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Will warming affect food web structure?

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WILL WARMING AFFECT FOOD WEB STRUCTURE?

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“If you ask a stupid question Tom, you’ll get an equally stupid answer…”

My Dad, (pers. comm. Circa 1985)

SUMMARY

The question is: Will warming affect food web structure? The rationale for asking this question comes from theories and laboratory observations that predict warming to decrease the quantity of producer relative to consumer biomass because rates of consumption increase more rapidly with warming than do rates of production. However, in natural ecosystems this is seldom observed. To explain this dichotomy, I posit the hypothesis that organisms adapt to their environment in many ways, and over various timescales such that the way in which individuals respond to temperature is contextual and dependent upon many other variables. Beginning with the contextual effects on the individuals themselves, in Chapters 2 and 3 I conduct laboratory experiments to investigate the effects of warming upon individual level rates of production and consumption and I then investigate how those individual level effects of warming govern the ratio of producer to consumer biomass. These experiments demonstrate that the initial ratio of consumer to producer body size is more important than temperature in determining change in the ratio of consumer to producer biomass. I then conduct field observations of the rocky shore community to investigate which key processes determine the ratio of consumer to producer biomass in this natural ecosystem. In Chapter 4, I observe that wave exposure affects the causal link between producer and consumer biomass, but also that producers and consumers respond to wave exposure in different, and apparently weakly connected ways. In Chapter 5, I observe that heterogeneity in the biomass of producers within communities is key in determining producer species richness and that the interaction between these two variables determines the abundance and group richness of consumers. Overall therefore, the results indicate that variation in individual attributes, and variation in individual responses to their environment and each other, are key in determining both community structure and whether it will be affected by warming. Thus the answer to the question is: I doubt it.

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CHAPTER 1: INTRODUCTION

Within the next century, the mean surface temperature of the earth is expected to rise by up to 4°C (Thuiller, 2007). This is expected to have far-reaching effects on the earth's climatic systems, causing increases in the frequency and intensity of droughts, storms, and El Nino events (IPCC, 2014). These climatic changes are expected to alter physical environments, with increases in sea level and the frequency and intensity of floods and wild fires (Walther *et al.,* 2002). All aspects of the biosphere are expected to be affected by rising global temperatures, both directly, as a consequence of warming having direct effects upon organisms, and indirectly, as a consequence of climate change having other physical consequences (for review see Gitay *et al.,* 2002, Leemans & Eikhout, 2004, Bellard *et al.,* 2012). Despite these direct and indirect effects occurring simultaneously, the primary focus of this thesis is upon only the direct effects that rising temperatures have upon organisms.

To date, rising global temperatures have directly caused organisms to respond in three ways, branded as "*universal*" due to their ubiquity across the biosphere (Parmesan, 2006):

a) In response to warming decreasing the duration and intensity of winters, the phenology of species has shifted with earlier onset of events such as bud break in trees, flowering in plants (Parmesan, 2007, deValpine & Harte, 2001), reproduction by zooplankton etc (Penuelas, 2001).
b) In response to warming increasing temperatures at higher latitudes, a pole-ward shift in the range distributions of species has occurred (Parmesan, 1999, Mieszkowska *et al.,* 2006).
c) In response to warming increasing the metabolic rates of ectotherms, the body size of individual ectotherms has decreased (Daufresne *et al.,* 2009, Gardner *et al.,* 2011, Sheridan, 2011).

Whilst general to the biosphere, these observed responses to warming are specific to the species or individuals observed and offer little insight into how warming affects systems of interacting organisms. In efforts to improve upon this, an array of laboratory studies (Petchey *et al.,* 1999, O'Connor *et al.,* 2009, O'Connor *et al.,* 2011, Kratina *et al.,* 2012, Shurin *et al.,* 2012, Seifert *et al.,* 2014) investigating the effects of warming upon trophic interactions has been conducted over the last decade or so and this has contributed to an emerging paradigm: Warming causes rates of consumption by higher trophic levels to outstrip rates of production by lower trophic levels and this causes the quantity of consumer biomass relative to the quantity of producer biomass to change. This theory however leads to a dichotomy. This is because whilst the theory has been developed and experimentally substantiated in laboratories, it has yet to be substantiated by broad-scale observations of nature in reality, with to my knowledge, only two reports of shifts in food web structure linked to warming (Schiel *et al.,* 2004, Möllman *et al.,* 2008). How our understanding has arrived in this situation is thus the question I set out to answer in this thesis.

In this introduction, I will expose the key issues surrounding this topic and crystalize those into two key lines of enquiry. This is achieved by first examining the theoretical foundations of how warming affects community structure and then discussing the laboratory studies that have supported this theory in relation to the universal effects of warming that are actually observed.

1.1 THEORETICAL FOUNDATIONS OF HOW WARMING AFFECTS ORGANISMS.

In 2004, the metabolic theory of ecology (MTE) (Brown *et al.,* 2004) built upon previous dynamic energy budget theories (Nisbet et al., 2000) to seemingly explain all of ecology as a purely mechanistic outcome of temperature (Van Der Meer, 2006, Kooijman 2009). This was achieved by explaining the metabolic rate of all individual organisms as being determined by the relationship between an individual's body size and the temperature at which it lives (Brown *et al.,* 2004). Due to the ubiquity of this relationship across all organisms, the theory was described by a single equation (Equation 1) where I is individual metabolic rate, i_0 a normalisation constant, M individual body mass and $e^{-E/kT}$ the Boltzmann factor in which e is the natural exponent, E the activation energy of metabolic processes and kT the temperature of the environment in degrees Kelvin.

$$I = i_0 M^{\frac{3}{4}} e^{-E/kT}$$

Equation 1.1

In this equation, only the normalisation constant, i_0 is species-specific, and the parameters describing the effects of body size upon metabolic rate ($M^{3/4}$), and temperature upon metabolic rate ($e^{-E/kt}$), are general to all organisms. This equation also states that the relationship between temperature and body size is multiplicative in determining the metabolic rate of all organisms (Clarke, 2006). The precision of these relationships has been extensively questioned (Kozlowski & Konarzewski, 2005, O'Connor *et al.,* 2007, delRio, 2008, Price et al., 2012) although the general theory, that temperature and body size interact to govern metabolic rate forms the basis of predictions regarding how warming will affect food web structure (O'Connor *et al.,* 2009).

1.1.1 EFFECTS OF TEMPERATURE UPON METABOLIC RATE.

The Boltzmann factor, ($e^{-E/kt}$) (Boltzmann, 1884), describes the effect of temperature t, upon the rate of all chemical reactions. If all other parameters in the Boltzman factor remain constant, then increases in temperature cause exponential increase in the rate of chemical reactions (Boltzmann, 1884). The normalisation constant, i_0, is incorporated into the metabolic theory of ecology to standardise the differences in chemistry between species (Brown *et al.,* 2004). This has the effect of causing all parameters of the Boltzmann factor to be normalised across different species such that the effects of temperature upon the rates of chemical reactions within an individual are the same for all species (Gillooly *et al.,* 2001). Metabolic theory also assumes that the metabolic rate of an individual is equal to the rate of all chemical reactions occurring within the individual. This enables the Boltzman factor to explicitly describe the effects of temperature upon individual metabolic rate. When fitted to data, this model describes the effects of temperature upon metabolic rate with ubiquity across both unicellular and multicellular organisms, encompassing both heterotrophs and autotrophs, and ectotherms and endotherms (Gillooly *et al.,* 2001, Brown *et al.,* 2004). In all cases, individual metabolic rate is observed to increase exponentially with temperature (figure 1.1) (Gillooly *et al.,* 2001).

