55	0.119
Error	12	56.80	4.73		
Total	14	80.93			

A18bii

Source	D.F.	SS	MS	*F*	P
Larvae species	2	0.000	0.000	0.00	1
Error	12	9.600	0.800		
Total	14	9.600			

A18ci

Source	D.F.	SS	MS	*F*	P
Larvae species	2	32.13	16.07	9.84	0.003
Error	12	19.60	1.63		
Total	14	51.73			

```
                Individual 95% CIs for mean based on pooled StDev
Level  N  Mean  StDev --+---------+---------+---------+-------
1      5 5.600  1.673                (-------*--------)
2      5 5.400  1.140                (-------*-------)
3      5 2.400  0.894  (-------*-------)
               --+---------+---------+---------+-------
                 1.5       3.0       4.5       6.0
Pooled StDev = 1.278

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of p.a prey id
Individual confidence level = 97.94%

p.a prey id = 1 subtracted from:
p.a prey id
    Lower  Center  Upper --------+---------+---------+---------+-
2   -2.355 -0.200  1.955         (------*-------)
3   -5.355 -3.200 -1.045  (------*-------)
                  --------+---------+---------+---------+-
                    -3.0      0.0       3.0       6.0

p.a prey id = 2 subtracted from:
p.a prey id
    Lower  Center  Upper --------+---------+---------+---------+-
3   -5.155 -3.000 -0.845  (------*------)
                  --------+---------+---------+---------+-
                    -3.0      0.0       3.0       6.0
```

A18cii

Source	D.F.	SS	MS	*F*	P
Larvae species	2	1.73	0.87	0.87	0.445
Error	12	12.00	1		
Total	14	13.73			

A18di

Source	D.F.	SS	MS	*F*	P
Larvae species	2	2.80	1.40	0.43	0.658
Error	12	38.80	3.23		
Total	14	41.60			

A18dii

Source	D.F.	SS	MS	*F*	P
Larvae species	2	2.800	1.400	1.91	0.191
Error	12	8.800	0.733		
Total	14	11.600			

A19 Tukey's (HSD) *post-hoc* test for initial larvae mass in each treatment, where 1= all three species with beetle, 2= all three species without beetle, 3= *C. pilipes* with beetle, 4= *C. pilipes* without beetle, 5= *D. anilis* with beetle, 6= *D. anilis* without beetle, 7= *C. frigida* with beetle, 8= *C. frigida* without beetle, 9= *C. pilipes* & *D. anilis* with beetle, 10= *C. pilipes* & *D. anilis* without beetle 11= *C. pilipes* & *C. frigida* with beetle, 12= *C. pilipes* & *C. frigida* without beetle, 13= *C. frigida, C. pilipes* & *D. anilis* with beetle, 14=*C. frigida, C. pilipes* & *D. anilis* with beetle.

Individual 95% CIs for mean based on pooled StDev

Level	N	Mean	StDev	---+---------+---------+---------+------
1	7	0.12126	0.01968	(---*--)
2	7	0.11811	0.00372	(---*--)
3	7	0.15763	0.02064	(---*---)
4	7	0.15373	0.01536	(---*---)
5	7	0.10636	0.00647	(--*---)
6	7	0.10617	0.00825	(--*---)
7	7	0.20641	0.00808	(---*---)
8	7	0.19197	0.02417	(---*--)
9	5	0.14050	0.00652	(---*---)
10	5	0.13186	0.00591	(----*---)
11	5	0.18426	0.02211	(----*---)
12	5	0.19808	0.02812	(----*---)
13	5	0.16792	0.02953	(---*---)
14	5	0.18982	0.00562	(---*---)

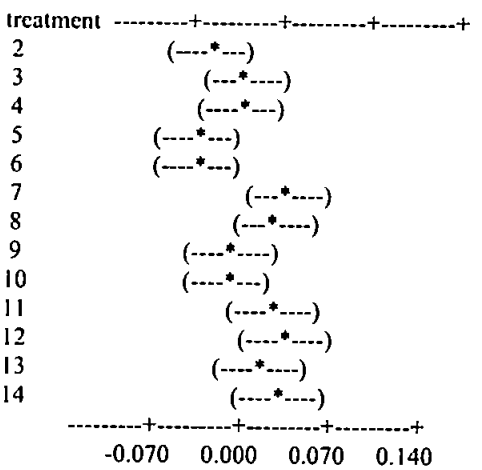
---+---------+---------+---------+------
0.105 0.140 0.175 0.210

Pooled StDev = 0.01666

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of larvae treatment
Individual confidence level = 99.91%

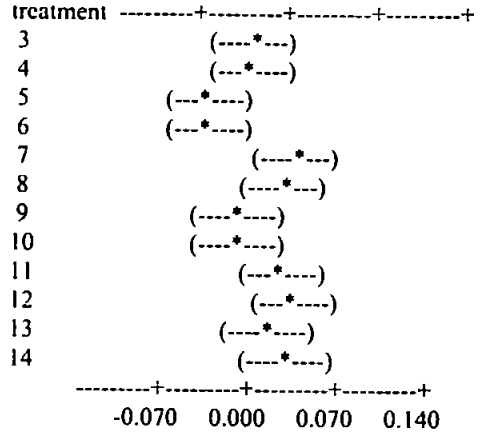
Larvae treatment = 1 subtracted from:

treatment	Lower	Center	Upper
2	-0.03405	-0.00314	0.02777
3	0.00546	0.03637	0.06728
4	0.00156	0.03247	0.06338
5	-0.04581	-0.01490	0.01601
6	-0.04600	-0.01509	0.01583
7	0.05425	0.08516	0.11607
8	0.03980	0.07071	0.10163
9	-0.01462	0.01924	0.05311
10	-0.02326	0.01060	0.04447
11	0.02914	0.06300	0.09687
12	0.04296	0.07682	0.11069
13	0.01280	0.04666	0.08053
14	0.03470	0.06856	0.10243



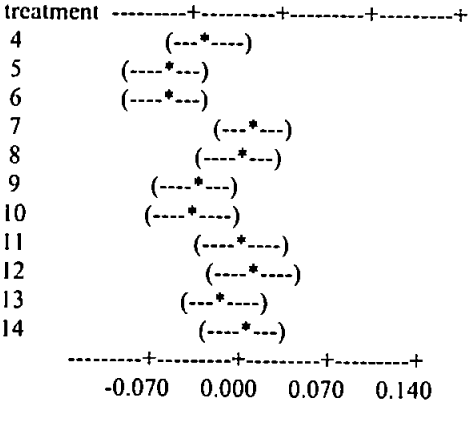
Larvae treatment = 2 subtracted from:

treatment	Lower	Center	Upper
3	0.00860	0.03951	0.07043
4	0.00470	0.03561	0.06653
5	-0.04267	-0.01176	0.01915
6	-0.04285	-0.01194	0.01897
7	0.05739	0.08830	0.11921
8	0.04295	0.07386	0.10477
9	-0.01148	0.02239	0.05625
10	-0.02012	0.01375	0.04761
11	0.03228	0.06615	0.10001
12	0.04610	0.07997	0.11383
13	0.01594	0.04981	0.08367
14	0.03784	0.07171	0.10557



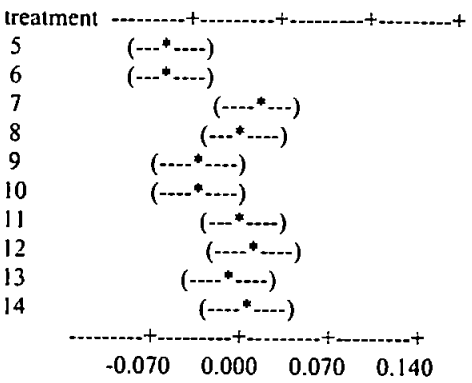
Larvae treatment = 3 subtracted from:

treatment	Lower	Center	Upper
4	-0.03481	-0.00390	0.02701
5	-0.08218	-0.05127	-0.02036
6	-0.08237	-0.05146	-0.02055
7	0.01787	0.04879	0.07970
8	0.00343	0.03434	0.06525
9	-0.05099	-0.01713	0.01673
10	-0.05963	-0.02577	0.00809
11	-0.00723	0.02663	0.06049
12	0.00659	0.04045	0.07431
13	-0.02357	0.01029	0.04415
14	-0.00167	0.03219	0.06605



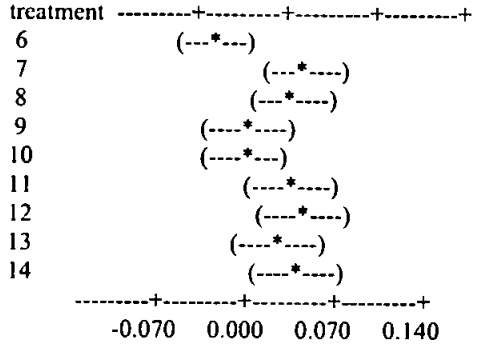
Larvae treatment = 4 subtracted from:

treatment	Lower	Center	Upper
5	-0.07828	-0.04737	-0.01646
6	-0.07847	-0.04756	-0.01665
7	0.02177	0.05269	0.08360
8	0.00733	0.03824	0.06915
9	-0.04709	-0.01323	0.02063
10	-0.05573	-0.02187	0.01199
11	-0.00333	0.03053	0.06439
12	0.01049	0.04435	0.07821
13	-0.01967	0.01419	0.04805
14	0.00223	0.03609	0.06995



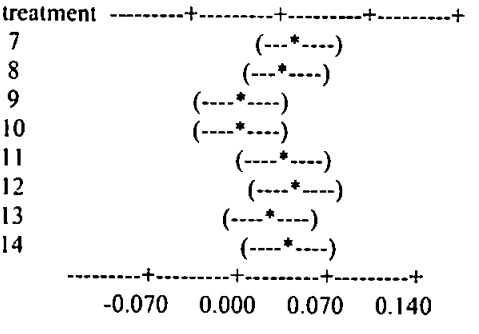
Larvae treatment = 5 subtracted from:

treatment	Lower	Center	Upper
6	-0.03110	-0.00019	0.03073
7	0.06915	0.10006	0.13097
8	0.05470	0.08561	0.11653
9	0.00028	0.03414	0.06801
10	-0.00836	0.02550	0.05937
11	0.04404	0.07790	0.11177
12	0.05786	0.09172	0.12559
13	0.02770	0.06156	0.09543
14	0.04960	0.08346	0.11733



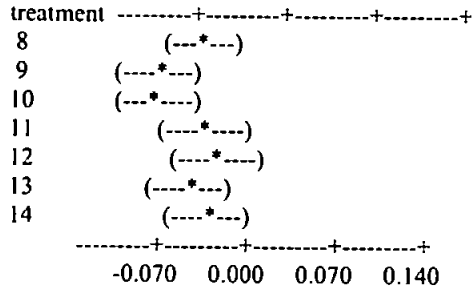
Larvae treatment = 6 subtracted from:

treatment	Lower	Center	Upper
7	0.06933	0.10024	0.13115
8	0.05489	0.08580	0.11671
9	0.00047	0.03433	0.06819
10	-0.00817	0.02569	0.05955
11	0.04423	0.07809	0.11195
12	0.05805	0.09191	0.12577
13	0.02789	0.06175	0.09561
14	0.04979	0.08365	0.11751



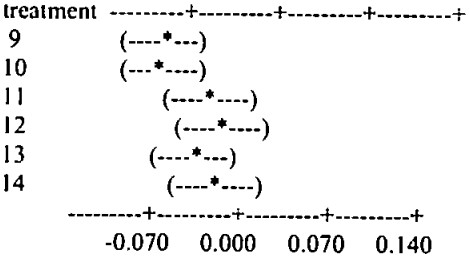
Larvae treatment = 7 subtracted from:

treatment	Lower	Center	Upper
8	-0.04535	-0.01444	0.01647
9	-0.09978	-0.06591	-0.03205
10	-0.10842	-0.07455	-0.04069
11	-0.05602	-0.02215	0.01171
12	-0.04220	-0.00833	0.02553
13	-0.07236	-0.03849	-0.00463
14	-0.05046	-0.01659	0.01727



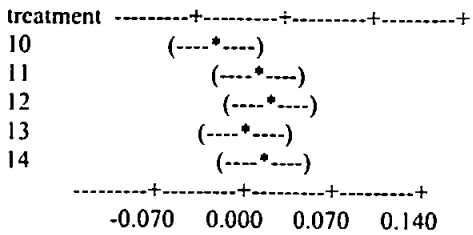
Larvae treatment = 8 subtracted from:

treatment	Lower	Center	Upper
9	-0.08533	-0.05147	-0.01761
10	-0.09397	-0.06011	-0.02625
11	-0.04157	-0.00771	0.02615
12	-0.02775	0.00611	0.03997
13	-0.05791	-0.02405	0.00981
14	-0.03601	-0.00215	0.03171



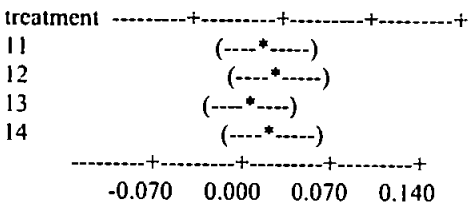
Larvae treatment = 9 subtracted from:

Lower	Center	Upper
-0.04522	-0.00864	0.02794
0.00718	0.04376	0.08034
0.02100	0.05758	0.09416
-0.00916	0.02742	0.06400
0.01274	0.04932	0.08590



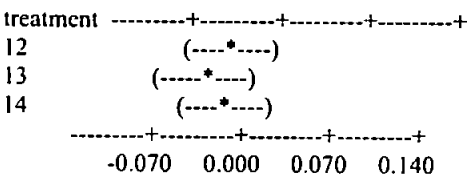
Larvae treatment = 10 subtracted from:

treatment	Lower	Center	Upper
11	0.01582	0.05240	0.08898
12	0.02964	0.06622	0.10280
13	-0.00052	0.03606	0.07264
14	0.02138	0.05796	0.09454