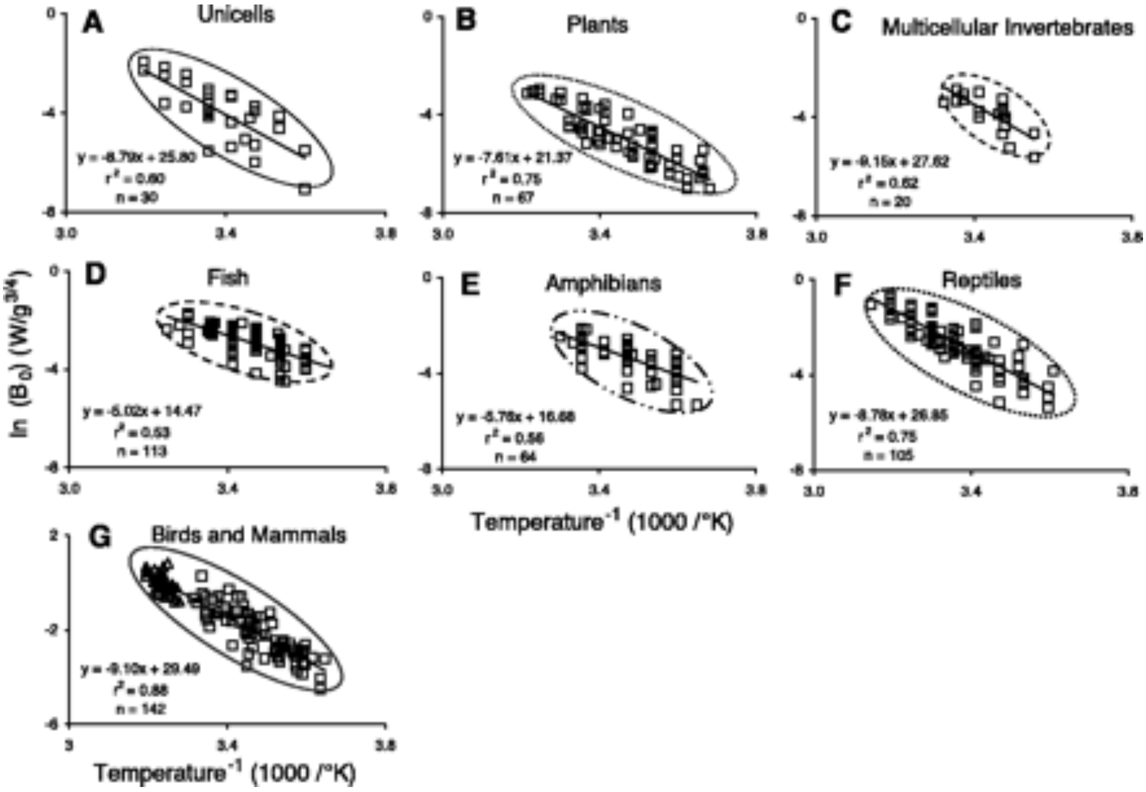


Figure 1.1 Relationships between temperature and mass-corrected metabolic rate (Giloolly *et al.,* 2001). Temperature has ubiquitous effects upon the mass-corrected metabolic rates (expressed as Watts per gram) of a diverse range of taxa, from unicellular organisms (top left) to plants (top middle), multicellular invertebrates (top right) and birds and mammals (bottom left). For each taxa the relationship is described by a linear model. This means that any variation between taxa, which is explained by differences in chemistry, can be accounted for by incorporating a normalisation constant.

1.1.2 EFFECTS OF BODY SIZE UPON METABOLIC RATE

Individual metabolic rate increases exponentially with body size but with an exponent that is less than one (Kleiber, 1947). This means that whilst individual metabolic rate increases with body size, the mass-specific metabolic rate of individuals decreases (Anderso-Teixeiras *et al.,* 2001, Savage *et al.,* 2004, Isaac & Carbone, 2010). Although various exponents of less than 1 have been hypothesised to describe the effects of body size upon individual metabolic rate (Agutter & Wheatley, 2004), it is now generally accepted that an exponent of 3/4 is ubiquitous to all organisms (figure 1.2) (West *et al.,* 2003, Savage *et al.,* 2004, Riveros & Enquist, 2010). The explanation for this is that the anatomy of all individual organisms is essentially a network that distributes resources to the tissues where they are metabolised (West *et al.,* 1999, West *et al.,* 2002). Because the branching of these networks distributes resources optimally over time within a three-dimensional space, they are described using fractal geometry and this method offers a mechanistic explanation for ¾ scaling (West *et al.,* 1999). Metabolic theory, by assuming that this optimisation of the internal resource distribution network is common to all organisms, incorporates the ¾ exponent to describe the effects of body size upon metabolic rate (Brown *et al.,* 2004).

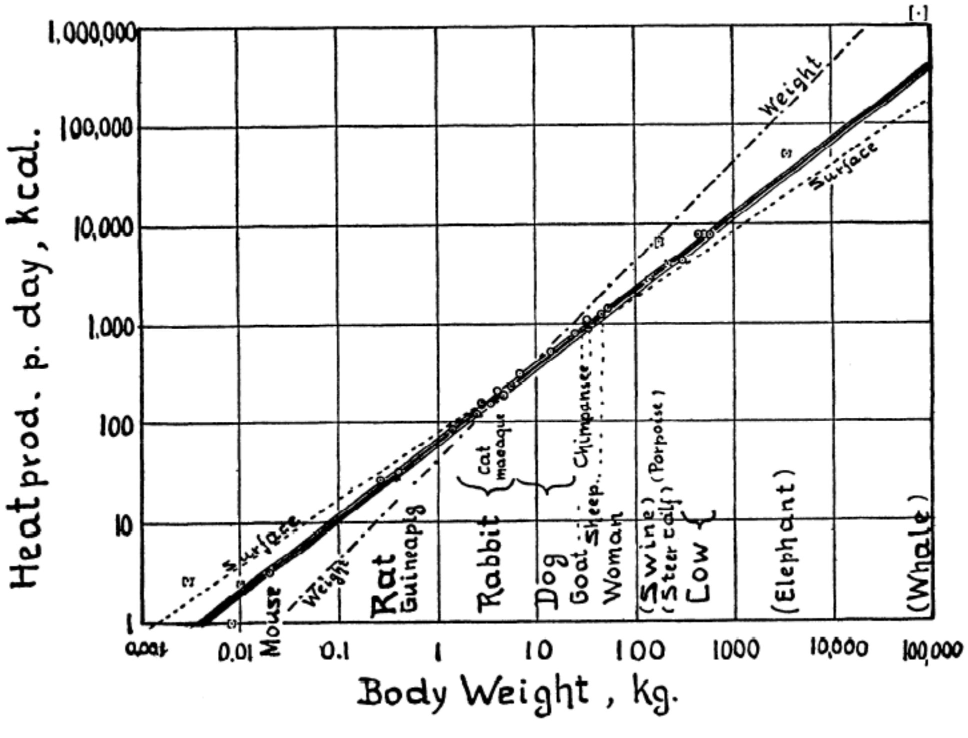


Figure 1.2 Relationship between body size and metabolic rate for mammals, from mice to whales (Kleiber, 1947). The slope of 3/4 indicates that mass-specific metabolic rate declines with increasing body size. At the time of publication, this exponent of ¾ could not be mechanistically explained. Instead, an exponent of 2/3 was expected because it was hypothesised that metabolic rate scaled according to the ratio between individual surface area and volume as per Euclidian geometry. However, a contemporary explanation for ¾ scaling is provided by West *et al.,* (1999). This explanation describes an individual as a branching resource distribution network, optimised according to fractal geometry.

1.1.3 THE RELATIONSHIP BETWEEN BODY SIZE AND TEMPERATURE IN DETERMINING METABOLIC RATE

The effects of temperature and body size are multiplicative in determining individual metabolic rate (Robinson *et al.,* 1983). This means that despite increases in temperature, the metabolic rate of an individual can remain constant provided there is a reduction in body size (Brown *et al.,* 2004). Individual body size can therefore be described as being determined by the product of the individual's metabolic rate and the temperature at which it lives by re-arrangement and simplification of equation 1:

$$M^{\frac{3}{4}} \propto \frac{I}{e^{-E/kT}}$$

Equation 1.2

Expressing individual body size in this way demonstrates that when temperature increases but individual metabolic rate does not, individual body size decreases. However, because the relationship between temperature and individual metabolic rate scales with body size according to a ¾ exponent (West *et al.,* 1999, West *et al.,* 2002), a decrease in individual body size corresponds with an increase in the mass-specific metabolic rate of individuals (Brown *et al.,* 2004, Gillooly *et al.,* 2001). This has important ramifications because it means that in response to changes in temperature, the body size, overall metabolic rate, and mass-specific metabolic rate of individuals change non-linearly with respect to each other (Ohlberger, 2013). In theory therefore, changes in temperature can elicit either large changes in body size that correspond to small changes in individual metabolic rate or reciprocally, large changes in individual metabolic rate that correspond with little change in body size (Brown *et al.,* 2004). This mechanism explains one of the universal responses to warming: The decrease in ectotherm body size (Gardner *et al.,* 2009). Here, it is hypothesised that increases in temperature do not drive increases in individual metabolic rate because resource availability does not increase and therefore metabolism is constrained by resource supply (Brown *et al.,* 2004). This has the effect of driving a decrease in individual body size, which is realised as an adaptive response by a species over multiple generations (Parmesan, 2006). As a consequence of individual metabolic rate being constrained by resource supply, and individual body size thereby decreasing in response to warming, the mass-specific metabolic rate of each individual increases (Gillooly *et al.,* 2001).