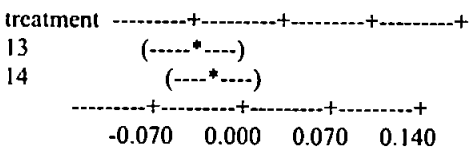
Larvae treatment = 11 subtracted from:

treatment	Lower	Center	Upper
12	-0.02276	0.01382	0.05040
13	-0.05292	-0.01634	0.02024
14	-0.03102	0.00556	0.04214



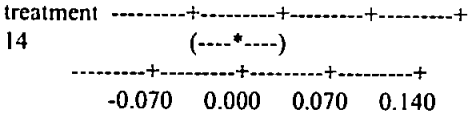
Larvae treatment = 12 subtracted from:

treatment	Lower	Center	Upper
13	-0.06674	-0.03016	0.00642
14	-0.04484	-0.00826	0.02832



Larvae treatment = 13 subtracted from:

treatment	Lower	Center	Upper
14	-0.01468	0.02190	0.05848



A20 Tukey's (HSD) *post-hoc* test between the total number of larvae killed by *C. xantholoma* in each treatment type, where 1= all three species together, 3= *C. pilipes*, 5= *D. anilis*, 7= *C. frigida*, 9= *C. frigida* & *C. pilies*, 11= *C. frigida* & *D. anilis*, 13= *C. pilipes* & *D. anilis*.

```
 Individual 95% CIs for mean based on pooled
StDev
Level N  Mean StDev --------+---------+--------
-+---------+-
1   7 4.143 1.215          (------*-----)
3   7 1.571 0.976 (-----*-----)
5   7 4.571 1.397            (-----*-----)
7   7 5.571 2.440              (-----*-----)
9   5 2.600 1.817    (------*------)
11  5 2.400 1.817    (------*------)
13  5 5.400 1.517              (------*------)
              --------+---------+--------+--------
                    2.0     4.0     6.0     8.0
```

Pooled StDev = 1.647

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of treatment/without (w/o) control
Individual confidence level = 99.64%

Treatment/wo control = 1 subtracted from:

Treatment/wo control	Lower	Center	Upper
3	-5.316	-2.571	0.173
5	-2.316	0.429	3.173
7	-1.316	1.429	4.173
9	-4.549	-1.543	1.464
11	-4.749	-1.743	1.264
13	-1.749	1.257	4.264

```
Treatment/wo
control      +---------+---------+---------+--------
-
3             (-------*------)
5                  (-------*-------)
7                    (-------*-------)
9             (--------*-------)
11            (--------*--------)
13                   (--------*-------)
         +---------+---------+---------+---------
       -7.0     -3.5      0.0      3.5
```

Treatment/wo control = 3 subtracted from:

Treatment/wo control	Lower	Center	Upper
5	0.256	3.000	5.744
7	1.256	4.000	6.744
9	-1.978	1.029	4.035
11	-2.178	0.829	3.835
13	0.822	3.829	6.835

```
Treatment/wo
control      +---------+---------+---------+--------
-
5                    (-------*------)
7                      (------*-------)
9                 (--------*--------)
11                (--------*--------)
13                   (--------*--------)
         +---------+---------+---------+---------
       -7.0     -3.5      0.0      3.5
```

Treatment/wo control = 5 subtracted from:

Treatment/wo control	Lower	Center	Upper
7	-1.744	1.000	3.744
9	-4.978	-1.971	1.035
11	-5.178	-2.171	0.835
13	-2.178	0.829	3.835

```
Treatment/wo
control      +---------+---------+---------+--------
-
7                    (-------*-------)
9             (-------*--------)
11            (--------*-------)
13                   (-------*--------)
         +---------+---------+---------+---------
       -7.0     -3.5      0.0      3.5
```

Treatment/wo control = 7 subtracted from:

Treatment/wo control	Lower	Center	Upper
9	-5.978	-2.971	0.035
11	-6.178	-3.171	-0.165
13	-3.178	-0.171	2.835

```
Treatment/wo
control      +---------+---------+---------+--------
-
9             (--------*-------)
11            (--------*--------)
13                   (--------*-------)
         +---------+---------+---------+---------
       -7.0     -3.5      0.0      3.5
```

Treatment/wo control = 9 subtracted from:

Treatment/wo control	Lower	Center	Upper
11	-3.447	-0.200	3.047
13	-0.447	2.800	6.047

```
Treatment/wo
control      +---------+---------+---------+--------
-
11                 (--------*---------)
13                          (--------*--------)
           +---------+---------+---------+---------
         -7.0      -3.5       0.0       3.5
```

Treatment/wo control = 11 subtracted from:

Treatment/wo control	Lower	Center	Upper
13	-0.247	3.000	6.247

```
Treatment/wo
control      +---------+---------+---------+--------
-
13                          (--------*--------)
           +---------+---------+---------+---------
         -7.0      -3.5       0.0       3.5
```

A21 Tukey's (HSD) post-hoc test between the number of total larvae pupating in each treatment with *C. xantholoma*. 1= *C. pilipes*, 2= *C. frigida*, 3= *D. anilis*, 4= *C. pilipes* & *D. anilis*, 5= *C. pilipes* & *C. frigida*, 6= *C. frigida* & *D. anilis*, and 7= all three species.

Individual 95% CIs for mean based on pooled StDev

Level	N	Mean	StDev	------+---------+---------+---------+---
1	7	2.429	1.397	(-----*-----)
2	7	0.714	0.756	(-----*-----)
3	7	0.000	0.000	(-----*-----)
4	5	3.000	2.236	(------*------)
5	5	3.000	1.414	(------*------)
6	5	0.600	0.548	(------*------)
7	7	0.714	0.756	(-----*-----)

```
------+---------+---------+---------+---
      0.0       1.5       3.0       4.5
```

Pooled StDev = 1.152

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of treatment
Individual confidence level = 99.64%

Treatment = 1 subtracted from:

Treatment	Lower	Center	Upper	-------+---------+---------+---------+--
2	-3.634	-1.714	0.206	(-----*------)
3	-4.349	-2.429	-0.508	(-----*-----)
4	-1.532	0.571	2.675	(------*------)
5	-1.532	0.571	2.675	(------*------)
6	-3.932	-1.829	0.275	(------*------)
7	-3.634	-1.714	0.206	(-----*------)

```
-------+---------+---------+---------+--
      -3.0       0.0       3.0       6.0
```

Treatment = 2 subtracted from:

Treatment	Lower	Center	Upper	-------+---------+---------+---------+--
3	-2.634	-0.714	1.206	(------*-----)
4	0.182	2.286	4.389	(------*------)
5	0.182	2.286	4.389	(------*------)
6	-2.218	-0.114	1.989	(------*------)
7	-1.920	0.000	1.920	(-----*-----)

```
-------+---------+---------+---------+--
      -3.0       0.0       3.0       6.0
```

Treatment = 3 subtracted from:

Treatment	Lower	Center	Upper	-------+---------+---------+---------+--
4	0.897	3.000	5.103	(------*------)
5	0.897	3.000	5.103	(------*------)
6	-1.503	0.600	2.703	(------*------)
7	-1.206	0.714	2.634	(-----*------)

```
-------+---------+---------+---------+--
      -3.0       0.0       3.0       6.0
```

```
Treatment = 4 subtracted from:
Treatment  Lower  Center  Upper -------+---------+---------+---------+--
5        -2.272  0.000   2.272        (-------*-------)
6        -4.672  -2.400  -0.128  (-------*-------)
7        -4.389  -2.286  -0.182  (------*------)
                      -------+---------+---------+---------+--
                        -3.0     0.0     3.0     6.0

Treatment = 5 subtracted from:
Treatment  Lower  Center  Upper -------+---------+---------+---------+--
6        -4.672  -2.400  -0.128  (-------*-------)
7        -4.389  -2.286  -0.182  (------*------)
                      -------+---------+---------+---------+--
                        -3.0     0.0     3.0     6.0

Treatment = 6 subtracted from:
Treatment  Lower  Center  Upper -------+---------+---------+---------+--
7        -1.989  0.114   2.218        (------*------)
                      -------+---------+---------+---------+--
                        -3.0     0.0     3.0     6.0
```

A22 Tukey's (HSD) post-hoc test between the number of total larvae pupating in each treatment without C. xantholoma. 1= *C. pilipes*, 2= *C. frigida*, 3= *D. anilis*, 4=*C. pilipes* & *D. anilis*, 5=*C. pilipes* & *C. frigida*, 6=*C. frigida* & *D. anilis*, and 7= all three species.

```
Individual 95% CIs For mean based on pooled StDev
Level  N  Mean  StDev --------+---------+---------+---------+-
1      7 2.714 1.496              (-------*-------)
2      7 2.286 2.812            (-------*-------)
3      7 0.000 0.000 (-------*-------)
4      5 1.600 0.894        (---------*--------)
5      5 2.600 1.673             (--------*---------)
6      5 0.400 0.894  (---------*--------)
7      7 0.714 0.951     (-------*-------)
               --------+---------+---------+---------+-
                  0.0     1.5     3.0     4.5
Pooled StDev = 1.526

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of treatment
Individual confidence level = 99.64%

Treatment = 1 subtracted from:
Treatment  Lower  Center  Upper --------+---------+---------+---------+-
2        -2.973  -0.429  2.116        (--------*-------)
3        -5.259  -2.714  -0.170 (--------*-------)
4        -3.902  -1.114  1.673      (--------*---------)
5        -2.902  -0.114  2.673       (---------*--------)
6        -5.102  -2.314  0.473  (--------*---------)
7        -4.544  -2.000  0.544    (-------*--------)
                      --------+---------+---------+---------+-
                        -3.0     0.0     3.0     6.0

Treatment = 2 subtracted from:
Treatment  Lower  Center  Upper --------+---------+---------+---------+-
3        -4.830  -2.286  0.259   (-------*--------)
4        -3.473  -0.686  2.102      (---------*--------)
5        -2.473  0.314   3.102        (--------*--------)
6        -4.673  -1.886  0.902   (---------*--------)
7        -4.116  -1.571  0.973    (--------*-------)
                      --------+---------+---------+---------+-
                        -3.0     0.0     3.0     6.0
```

```
Treatment = 3 subtracted from:
Treatment  Lower  Center  Upper  --------+---------+---------+---------+-
4        -1.187  1.600   4.387          (--------*---------)
5        -0.187  2.600   5.387            (---------*--------)
6        -2.387  0.400   3.187        (--------*---------)
7        -1.830  0.714   3.259         (-------*--------)
                --------+---------+---------+---------+-
                  -3.0      0.0       3.0       6.0

Treatment = 4 subtracted from:
Treatment  Lower  Center  Upper  --------+---------+---------+---------+-
5        -2.011  1.000   4.011          (---------*---------)
6        -4.211  -1.200  1.811    (---------*---------)
7        -3.673  -0.886  1.902     (--------*--------)
                --------+---------+---------+---------+-
                  -3.0      0.0       3.0       6.0

Treatment = 5 subtracted from:
Treatment  Lower  Center  Upper  --------+---------+---------+---------+-
6        -5.211  -2.200  0.811  (---------*---------)
7        -4.673  -1.886  0.902  (---------*--------)
                --------+---------+---------+---------+-
                  -3.0      0.0       3.0       6.0

Treatment = 6 subtracted from:
Treatment  Lower  Center  Upper  --------+---------+---------+---------+-
7        -2.473  0.314   3.102         (--------*--------)
                --------+---------+---------+---------+-
                  -3.0      0.0       3.0       6.0
```

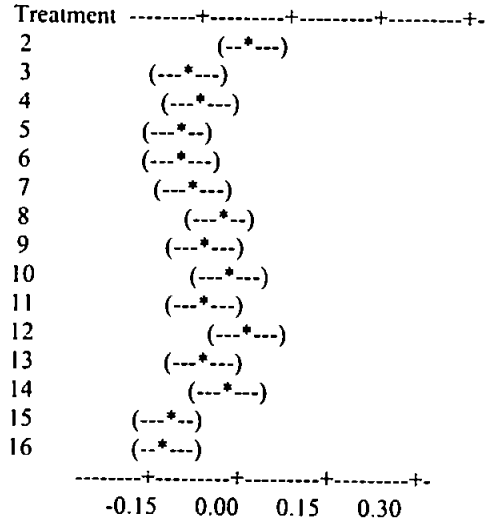
A23 Tukey's (HSD) *post-hoc* test between the actual *L. digitata* mass loss by treatment. 1= all three species, W, 2= All three species W/O, 3= *C. pilipes W*, 4= *C. pilipes W/O* , 5=*C. frigida W* , 6=*C. frigid W/O*, 7= *D. anilis W* 8= *D. anilis W/O*, 9=*C. pilipes* & *D. anilisW*, 10= *C. pilipes* & *D. anilisW/O*, 11=C. *pilipes* & *C. frigidaW*, 12 =C. *pilipes* & *C. frigidaW* /O 13=*C. frigida* & *D. anilis* W, 14= *C. frigida* & *D. anilis* W/O and 15=*C. xanhtoloma* only, 16= no species. Where W= with *C. xantholoma* and W/O=Without *C. xantholoma.*

```
                    Individual 95% CIs for mean based on pooled StDev
Level  N    Mean   StDev  ---+---------+---------+---------+------
1      7  0.11949  0.04364            (--*--)
2      7  0.21672  0.02152                      (--*--)
3      7  0.05865  0.02181       (--*--)
4      7  0.08910  0.02037          (--*--)
5      7  0.03977  0.00997      (--*--)
6      7  0.04497  0.01387      (--*---)
7      7  0.07520  0.02519         (--*--)
8      7  0.14530  0.04986               (--*--)
9      5  0.10148  0.05916          (--*---)
10     5  0.15658  0.03066                (--*---)
11     5  0.08925  0.02466          (---*--)
12     5  0.19041  0.01341                   (--*---)
13     5  0.08596  0.02707          (--*---)
14     5  0.15660  0.02181                (--*---)
15     7  0.00889  0.01431  (--*--)
16     7  0.00201  0.02209  (--*--)
                  ---+---------+---------+---------+----
                     0.000     0.070     0.140     0.210
Pooled StDev = 0.02885
```

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of treatment
Individual confidence level = 99.93%