1.1.4 THE RELATIONSHIP BETWEEN METABOLIC RATE, CONSUMPTION AND GROWTH

The total metabolic rate of an individual represents both the rate at which molecules are broken down to release energy (catabolism) and the rate at which new molecules are constructed (anabolism) (Van der Meer, 2006). Within every cell of every individual organism, the catabolic break down of molecules releases energy that is in part lost as heat but mainly used to synthesise the molecule adenosine triphosphate (ATP) (Russell & Cook, 1995). ATP is then distributed within cells to structures and tissues in need of repair, where ATP is broken down and the energy released used in cell maintenance. When the maintenance requirements of cells are low, and the supply of molecules for catabolic metabolism high, surplus ATP may be produced. In this instance the energy released from the break down of ATP is used to synthesise molecules in anabolism and it is these molecules that constitute individual growth (Pospispilova, 2003).

In autotrophs, glucose is synthesised by photosynthesis and this molecule is then used for catabolism (Pospispilova, 2003). In heterotrophs, molecules for catabolism are supplied by the consumption of food (Russell & Cook, 1995). Despite this difference, the rate of catabolism for both groups is dependent upon the availability, and the rate of consumption, of resources. In both groups, the rate of individual growth is then determined by the maintenance demands of the individual, because only the residual proportion of catabolism is available to anabolic growth (Brown *et al.,* 2004).

1.1.4.1 WARMING DECREASES GROWTH RELATIVE TO CONSUMPTION

All chemical reactions within an individual organism increase with temperature, both those that are beneficial to the organism and those that are not (Gillooly *et al.,* 2001). As a consequence of detrimental chemical reactions cellular structures and tissues are damaged, and therefore increases in temperature cause the maintenance demands of an individual to increase. Because of this, a greater proportion of catabolic energy is allocated to maintenance as opposed to growth such that if the catabolic rate remains constant, the portion of energy available to anabolism diminishes (Angiletta *et al.,* 2004). Thus relative to the rate with which resources are consumed, the growth rate of individuals decreases with warming.

1.1.4.2 WARMING DECREASES BODY SIZE RELATIVE TO CONSUMPTION

In homeotherms, animals that maintain a constant body temperature, catabolic demands are imposed when the ambient temperature deviates from the individual's body temperature. This is because energetic costs are incurred by the homeostatic mechanisms that enable heat to be both gained from, and lost to, the environment. As a consequence of this, the relationship between ambient temperature, metabolic rate and body size in homeotherms is dependent on the precise metabolic costs of thermoregulation, with warming actually decreasing the catabolic demands of homeotherms when ambient temperature is below body temperature (Peters, 1986). However, in poikilotherms, which are animals whose body temperature fluctuates according to the ambient temperature, no metabolic costs are associated with thermoregulation and therefore a simpler relationship between ambient temperature, metabolic rate and body size exists. It is with specific reference to poikilotherms that this is introduced:

As individuals increase in body size, the quantity of biomass demanding maintenance increases. This means that if the rate with which resources are consumed does not increase, the proportion of catabolic energy available to anabolism will diminish, and the individual growth rate will decrease. The maximum body size of an individual is therefore attained when catabolic energy available to anabolism diminishes to zero, and this occurs at the body size where the rate at which resources are consumed equates to the maintenance costs of the individual (Angiletta *et al.,* 2004). Because these individual maintenance costs increase with temperature, the maximum body size of individuals relative to the rate at which resources are consumed decreases with warming (Brown *et al.,* 2004).

1.1.5 ELTON'S RULE AND THE TROPHIC PYRAMID

Elton's rule is that a "pyramid of numbers" exists in ecosystems with the abundance of organisms decreasing as trophic level increases (Elton 1927) (figure 1.3). This rule is explained by the efficiency with which energy is transferred between trophic levels: Of the energy captured by autotrophs, some is lost as heat, some is allocated to maintenance and the remainder is allocated to anabolic growth. That productivity is consumed by herbivores and in turn is catabolised, with a proportion lost as heat, some allocated to maintenance and the remainder apportioned to growth. In turn this herbivore biomass is the food resource of higher trophic consumers (Jennings & Mackinson, 2003). As a general rule, an average 10% of the energy contained in the biomass of one trophic level is incorporated as biomass in the subsequent level, although much variation exists around this mean (for example see Pauly & Christensen, 1995) (figure 1.4)

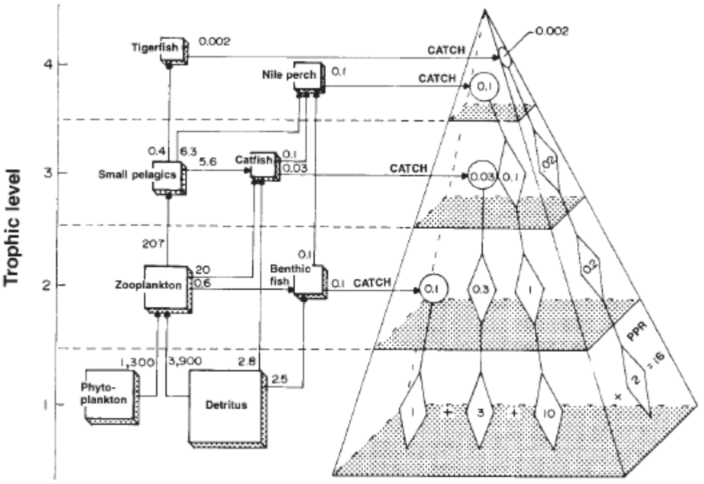


Figure 1.3 Diagrammatic representation of an energy pyramid, characteristic of all food webs (Pauly & Christensen, 1995). Due to the transfer of energy between trophic levels being less than 100%, the proportion of energy available to each successive level becomes exponentially smaller. The maximum number of trophic levels is thus determined by both the quantity of energy in the bottom trophic level, and the efficiency with which energy is transferred between levels.

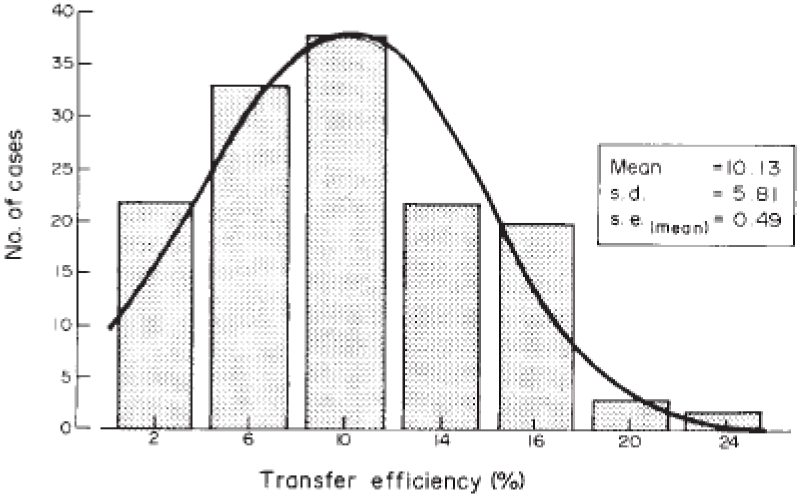


Figure 1.4 Frequency distribution of energy transfer efficiencies (Pauly and Christensen, 1995). 140 transfer efficiencies were estimated for aquatic systems spanning 48 trophic models. This demonstrated that great variation exists in transfer efficiencies. However, the mean transfer efficiency is consistently close to 10%, and therefore the general transfer efficiency of ecosystems is expected to be around 10%.

1.1.5.1 THE EFFECT OF WARMING ON ELTON'S LAW

Elton's law describes a pattern observed in natural ecosystems that are at stable equilibrium. This means that it describes the pattern in food web structure that is observed when the relative biomass of each trophic level is constant (Begon *et al.,* 2006). The process that explains the pattern of Elton's law is the exponential decline in the quantity of energy that is transferred from one trophic level to the next, and by affecting this process, warming is expected to affect the resulting pattern in biomass that is observed (Jennings & Mackinson, 2003).

Warming affects the process of energy transfer between trophic levels because it increases the catabolic demands of individuals. This means that relative to the rate at which resources are consumed, the growth rate and maximum body size of individuals is lower (Petchey *et al.,* 2007) and therefore a smaller proportion of the energy consumed by one trophic level is allocated to anabolism. This means that relative to the biomass of a consumer, the rate at which resources are consumed must increase, and therefore this represents a decrease in the transfer efficiency of energy (Brown *et al.,* 2004). This is predicted to affect the pattern in food web structure described by Elton's law (Petchey *et al.,* 1999) because a decrease in the energy transfer efficiency between each trophic level accentuates the rate at which the biomass of successive trophic levels diminishes (Petchey *et al.,* 2007). Thus warming is expected to have a general effect upon the pattern of food web structure: Relative to their food resource, the biomass of consumers is expected to decrease with warming (O'Connor *et al.,* 2009) and this also leads to another general prediction of how warming will affect the underlying process of food web structure: Relative to consumer biomass, the rate of consumption is expected to increase with warming (Brown et al., 2004).