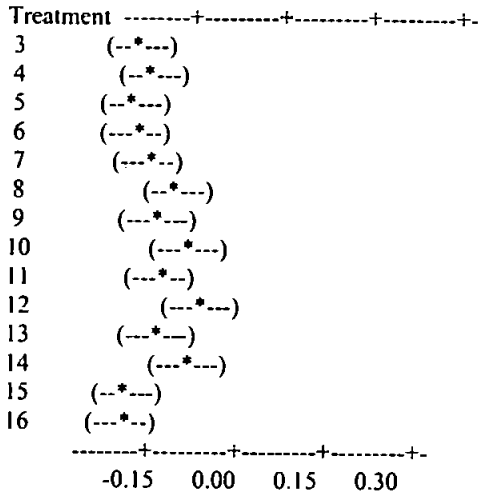
Treatment = 1 subtracted from:

Treatment	Lower	Center	Upper
2	0.04271	0.09723	0.15175
3	-0.11537	-0.06084	-0.00632
4	-0.08492	-0.03040	0.02413
5	-0.13425	-0.07973	-0.02520
6	-0.12904	-0.07452	-0.02000
7	-0.09882	-0.04430	0.01023
8	-0.02872	0.02581	0.08033
9	-0.07775	-0.01802	0.04171
10	-0.02264	0.03709	0.09682
11	-0.08998	-0.03025	0.02948
12	0.01119	0.07092	0.13065
13	-0.09327	-0.03354	0.02619
14	-0.02263	0.03710	0.09683
15	-0.16512	-0.11060	-0.05608
16	-0.17201	-0.11749	-0.06296



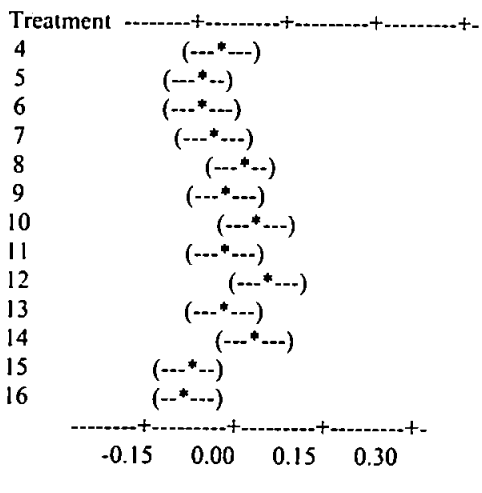
Treatment = 2 subtracted from:

Treatment	Lower	Center	Upper
3	-0.21260	-0.15807	-0.10355
4	-0.18215	-0.12763	-0.07310
5	-0.23148	-0.17696	-0.12243
6	-0.22627	-0.17175	-0.11723
7	-0.19605	-0.14153	-0.08700
8	-0.12595	-0.07142	-0.01690
9	-0.17497	-0.11525	-0.05552
10	-0.11987	-0.06014	-0.00041
11	-0.18721	-0.12748	-0.06775
12	-0.08604	-0.02631	0.03342
13	-0.19050	-0.13077	-0.07104
14	-0.11986	-0.06013	-0.00040
15	-0.26235	-0.20783	-0.15331
16	-0.26924	-0.21472	-0.16019



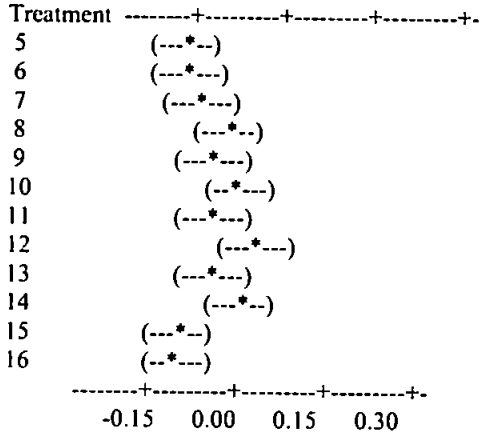
Treatment = 3 subtracted from:

Treatment	Lower	Center	Upper
4	-0.02408	0.03045	0.08497
5	-0.07341	-0.01888	0.03564
6	-0.06820	-0.01368	0.04085
7	-0.03798	0.01655	0.07107
8	0.03213	0.08665	0.14118
9	-0.01690	0.04283	0.10256
10	0.03821	0.09793	0.15766
11	-0.02913	0.03060	0.09032
12	0.07203	0.13176	0.19149
13	-0.03242	0.02731	0.08703
14	0.03822	0.09795	0.15767
15	-0.10428	-0.04976	0.00477
16	-0.11117	-0.05664	-0.00212



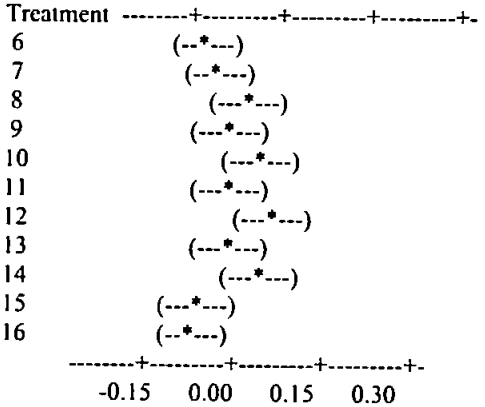
Treatment = 4 subtracted from:

Treatment	Lower	Center	Upper
5	-0.10385	-0.04933	0.00520
6	-0.09865	-0.04412	0.01040
7	-0.06842	-0.01390	0.04063
8	0.00168	0.05621	0.11073
9	-0.04735	0.01238	0.07211
10	0.00776	0.06749	0.12722
11	-0.05958	0.00015	0.05988
12	0.04159	0.10132	0.16104
13	-0.06287	-0.00314	0.05659
14	0.00777	0.06750	0.12723
15	-0.13473	-0.08020	-0.02568
16	-0.14161	-0.08709	-0.03256



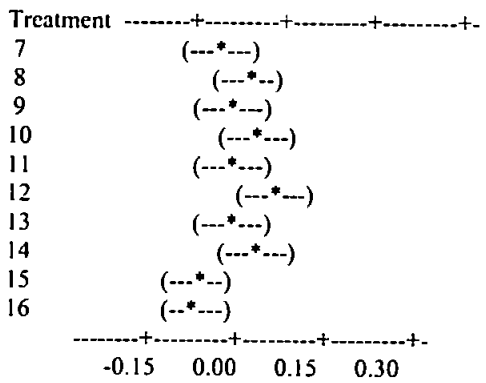
Treatment = 5 subtracted from:

Treatment	Lower	Center	Upper
6	-0.04932	0.00521	0.05973
7	-0.01910	0.03543	0.08995
8	0.05101	0.10553	0.16006
9	0.00198	0.06171	0.12144
10	0.05709	0.11682	0.17654
11	-0.01025	0.04948	0.10921
12	0.09092	0.15064	0.21037
13	-0.01354	0.04619	0.10592
14	0.05710	0.11683	0.17656
15	-0.08540	-0.03087	0.02365
16	-0.09228	-0.03776	0.01676