1.1.5.2 Pinning down predictions with consumer biomass as a point of reference

Predictions of how warming will affect both the process and pattern of food web structure are made in relation to consumer biomass. This means that in order for patterns and processes to be linked in this thesis, those predictions must be standardised according to consumer biomass. I achieve this by crystalizing the two predictions into a single key concept that is specific to consumer biomass and general throughout food webs. The rate of consumption relative to consumer biomass is equal to the mass specific consumption rate (Savage *et al.,* 2004) and therefore the first prediction, that warming will drive an increase in consumption relative to consumer biomass can be generalised as: *Warming will cause the mass specific consumption rate to increase.* Regarding the second prediction, that warming will cause the biomass of consumers to decrease relative to their food resource, this can be rephrased. Firstly, the food resource can be generally termed as "producer biomass" because it is the anabolic production by one trophic level that constitutes the food resource of a subsequent trophic level. Thus the prediction is clarified: Warming causes consumer biomass to decrease relative to producer biomass. This prediction can now be generalised with regard to consumer biomass as a point of reference, by describing the ratio between consumer and producer biomass. In doing so, it is predicted that warming will cause the ratio of consumer to producer biomass to decrease. Thus the two predictions can now be coupled into a key theory: *Warming increases the mass specific consumption rate and thereby drives decrease in the ratio of consumer to producer biomass.*

1.2 EMPIRICAL OBSERVATION OF WARMING INDUCED SHIFTS IN FOOD WEB STRUCTURE

Empirical observations of warming driven shifts in food web structure are largely limited to laboratory observations. The earliest of these was reported by Petchey *et al.* (1999), who observed that in microbial food webs, warming increased the probability of extinction for organisms at higher trophic levels. This was because the trophic pyramid described by Elton's law was accentuated by warming in their model food webs, causing populations of microbes at the highest trophic levels to be diminished to extinction (Petchey *et al.* 1999). Thus in accordance with the prediction of how warming affects the pattern of food webs, the ratio of consumer relative to producer biomass was observed to decrease. From this result, it was inferred that the mechanism driving this change in the trophic pyramid was an increase in the rates of consumption relative to biomass at each trophic level. Subsequent studies, involving organisms and model food webs of varying complexity have offered deeper insight into the mechanisms that cause warming to drive shifts in food web structure.

1.2.1 MECHANISTIC INSIGHT FROM LABORATORY STUDIES

Petchey *et al.* (1999), used microbial food webs as their model system and this enabled them to observe how warming affects the patterns in food web structure. This is because the adaptability of microbes to laboratory conditions, combined with their short generation time and small body size, enabled their model food webs to reach equilibrium, whereby the biomass of each trophic level remained constant over time (Petchey *et al.,* 1999). In other laboratory studies, where the effects of warming upon food web processes have been investigated, model organisms with longer generation times and increasingly complex life cycles have been employed (O'Connor, 2009, O'Connor *et al.,* 2009, O'Connor *et al.,* 2011, Kratina *et al.,* 2012, Shurin *et al.,* 2012, Seifert *et al.,* 2014). In these examples, food webs have not been observed (or intended) to reach a stable equilibrium and therefore these studies show divergent patterns in the effects of warming on food web structure. For example, in order to investigate the effects of warming upon plant-herbivore interaction strengths, O'Connor (2009) observed the interaction between an amphipod herbivore and macroalgae producer. Here, warming was shown to increase the mass specific rate of consumption by the amphipod, supporting the hypothesis that relative to consumer body size, warming causes rate of consumption to increase. However, because the experimental was short term, this increase in consumption caused producer biomass to decrease, and therefore the ratio of consumer to producer biomass was observed to increase in response to warming. Yet this result is not contrary to the predictions of how warming affects food web structure because common sense dictates that the results are interpreted in proper context: Studies attaining equilibrium such as Petchey (1999) inform us of how warming affects the pattern of food web structure, whilst those not attaining equilibrium such as O'Connor (2009) inform us only of how warming affects the processes underlying that pattern.

1.2.1.1 INTERACTION STRENGTH

For the purposes of this thesis, interaction strength is defined as the quantity of biomass flowing between two trophic levels (*sensu* Bersier *et al.* (2002)). In this context, O' Connor's (2009) study demonstrated that warming increased both rates of consumption by the amphipod herbivore, and rates of production by the macroalgae producer and therefore because the flow of biomass increased within the interaction, interaction strength increased. This observation was supported by a further study (Pennings and Silliman, 2005) which demonstrated that the strength of interactions between plants and herbivores decreased with increasing latitude; indicating towards a biogeographical pattern in interaction strengths that corresponded with temperature. The implications of these results are interesting because the strength of interactions between organisms are understood to determine food web stability (Ives & Cardinale, 2004, Emmerson & Raffaelli, 2004, O'Gormon & Emmerson, 2009) and the majority of interactions in food webs tend to be weak (Paine, 1980, O'Gormon *et al.,* 2010). Thus a strengthening of trophic interactions by warming has the potential to destabilise food webs (Rall *et al.,* 2010).

1.2.1.2 POPULATION DYNAMICS

Based on laboratory observations of Daphnia interacting with phytoplankton, O'Connor *et al.,* (2011) made theoretical predictions regarding the effects of warming upon the dynamics of a consumer-producer interaction. Contrary to the notion that warming destabilises food webs, they predicted that the interaction between producers and consumers would be stabilised by warming. This prediction is based upon warming increasing rates of both production and consumption, and thereby decreasing both the time necessary for populations to reach equilibrium and decreasing the amplitude of oscillatory population dynamics (O'Connor *et al.,* 2011). However, when considered in the context of a multi-species system, this finding equates to a strengthening of a producer consumer interaction, and may therefore have destabilising effects upon the overall system.

1.2.1.3 INCREASES IN TOP- DOWN CONTROL OF PRODUCERS

Shurin *et al.,* (2012) reported an increase in the top-down control of producers in model freshwater food webs in response to warming. A similar field based observation was also reported by Kishi *et al.,* (2005) who observed a warming induced increase in the top down control of natural food webs in Japanese streams. Both observations are explained by warming causing disproportionate increase in the mass specific consumption rates of consumers at higher trophic levels, such that greater control is imposed upon producer biomass.

1.2.1.4 RESOURCE AVAILABILITY

The effects of warming upon the top-down control of producer biomass may be mediated by increases in the availability of resources to producers. This was demonstrated empirically by O'Connor *et al.,* (2009) who found that nutrient enrichment under warming could promote primary production to levels that compensated for increases in consumption. This effect of eutrophication was also observed by Shurin *et al.,* (2012), bolstering the hypothesis that shifts in food web structure that occur in response to warming are the consequence of shifts in the ratio of bottom-up versus top down control of food webs (Jochum *et al.,* 2012). Temperature and nutrient resource availability are further interactive in determining the outcome of multi-trophic interactions because nutrient resource availability can affect the nutritional quality, and final biomass of plants and herbivores. Specifically, nutrient limitation reduces the food quality of producer biomass by altering the stoichiometry of primary producer tissues, and this leads to an increase in feeding by herbivores, but decrease in final herbivore biomass. For reasons outlined above, warming enhances this effect. However, the food quality of producer biomass may also be increased by increases in nutrient uptake by producers, causing a decrease in feeding rates, and increase in biomass of herbivores (Moorthi *et al.,* 2016). Thus an increase in the food quality of producer biomass can limit the effects of warming upon rates of herbivory and herbivore biomass. In addition to changes in nutrient resource supply, the food quality of producer biomass may be affected by the physiological responses of individual producers to warming, by the species composition of producer communities, and a combination thereof, with the food quality of a producer assemblage varying with temperature according to the combined responses of individuals (Renaud *et al.,* 1995). Thus whilst warming has the general effect of increasing the top-down versus bottom up control of food webs, this may in turn be affected by changes in the stoichiometry of individuals.

1.2.2 LABORATORY STUDIES IN THE CONTEXT OF UNIVERSAL RESPONSES TO WARMING

Species that constitute natural food webs exhibit three "*universal responses to warming*" (Parmesan, 2006): Pole-ward range extensions (Parmesan, 1999, Mieszkowska *et al.,* 2006) shifts in phenology (often to earlier dates (Parmesan, 2007)), and decreases in individual body size (Daufresne *et al.,* 2009, Gardner *et al.,* 2011). These three responses to warming fall into two classes: Firstly, ectotherm body size decreases in response to warming, and therefore this is driven by an adaptive response by individuals whose maximum body size is limited by the temperature of their environment. These individuals therefore exist at temperatures close to the upper thermal tolerance limit of that species (Ohlberger, 2013). Secondly, shifts in species range distributions and phenology are driven by the adaptive response of individuals living at the lower thermal tolerance limit for a species. This is because species range distributions extend pole-ward into newly warmed environments, and phenological shifts occur towards earlier, newly warmed, dates of the year (Thomas *et al.,* 2001). Categorising the universal responses to warming into these two classes illustrates that species adapt to warming in two fundamental ways depending upon the temperature of the environment in which they live relative to the upper and lower thermal tolerance limits for that species.

As a general rule, the reproductive rate of individuals increases with body size within species yet decreases with body size between species (Kooijman, 1986). This means that a decrease in the body size of individuals incurs an immediate disadvantage to that species because it causes a decrease in the reproductive rate of the population. However, it also leads to an immediate advantage over different species with larger bodied individuals because the reproductive rate of the smaller bodied population is greater per unit of population biomass. Thus whether adaptation of individual body size in response to warming incurs fitness costs or benefits is dependent upon the precise response of individuals relative to other species.

1.2.2.1 Species response to warming in relation to thermal performance

Temperature affects the ability of individuals to perform functions such as foraging, consumption and growth that are necessary for survival. Because of this, where performance is the ability of an individual to complete these functions that determine fitness, temperature affects individual performance (Kingsolver & Huey, 2008). The general effects of temperature upon individual performance are described for all species by thermal performance curves (Angiletta, 2009) (figure 1.5). These curves demonstrate that individual performance has a thermal optimum at which maximum performance is attained, and that performance is limited at temperatures both above and below the optimum.

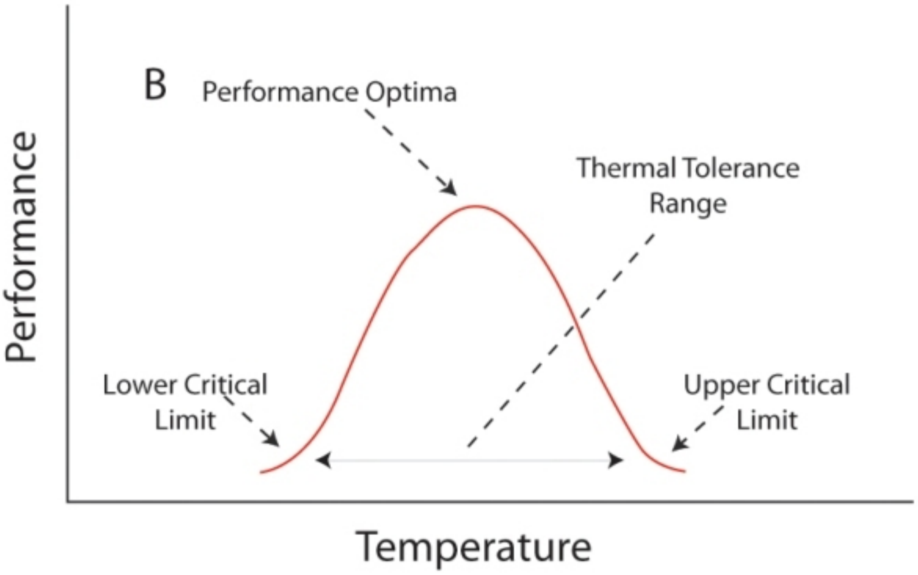


Figure 1.5 **Theoretical thermal performance curve of an individual (Miller & Stillman, 2012).** Performance describes the ability of an individual to complete the functions that contribute to its fitness and therefore thermal performance curves provide a conceptual model by which to understand the effects of temperature upon fitness. The thermal tolerance range of a species is defined by the lower critical and upper critical limits of temperature. At these extremes, the performance of individuals is zero. The optimal performance of individuals occurs at a temperature between these two extremes. Thus the thermal performance of individuals is determined by the temperature of the environment experienced by that individual in relation to thermal tolerance range of the species.

Whilst individual performance is greatest at the optimum temperature, species are adapted to tolerate a variety of temperatures (Miller and Stillman, 2012) and the extent of this thermal range between the upper and lower critical limits are determined by genotype. Because of this, the genotype of a species encodes for both the positive and negative responses to temperature that an individual may exhibit, depending upon the temperature of its environment (Kingsolver & Huey, 2008). This means that instead of individual fitness being determined by the species genotype encoding for optimum performance at a specific temperature, individual fitness is determined by phenotypic adaptation around that specific genotype according to the temperature at which an individual lives (Kingsolver & Huey, 2008).

Thus the individual response to temperature may not be entirely prescribed by the laws of physics as metabolic theory predicts, but instead realised within the range of thermal tolerance to which the genotype is adapted (Ohlberger, 2013). This has important consequences for food webs because it illustrates that the temperature of the environment may not determine the effects of temperature upon individuals that constitute food webs in a purely mechanical way. Instead, the temperature of the environment has effects upon each individual that are determined by that temperature relative to the range of temperatures that species is adapted to. This means that in any natural food web, some species may respond positively to a specific temperature whilst others respond negatively. For example, a natural food web may contain individuals of one species at their upper latitudinal limit, and individuals of another species at their maximum body size. In this example, the environmental temperature is at the lower thermal tolerance limit for individuals of the species at their upper latitudinal limit and therefore an increase in temperature may have a positive effect upon those individuals. Conversely, for individuals of the species that is at maximum body size, the environmental temperature is at the upper thermal tolerance limit for individuals and therefore an increase in temperature may have a negative effect upon those individuals. Thus the effects of warming upon food web structure may be dependent upon context, depending upon the specific environmental temperature in relation to the spectrum of thermal tolerance ranges of the species employed. Thus contrary to the predictions of metabolic theory and laboratory studies, the effects of warming upon natural food webs may be difficult to generalise.

1.3 VARIATION IN INDIVIDUAL RESPONSES TO TEMPERATURE

In the context of the three universal responses to warming, metabolic theory and subsequent laboratory studies appear inadequate in entirely explaining the effects of temperature upon individuals and the food webs they comprise. This is because whilst temperature apparently has ubiquitous metabolic effects upon all individuals, those metabolic effects may only elicit a response in body size or mass-specific consumption rate for the small proportion of individuals which exist close to the upper limit of their thermal tolerance range (Ohlberger, 2013).

This means that despite warming having predictable effects upon individuals, in as much as it causes metabolic rates to increase, the effects of those increases in metabolism is dependent on context. Therefore the effects of temperature upon food web structure may also be context dependent. This woolly idea can be distilled into a key concept: Food webs are composed of a variety of individual responses to warming. From this concept, two basic lines of enquiry now emerge: Firstly, How does variation in the effects of responses to warming occur? And secondly, what are the effects of variation in responses to warming?

1.4 DEVELOPING A MODEL SYSTEM

In essence, the aim of this thesis is to examine whether variation exists in the temperature dependence of relationships between biomass, consumption and growth and to make this examination as relevant as possible to the real world. In achieving this, it is therefore necessary to both manipulate temperature and precisely monitor organisms, but at the same time make those observations within the context of a real world scenario. In order to achieve this, I have chosen to use the rocky intertidal as a model ecosystem.

1.4.1 THE ROCKY SHORE ECOSYSTEM

The relative accessibility of the environment and diversity of organisms found within it has meant that for many years, the intertidal rocky shore has provided the backdrop for studying the interactions between species and structure of food webs (Dayton, 1971, Lubchenco & Menge, 1978, Paine, 1980, Menge, 1995, Crowe *et al.,* 2009, Griffin *et al.,* 2010). More recently this ecosystem has also received much attention as one affected by climate change (Hawkins *et al.,* 2008), in particular because pole-ward range expansions have been observed in several rocky shore organisms in response to warming (Mieszkoska *et al.,* 2006, Hawkins *et al.,* 2009).