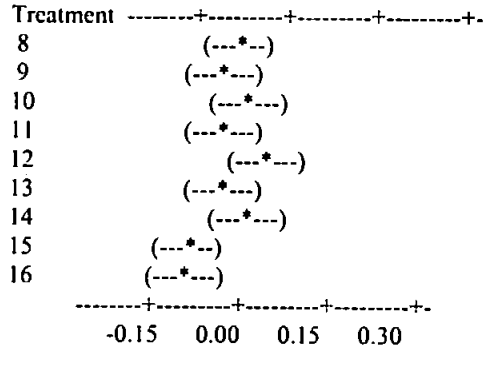
Treatment = 6 subtracted from:

Treatment	Lower	Center	Upper
7	-0.02430	0.03022	0.08475
8	0.04580	0.10033	0.15485
9	-0.00322	0.05650	0.11623
10	0.05188	0.11161	0.17134
11	-0.01546	0.04427	0.10400
12	0.08571	0.14544	0.20517
13	-0.01875	0.04098	0.10071
14	0.05189	0.11162	0.17135
15	-0.09060	-0.03608	0.01844
16	-0.09749	-0.04297	0.01156



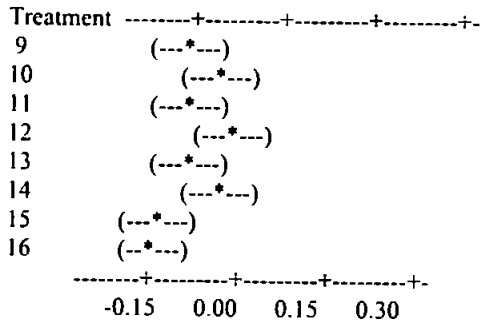
Treatment = 7 subtracted from:

treatment	Lower	Center	Upper
8	0.01558	0.07011	0.12463
9	-0.03345	0.02628	0.08601
10	0.02166	0.08139	0.14112
11	-0.04568	0.01405	0.07378
12	0.05549	0.11522	0.17494
13	-0.04897	0.01076	0.07049
14	0.02167	0.08140	0.14113
15	-0.12083	-0.06630	-0.01178
16	-0.12771	-0.07319	-0.01866



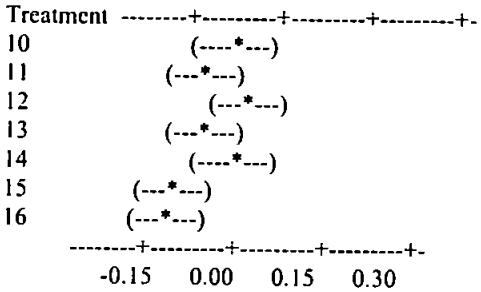
Treatment = 8 subtracted from:

Treatment	Lower	Center	Upper
9	-0.10355	-0.04383	0.01590
10	-0.04845	0.01128	0.07101
11	-0.11579	-0.05606	0.00367
12	-0.01462	0.04511	0.10484
13	-0.11908	-0.05935	0.00038
14	-0.04844	0.01129	0.07102
15	-0.19093	-0.13641	-0.08188
16	-0.19782	-0.14330	-0.08877



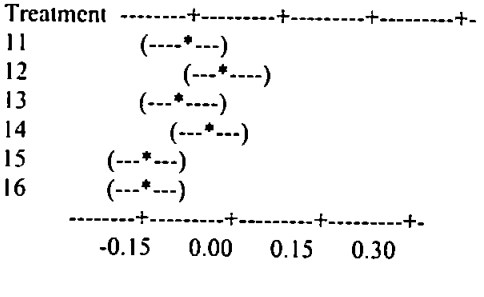
Treatment = 9 subtracted from:

Treatment	Lower	Center	Upper
10	-0.00941	0.05511	0.11962
11	-0.07675	-0.01223	0.05228
12	0.02442	0.08893	0.15345
13	-0.08004	-0.01552	0.04899
14	-0.00940	0.05512	0.11963
15	-0.15231	-0.09258	-0.03286
16	-0.15920	-0.09947	-0.03974



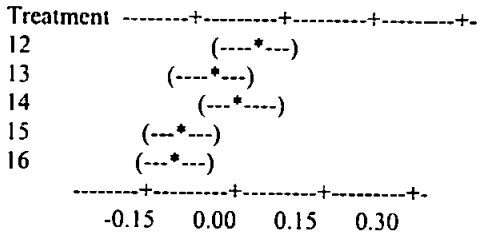
Treatment = 10 subtracted from:

Treatment	Lower	Center	Upper
11	-0.13185	-0.06734	-0.00283
12	-0.03069	0.03383	0.09834
13	-0.13514	-0.07063	-0.00611
14	-0.06450	0.00001	0.06453
15	-0.20742	-0.14769	-0.08796
16	-0.21431	-0.15458	-0.09485



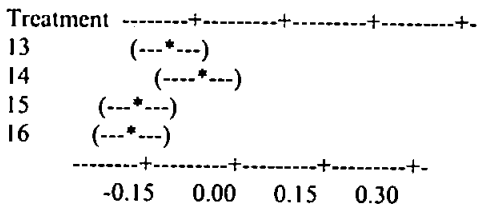
Treatment = 11 subtracted from:

Treatment	Lower	Center	Upper
12	0.03665	0.10117	0.16568
13	-0.06780	-0.00329	0.06122
14	0.00284	0.06735	0.13186
15	-0.14008	-0.08035	-0.02062
16	-0.14697	-0.08724	-0.02751



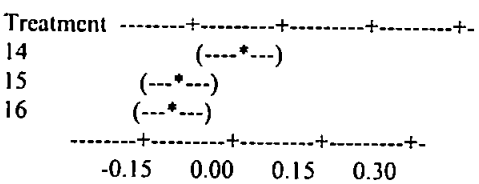
Treatment = 12 subtracted from:

Treatment	Lower	Center	Upper
13	-0.16897	-0.10446	-0.03994
14	-0.09833	-0.03382	0.03070
15	-0.24125	-0.18152	-0.12179
16	-0.24813	-0.18840	-0.12868



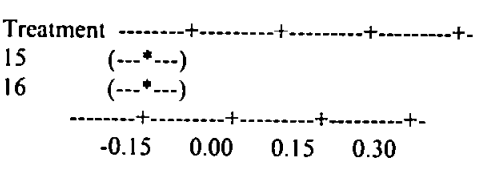
Treatment = 13 subtracted from:

Treatment	Lower	Center	Upper
14	0.00613	0.07064	0.13515
15	-0.13679	-0.07706	-0.01733
16	-0.14368	-0.08395	-0.02422



Treatment = 14 subtracted from:

Treatment	Lower	Center	Upper
15	-0.20743	-0.14770	-0.08797
16	-0.21432	-0.15459	-0.09486



Treatment = 15 subtracted from:
Treatment Lower Center Upper
16 -0.06141 -0.00689 0.04764

Treatment --------+---------+---------+---------+-
16 (---*--)
--------+---------+---------+---------+-
-0.15 0.00 0.15 0.30

A24a Tukey's (HSD) post-hoc test of variability in transformed *L. digitata*/initial larvae mass g by species level (Diversity) without *C. xantholoma*.

Individual 95% CIs for mean based on pooled StDev
Level N Mean StDev ---+---------+---------+---------+------
1 21 0.02181 0.01125 (-*-)
2 15 0.04260 0.01120 (-*--)
3 7 0.09035 0.01538 (---*---)
---+---------+---------+---------+------
0.025 0.050 0.075 0.100
Pooled StDev = 0.01194

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of diversity
Individual confidence level = 98.04%

diversity = 1 subtracted from:
diversity lower center upper -----+---------+---------+---------+----
2 0.01097 0.02079 0.03061 (-*--)
3 0.05586 0.06854 0.08122 (--*--)
-----+---------+---------+---------+----
-0.040 0.000 0.040 0.080

diversity = 2 subtracted from:
diversity lower center upper -----+---------+---------+---------+----
3 0.03446 0.04775 0.06105 (--*--)
-----+---------+---------+---------+----
-0.040 0.000 0.040 0.080

A24b Tukey's (HSD) post-hoc test of variability in *L. ditigata* mass loss g /initial larvae mass g per treatment (larvae identity combination) without *C. xantholoma*. 2= all three species, 4= *C. pilipes*, 6= *D. anilis*, 8= *C. frigida*, 10= *C. pilipes* & *D. anilis*, 12= *C. pilipes* & *C. frigida*, 14= *C. frigida* & *D. anilis*.

Tukey 95% simultaneous confidence intervals
all pairwise comparisons among levels of identity
individual confidence level = 99.64%

identity = 2 subtracted from:
identity lower center upper
4 -0.08710 -0.06954 -0.05199
6 -0.09429 -0.07673 -0.05917
8 -0.07691 -0.05935 -0.04180
10 -0.05963 -0.04040 -0.02117
12 -0.06578 -0.04655 -0.02731
14 -0.07555 -0.05631 -0.03708

identity ----+---------+---------+---------+-----
4 (----*---)
6 (----*---)
8 (---*----)
10 (----*----)
12 (---*----)
14 (----*----)
----+---------+---------+---------+-----
-0.080 -0.040 0.000 0.040

identity = 4 subtracted from:

identity	lower	center	upper	----+---------+---------+---------+-----
6	-0.02474	-0.00719	0.01037	(---*----)
8	-0.00737	0.01019	0.02774	(----*---)
10	0.00991	0.02914	0.04837	(----*----)
12	0.00377	0.02300	0.04223	(----*----)
14	-0.00600	0.01323	0.03246	(----*----)

----+---------+---------+---------+-----
-0.080 -0.040 0.000 0.040

identity = 6 subtracted from:

identity	lower	center	upper	----+---------+---------+---------+-----
8	-0.00018	0.01738	0.03493	(---*----)
10	0.01710	0.03633	0.05556	(----*----)
12	0.01095	0.03019	0.04942	(----*---)
14	0.00119	0.02042	0.03965	(----*----)

----+---------+---------+---------+-----
-0.080 -0.040 0.000 0.040

identity = 8 subtracted from:

identity	lower	center	upper	----+---------+---------+---------+-----
10	-0.00028	0.01895	0.03819	(----*----)
12	-0.00642	0.01281	0.03204	(----*----)
14	-0.01619	0.00304	0.02227	(----*----)

----+---------+---------+---------+-----
-0.080 -0.040 0.000 0.040

identity = 10 subtracted from:

identity	lower	center	upper	----+---------+---------+---------+-----
12	-0.02692	-0.00614	0.01463	(----*-----)
14	-0.03669	-0.01591	0.00486	(----*----)

----+---------+---------+---------+-----
-0.080 -0.040 0.000 0.040

identity = 12 subtracted from:

identity	lower	center	upper	----+---------+---------+---------+-----
14	-0.03054	-0.00977	0.01100	(-----*----)

----+---------+---------+---------+-----
-0.080 -0.040 0.000 0.040

A25 Tukey's (HSD) post-hoc test of variability in *L. digitata* mass loss g/final larvae mass loss g by species level (Diversity) without *C. xantholoma*.

Individual 95% CIs for mean based on pooled StDev

Level	N	Mean	StDev	-+---------+---------+---------+--------
1	21	0.03320	0.02582	(---*---)
2	15	0.05251	0.02242	(----*----)
3	7	0.10190	0.03122	(-------*-------)

-+---------+---------+---------+--------
0.025 0.050 0.075 0.100

Pooled StDev = 0.02560

Tukey 95% simultaneous confidence intervals
all pairwise comparisons among levels of diversity
individual confidence level = 98.04%

diversity = 1 subtracted from:

diversity	lower	center	upper	------+---------+---------+---------+---
2	-0.00174	0.01931	0.04036	(---*---)
3	0.04153	0.06871	0.09588	(-----*----)

------+---------+---------+---------+---
-0.050 0.000 0.050 0.100

```
diversity = 2 subtracted from:
diversity  lower  center  upper ------+---------+---------+---------+---
3        0.02089 0.04939 0.07790              (-----*-----)
                        ------+---------+---------+---------+---
                          -0.050    0.000    0.05
```

A26a Tukey's (HSD) post-hoc test of variability in *L. digitata* mass loss g/mean larvae mass loss g by species level (Diversity) without *C. xantholoma*.

```
                    Individual 95% CIs for mean based on pooled StDev
Level  N    Mean   StDev ---+---------+---------+---------+------
1     21 0.02367 0.01053 (-*--)
2     15 0.04622 0.01381        (-*--)
3      7 0.09546 0.02179                  (---*---)
                   ---+---------+---------+---------+------
                    0.025    0.050    0.075    0.100
Pooled StDev = 0.01391

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of diversity
Individual confidence level = 98.04%

diversity = 1 subtracted from:
diversity  lower  center  upper ------+---------+---------+---------+---
2        0.01111 0.02254 0.03398             (--*-)
3        0.05702 0.07179 0.08656                    (---*---)
                        ------+---------+---------+---------+---
                          -0.040    0.000    0.040    0.080

diversity = 2 subtracted from:
diversity  lower  center  Upper ------+---------+---------+---------+---
3        0.03376 0.04924 0.06473                  (---*---)
                        ------+---------+---------+---------+---
                          -0.040    0.000    0.040    0.080
```

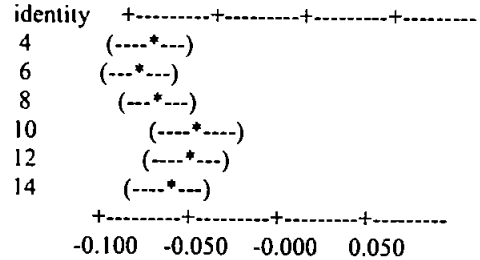
A26b Tukey's (HSD) post-hoc test of variability in *L. digitata* mass loss g/mean larvae mass loss g by treatment (larvae identity combination) without *C. xantholoma*.
Where 2= all three species, 4= *C. pilipes*, 6= *D. anilis*, 8= *C. frigida*, 10= *C. pilipes* & *D. anilis*, 12= *C. pilipes* & *C. frigida*, 14= *C. frigida* & *D. anilis*.

```
                    Individual 95% CIs for mean based on pooled StDev
Level  N    Mean   StDev -------+---------+---------+---------+--
2      7 0.09546 0.02179                    (---*---)
4      7 0.02358 0.00602   (--*---)
6      7 0.01598 0.00559 (--*---)
8      7 0.03146 0.01275     (---*--)
10     5 0.05539 0.01775          (---*----)
12     5 0.04862 0.00631         (---*----)
14     5 0.03464 0.00577     (----*---)
                   -------+---------+---------+---------+--
                    0.025    0.050    0.075    0.100
Pooled StDev = 0.01267
```