In general, the rocky shore is an example of an ecosystem dominated by the abiotic disturbance of wave exposure (Dayton, 1971). Very generally, high levels of wave exposure cause shearing and damage of macroalgae and this means that as wave exposure increases, the dominance of rocky shore organisms shifts from macroalgae to filter feeding sedentary heterotrophs, such as barnacles and mussels (Ballantine, 1961). Whilst the dominance of organisms follows this broad-scale pattern across coastlines, local topography and geology can affect it. This is because on coastlines that experience a high degree of wave exposure, certain shores may be sheltered by headlands or promontories (Burrows *et al.,* 2008), and within those shores, large boulders or rocky outcrops may shelter small microhabitats (Hartnoll *et al.,* 1985). Thus interactions between wave exposure, topology and geology determine the extent to which the rocky shore ecosystem represents a mosaic of different habitats (Hartnoll & Hawkins, 1985) and this can cause the outcome of species interactions on the rocky shore to be heavily dependent upon context (Crowe *et al.,* 2011). A predicted indirect effect of global warming in temperate regions is an increase in the duration and intensity of storms (Dawson *et al.,* 2004, IPCC, 2014). This is likely to intensify the effects of wave exposure upon rocky shore ecosystems and therefore may have diverse effects upon the contextual response of rocky shore organisms to their environment. Because of this, the rocky shore provides an interesting model system in which to study both the direct and indirect effects of rising global temperatures upon ecosystems.

1.4.2 Choosing a Model Interaction between producers and consumer

In order to conduct laboratory experiments with temperature as controlled variable, and for the results of these experiments to be relevant to field observations of the rocky shore ecosystem, it was necessary to choose a model producer-consumer interaction that was both adaptable to laboratory conditions and widely observed in nature. This was achieved by choosing *Ulva lactuca* as a model producer and *Idotea granulosa* as a model consumer. These species have proven adaptability to laboratory conditions, both in isolation and interaction, (Steffenson, 1976, Sagerman *et al.,* 2014, Enge *et al.,* 2013) and *U. lactuca* has been observed to be preferentially grazed upon by *I. granulosa* (Karez *et al.,* 2000).

1.4.2.1 *Ulva lactuca*: Model producer

Ulva lactuca is an ephemeral macroalgae common to European rocky shores. Whilst isomorphic in anatomy, *U. lactuca* has a modular distromatic construction with a colony of cells functioning as individual modules (Loughnane *et al.,* 2008). This species of macroalgae was chosen as a model for use in laboratory experiments in this study because the lack of complex anatomical features such as fruiting bodies or stipe was expected to limit confounding effects in the size dependence of growth rates. Furthermore, *U. lactuca* naturally exists as a fast growing, ephemeral alga, reproducing and growing year round, growing either upon the basal substrate of the rocky shore, as an epiphyte on other macroalgae, or as free-living fragments in the water column (Sand-Jensen, 1988).

1.4.2.2 *IDOTEA GRANULOSA*: MODEL CONSUMER

Idotea granulosa is a generalist herbivore, widespread around the coast of Europe (Salemaa, 1986, Leifsson, 1998). Because *I. granulosa* breeds throughout the year and has no larval phase in its life cycle (Healy & O'Neill, 1984, Hull *et al.,* 2001), individuals spanning a wide range of body sizes could be continually collected from local rocky shores. This ensured that a constant supply of individuals was available for investigations into the effects of temperature upon mass specific growth and consumption rates.

1.4.2.3 MODEL TEMPERATURES: 9°C TO 15°C

Ulva lactuca and *Idotea granulosa* individuals were collected from rocky shores around the coast of Anglesey, North Wales. In these locations, mean sea surface temperatures range annually from around 7°C to 15°C (Hayward & Ryland, 1995). Based on the assumption that these organisms would be adapted to the annual range of temperatures experienced in their local environment, test temperatures of 9°C, 12°C and 15°C were used throughout this study. These test temperatures were chosen to be at the upper limit of those to which the organisms were assumed to be adapted. This meant that temperature was studied as a fundamental attribute of the environment, as opposed to a factor imposing physiological stress upon organisms.

1.4.3 THESIS OUTLINE

In order to answer the question "*Will warming affect food web structure?*" I pursue two lines of enquiry. The first of these is to investigate whether warming has universal effects upon producer-consumer interactions, and the second of these is to investigate what determines the structure of natural food webs.

Because predictions of how warming will affect food web structure are underpinned by theory describing the effects of warming upon individuals (Brown et al., 2004), I investigate whether warming has universal effects upon producer-consumer interactions by examining individual responses to warming. Specifically, I conduct laboratory experiments using the model interaction between *I. granulosa* and *U. lactuca* described in section 1.4.2 to examine the way in which individuals respond to warming, and whether those individual responses affect trophic interactions. I begin in Chapter 2 by focusing on producer body size and investigate whether increases in rates of consumption caused by warming always lead to ubiquitous decrease in producer biomass. The rationale for this investigation is that rates of producer growth are determined by producer body size and temperature (Cooper, 1973), and therefore changes in producer body size that occur because of consumption can affect the temperature dependence of producer growth rates. Thus in this chapter, I investigate whether warming causes consumption rates to universally outstrip rates of production, and whether this leads to predictable shifts in the ratio of consumer to producer biomass.

In Chapter 3 I focus on consumer body size as a confounding variable in determining the effects of temperature upon food web structure. Here, I investigate whether the average body size of consumers determines the effects of warming on the ratio of consumer to producer biomass. The rationale for this investigation is that the rate at which consumers grow relative to the rate at which they consume resources can be dependent not only upon temperature, but also ontogenetic factors, and therefore body size (Ohlberger, 2013).

The first two chapters indicate that variation in the body size of producers and consumers can lead to variation in the effects of warming upon the ratio of consumer to producer biomass. From this, I derive the tenet that the ratio of consumer to producer biomass is not dependent upon temperature alone and investigate other factors that determine food web structure. In Chapter 4, I investigate whether wave exposure may be an abiotic variable that determines the causal link between producer and consumer biomass. The rationale for this investigation is that hydrodynamic forces can dislodge individuals and prune macroalgae on the rocky shore, and therefore this may alter the relative proportion of consumer to producer biomass (Menge *et al.,* 1995). I then investigate the role of species interactions in determining food web structure. In Chapter 5, I investigate the role of small-scale variation in producer biomass in determining the species richness of macroalgae communities, and investigate how the interaction between these two variables determines the abundance and group richness of consumers. These final two chapters indicate that the ratio between consumer and producer biomass is determined by complex species interactions within communities and that those interactions are dependent upon context.

CHAPTER 2: INDIVIDUAL LEVEL RESPONSES TO THE SIMULTANEOUS EFFECTS OF WARMING UPON PRODUCTION AND CONSUMPTION

Abstract

The ratio of consumer to producer biomass is expected to increase with warming because consumption rates increase in temperature faster than rates of primary production. However, this effect is dependent upon increases in consumption leading to predictable declines in producer biomass. In this chapter, I investigate the effects of warming upon interactions between individuals of the ephemeral algae, *Ulva lactuca* and the generalist intertidal herbivore, *Idotea granulosa*. I cultured individuals in the laboratory and measured the effects of body size and temperature upon producer growth and consumer consumption rates. This enabled the simultaneous rates of growth and consumption that occur in an interaction to be predicted from observations of the relative body sizes of consumers and producers. I found that whilst the consumption rate of *I. granulosa* individuals increased with warming, this had no effect upon *U. lactuca* body size and this was explained by estimates of simultaneous growth and consumption: In short term experiments where consumers did not grow, warming caused sufficient increases in *U. lactuca* growth rates to compensate for the effects of consumption upon *U. lactuca* biomass. In longer-term experiments, *I. granulosa* growth was dependent upon temperature and body size and therefore rates of consumption increased throughout the duration of the experiment according to body size and temperature. This meant that relative to consumer body size, the effect of consumption upon *U. lactuca* biomass was independent of temperature: Whilst consumer body size drove increases in the consumption rate through time, this did not lead to a significant effect of temperature upon the ratio of consumer to producer biomass. This was because the positive effects of temperature upon producer growth were sufficient to compensate for the effects of temperature upon consumption. These results are explained by the effects of warming upon *U. lactuca* in the absence of consumption. This is because warming caused both growth rates and maximum body size of *U. lactuca* to increase. It is this effect of temperature upon the relationship between *U. lactuca* body size and growth rates that enables the compensatory response by *U. lactuca* individuals to consumption. This work indicates therefore that when warming promotes primary producer body size and growth rates, a shift in the ratio of consumer to producer biomass is unlikely.