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of identity
individual confidence level = 99.64%

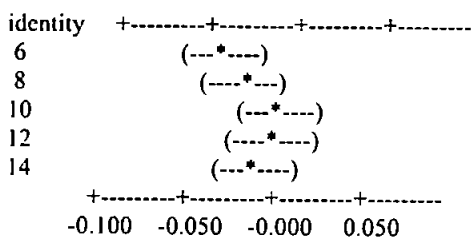
identity = 2 subtracted from:

identity	lower	center	upper
4	-0.09300	-0.07188	-0.05075
6	-0.10061	-0.07948	-0.05836
8	-0.08513	-0.06400	-0.04288
10	-0.06322	-0.04008	-0.01694
12	-0.06998	-0.04684	-0.02370
14	-0.08396	-0.06082	-0.03768



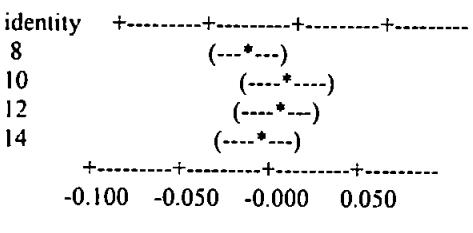
identity = 4 subtracted from:

identity	lower	center	upper
6	-0.02873	-0.00761	0.01352
8	-0.01325	0.00787	0.02900
10	0.00866	0.03180	0.05494
12	0.00190	0.02504	0.04818
14	-0.01208	0.01106	0.03420



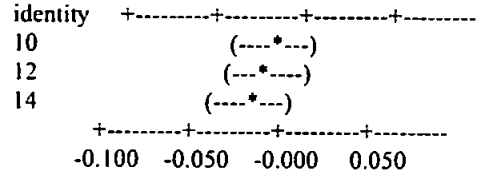
identity = 6 subtracted from:

identity	lower	center	upper
8	-0.00564	0.01548	0.03660
10	0.01627	0.03941	0.06255
12	0.00950	0.03264	0.05579
14	-0.00448	0.01866	0.04180



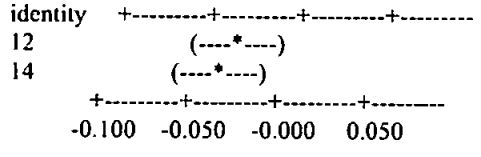
identity = 8 subtracted from:

identity	lower	center	upper
10	0.00079	0.02393	0.04707
12	-0.00597	0.01717	0.04031
14	-0.01996	0.00318	0.02632



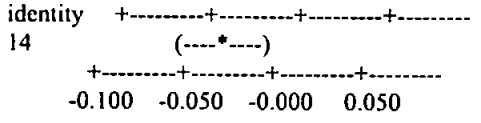
identity = 10 subtracted from:

identity	lower	center	upper
12	-0.03176	-0.00676	0.01823
14	-0.04574	-0.02074	0.00425



identity = 12 subtracted from:

identity	lower	center	upper
14	-0.03898	-0.01398	0.01101



A27 Tukey's (HSD) post-hoc test of variability in log10*L. digitata* mass loss g/initial larvae mass loss g by species level (Diversity) with *C. xantholoma*.

```
Individual 95% CIs for mean based on pooled StDev
Level  N    Mean  StDev ---+---------+---------+---------+------
1     21 -4.4707 0.3578 (---*--)
2     15 -3.9979 0.5100       (---*---)
3      7 -3.3514 0.4097              (------*-----)
                  ---+---------+---------+---------+------
                  -4.50    -4.00    -3.50    -3.00
Pooled StDev = 0.4245

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of diversity
Individual confidence level = 98.04%

diversity = 1 subtracted from:
diversity  lower center  upper ------+---------+---------+---------+---
2         0.1237 0.4728 0.8219             (----*----)
3         0.6686 1.1193 1.5700                   (-----*-----)
                      ------+---------+---------+---------+---
                       -0.70     0.00     0.70     1.40

diversity = 2 subtracted from:
diversity  lower center  upper ------+---------+---------+---------+---
3         0.1739 0.6465 1.1192             (------*------)
                      ------+---------+---------+---------+---
                       -0.70     0.00     0.70     1.40
```

A28 Tukey's (HSD) post-hoc test of variability in *L. digitata* mass loss g/final larvae mass loss g by species level (Diversity) with *C. xantholoma*.

```
                    Individual 95% CIs for mean based on pooled StDev
Level  N    Mean  StDev  -+---------+---------+---------+--------
1     21 0.03104 0.03703  (------*-----)
2     15 0.03821 0.01899    (-------*-------)
3      7 0.06645 0.02082           (----------*----------)
                  -+---------+---------+---------+--------
                  0.020    0.040    0.060    0.080
Pooled StDev = 0.02961

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of diversity
individual confidence level = 98.04%

diversity = 1 subtracted from:
diversity   lower  center  upper -------+---------+---------+---------+--
2        -0.01717 0.00718 0.03153          (------*------)
3         0.00397 0.03541 0.06685              (--------*--------)
                       -------+---------+---------+---------+--
                            -0.035    0.000    0.035    0.070

diversity = 2 subtracted from:
diversity   lower  center  upper -------+---------+---------+---------+--
3        -0.00474 0.02823 0.06121            (--------*--------)
                       -------+---------+---------+---------+--
                            -0.035    0.000    0.035    0.070
```

A29 Tukey's (HSD) post-hoc test of variability in log10*L. digitata* mass loss g/mean larvae mass loss g by species level (Diversity) with *C. xantholoma*.

```
                    Individual 95% CIs for mean based on pooled StDev
Level  N    Mean  StDev --------+---------+---------+---------+-
1     21 -4.2429 0.3525 (--*---)
2     15 -3.7489 0.4481       (---*---)
3      7 -3.1049 0.3797              (-----*-----)
                  --------+---------+---------+---------+-
                    -4.00    -3.50    -3.00    -2.50
Pooled StDev = 0.3925

Tukey 95% simultaneous confidence intervals
All pairwise comparisons among levels of diversity
individual confidence level = 98.04%

diversity = 1 subtracted from:
diversity  lower  center  upper -----+---------+---------+---------+----
2         0.1713  0.4940  0.8168           (----*----)
3         0.7214  1.1380  1.5547                (-----*-----)
                  -----+---------+---------+---------+----
                    -0.70     0.00     0.70     1.40

diversity = 2 subtracted from:
diversity  lower  center  upper -----+---------+---------+---------+----
3         0.2070  0.6440  1.0810           (-----*-----)
                  -----+---------+---------+---------+----
                    -0.70     0.00     0.70     1.40
```