2.1 INTRODUCTION

The mechanisms that cause food web structure to shift with warming have been investigated in many studies (O'Connor *et al.,* 2009, O'Connor *et al.,* 2011, Shurin *et al.,* 2012, Seifert *et al.,* 2014). In all of these, populations of unicellular primary producers have been employed which in response to warming, increase in productivity. However, this increase in primary productivity coincides with warming causing an increase in consumption rates that outstrip rates of production by the primary producer population. Because of this, a decrease in primary producer population biomass is observed. Over multiple generations, this decrease in primary producer population biomass is stable because increases in consumption cause primary producer population biomass to decrease whilst increases in production enable consumption to be compensated for by producer production (O'Connor *et al.,* 2011). The effects of temperature upon the relationship between primary producer population biomass and production explain this result (Savage *et al.,* 2004, O'Connor *et al.,* 2011). This is because warming drives increase in the intrinsic growth rate, *r* (expressed as maximal productivity, P*, (figure 2.2)), of the primary producer population whilst increases in consumption simultaneously drive decreases in the carrying capacity, *K*, of the primary producer population (figure 2.1). The combined outcome of these effects is an increase in the maximum productivity of the primary producer population, and a decrease in the population biomass at which this optimal productivity occurs. As a consequence of these effects, warming causes lower levels of primary producer population biomass to operate with greater productivity (figure 2.2). By this mechanism, increased levels of consumption can be sustained over several generations without a persistent decline in producer biomass and these dynamics have been observed in experiments employing populations of phytoplankton grazed by zooplankton (O'Connor *et al.,* 2011) and microbial predator-prey interactions (Fussman *et al.,* 2014).

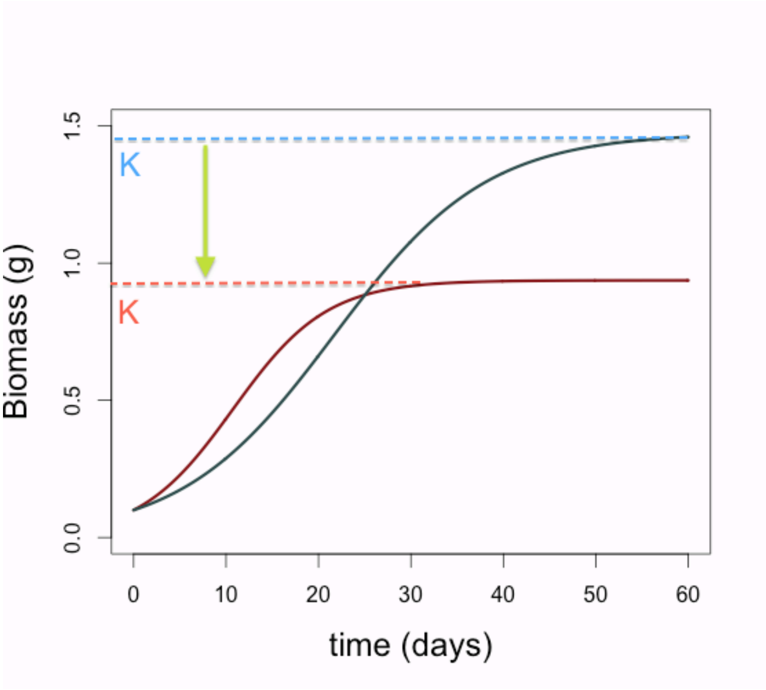


Figure 2.1 Theoretical effect of warming upon density dependent population growth through time. Warming causes carrying capacity (K) to decrease (green arrow) such that in cooler environments (blue), carrying capacity is greater than in warmer environments (red). This causes the population to reach carrying capacity at a later time in cooler environments.

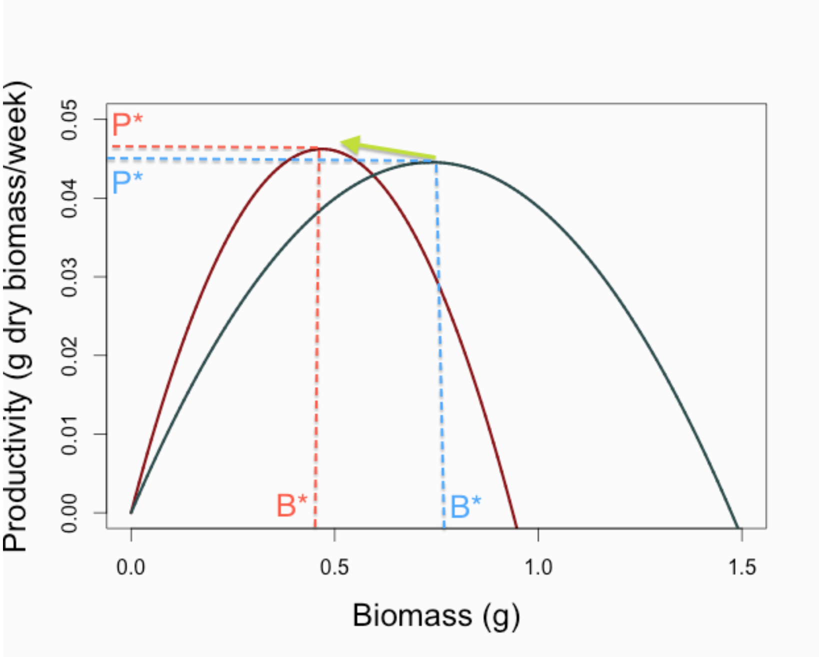


Figure 2.2 Theoretical effect of warming upon the relationship between population biomass and productivity. Warming causes maximum rates of productivity (P*) to increase, and the biomass at which this occurs (B*) to decrease (green arrow). This

causes rates of productivity to be higher in warmer environments (red) than in cooler environments (blue) only when population biomass is low.

2.1.1 SIGMOIDAL GROWTH AS A CAUSE OF COMPENSATORY RESPONSES TO CONSUMPTION

Sigmoidal growth patterns explain the fundamental mechanism by which rates of production by primary producer populations can increase in response to decreases in primary producer population biomass (figures 2.3 & 2.4) (Cooper, 1973, O'Connor *et al.,* 2011). In populations of unicellular phytoplankton, this compensatory response occurs because although the consumption of an individual necessitates mortality, the reproductive rate of survivors is sufficient for the remaining population to reproduce, and thereby compensate for consumption (Cooper, 1973). In modular primary producers, whereby consumption of individuals constitutes a decrease in the number of functioning modules as opposed to mortality, the same effect may be observed provided individual growth is sigmoidal (Brown & Allen, 1989). At both the population and individual level, sigmoidal growth enables a compensatory response by producers to consumption based on a core principle: The conditions for growth must become instantaneously more favorable as a consequence of consumption (Hilbert *et al.,* 1981, Williamson *et al.,* 1989, Belsky *et al.,* 1993, deMazancourt *et al.,* 1998, Wise & Abrahamson, 2008, Lebon *et al.,* 2014). This core principle may be adhered to, either as a consequence of a decrease in primary producer biomass, or a change in the environment caused by the consumer (Hilbert *et al.,* 1981). This is demonstrated by instances where primary production is limited by either light or CO_2: Light limitation can occur when primary production is limited by shading and therefore a decrease in producer biomass causes production rates to increase. This is because light is instantly replenished as a resource. In instances where CO_2 limits primary production, respiration by consumers instantaneously modifies the environment by increasing CO_2 concentrations and thereby causes rates of primary production to increase (Wise & Abrahamson, 2008, Cooper, 1973).

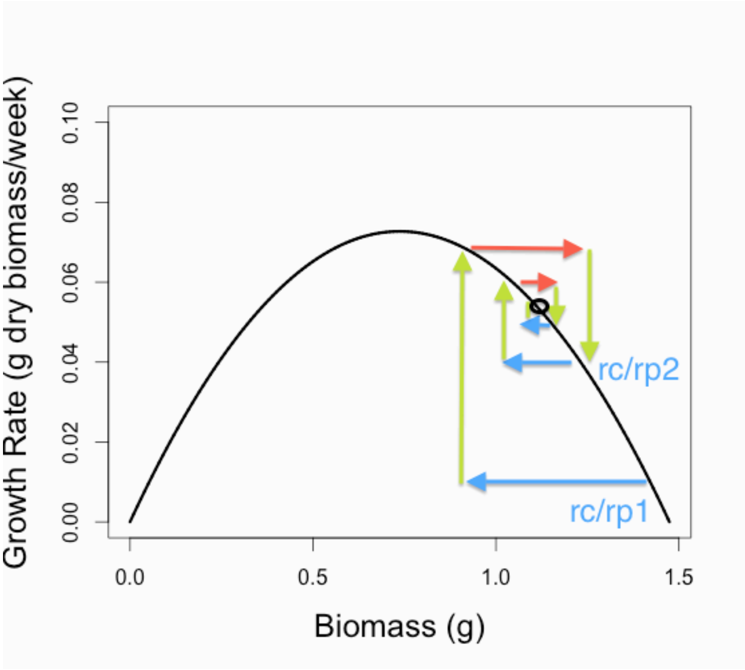


Figure 2.3 Theoretical compensatory response by primary producers to consumption. The initial ratio of consumption relative to production (rc/rp1) causes producer biomass to decrease (blue arrow) which causes the growth rate to increase (green arrow) and this in turn causes biomass to increase (red arrow) and a subsequent decrease in growth rates to the the second ratio of consumption relative to production (rc/rp2). The process is repeated, causing an equilibrium producer biomass (black circle) to be attained via damped oscillations through time.

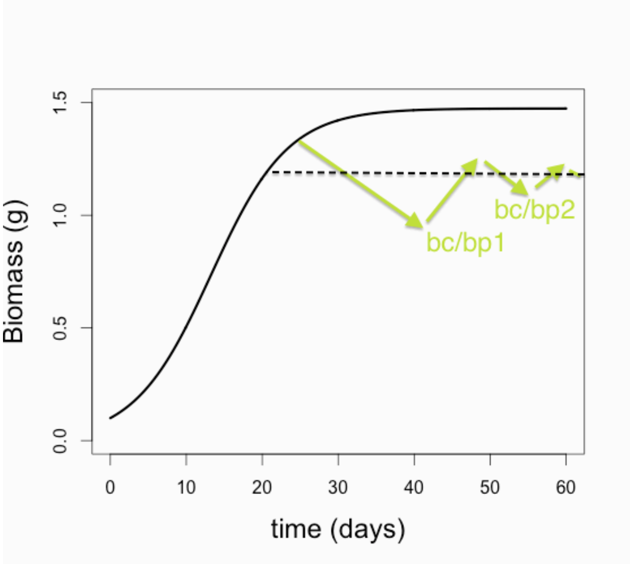


Figure 2.4 Theoretical effect of the compensatory response on biomass through time. Following consumption, producer biomass (green arrows) arrives at equilibrium (black dashed line) via damped oscillations.

2.1.2 EFFECTS OF CONSUMER BIOMASS UPON THE COMPENSATORY RESPONSE

In addition to conditions becoming instantaneously more favorable for growth, the compensatory response by either a population or individual depends upon producer biomass not decreasing to a level below that at which growth is optimal (figures 2.5 & 2.6). This is because at biomass below that at which growth is optimal, decreases in biomass cause growth rates to decline, irrespective of the availability of resources (Lebon *et al.,* 2014). For this situation not to arise is dependent upon both the consumption rate and the relationship between primary producer biomass and producer growth. Specifically, the rate of consumption must be sufficiently low for the consequent decrease in producer biomass to not cause a decrease in producer growth rates. Because consumption rates generally increase with consumer biomass, this means that the initial ratio of consumer to producer biomass is crucial in determining whether a compensatory response occurs.

2.1.3 EFFECTS OF CONSUMER GROWTH UPON THE COMPENSATORY RESPONSE

Consumer biomass increases through time as a consequence of consumer growth and the rate of consumer growth is dependent upon consumption rate. Because of this, initial consumer biomass determines not only consumption rate, but also the rate of change in consumer biomass, and the rate of increase in consumption rates through time. This means that in order for the compensatory response by primary producers to be effective over time, the initial biomass of consumers relative to producers must be scaled accordingly (Brown & Allen, 1989).

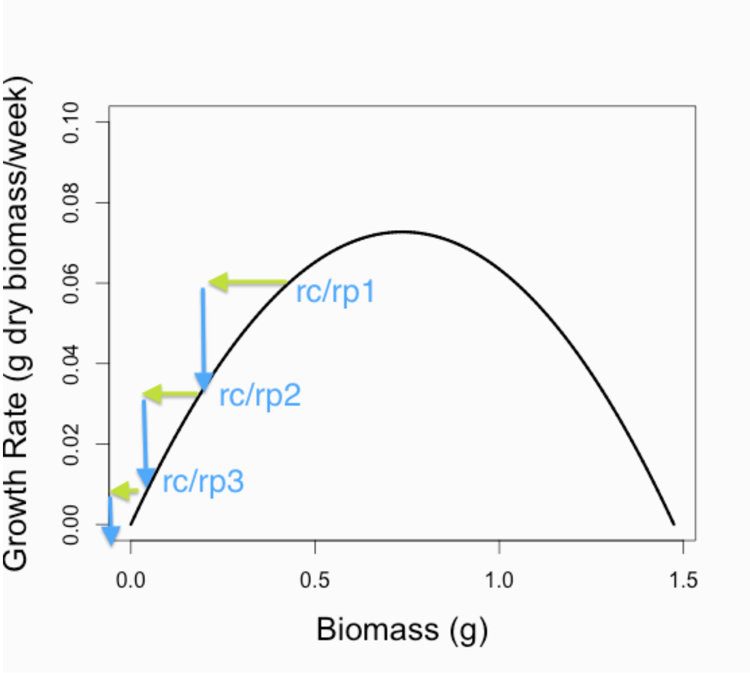


Figure 2.5 Inadequate compensatory response by primary producers to consumption. The initial ratio of consumption relative to production (rc/rp1) causes producer biomass to decrease (blue arrow) but because producer biomass is below that at which growth is optimal, growth rate decreases (green arrow) and this in turn causes biomass to decrease. Continued consumption leads to producer extinction.

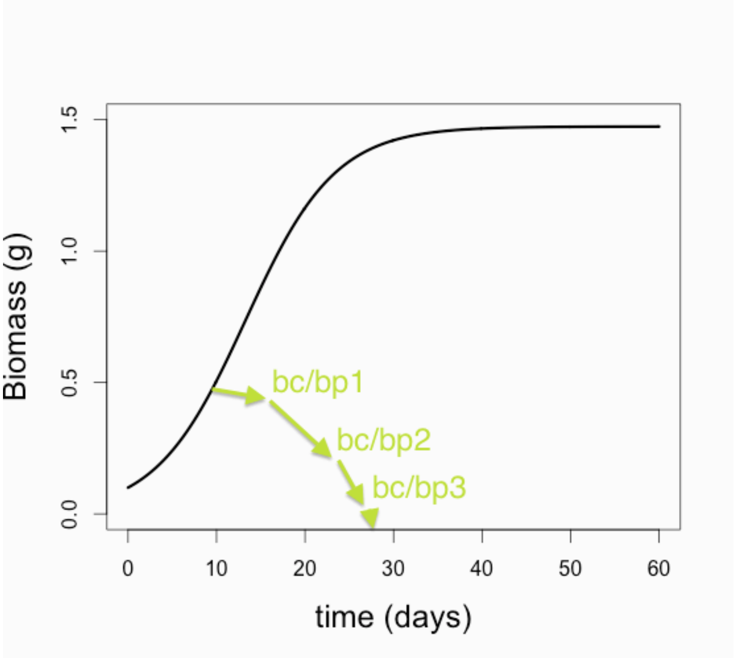


Figure 2.6 Effect of inadequate compensatory response on biomass through time. Following consumption, producer biomass (green arrows) declines to extinction

2.1.4 EFFECTS OF TEMPERATURE UPON THE COMPENSATORY RESPONSE

Primary producer growth, of both individuals and populations ultimately happens when individuals assimilate carbon. This process occurs when individual rates of photosynthesis (anabolism) exceed individual rates of respiration (catabolism). In general, rates of photosynthesis by individual primary producers increase with warming at a faster rate than do individual rates of respiration (Ribeiro *et al.,* 2006), and therefore rates of carbon assimilation increase with warming. This causes the intrinsic growth rate, *r*, of both primary producer individuals and populations to increase with warming. The effects of temperature upon the maximum biomass of primary producers are more complex however. This is because temperature affects the levels at which resources become limiting to primary production, warming increasing the supply levels at which rates of photosynthesis are saturated by CO2 (Idso *et al.,* 1987, Long, 2006) and light (Marsh *et al.,* 1986). Thus in warmer environments, provided other resources are not limiting, producers are able to utilize a greater proportion of the CO2 (Idso *et al.,* 1987) and light (Marsh *et al.,* 1986) available to them. This may cause both producer growth rates, and maximum producer biomass to increase (figures 2.7 & 2.8), and thereby create the conditions necessary for a compensatory response to occur. Specifically, where an increase in the ability to utilize available resources occurs, this may cause the maximum producer biomass to increase and thereby cause the biomass at which growth rates are optimal to increase also. This would have the effect of increasing the minimum producer biomass necessary for a compensatory response to occur and consequently limit the extent to producer biomass decreases as a consequence of warming (figures 2.9 & 2.10). In general terms, this means that the effects of warming upon the ratio of consumer to producer biomass are determined not only by temperature and the ratio between consumer and producer biomass, but also the effects of temperature upon the ability of producers to utilize available resources.

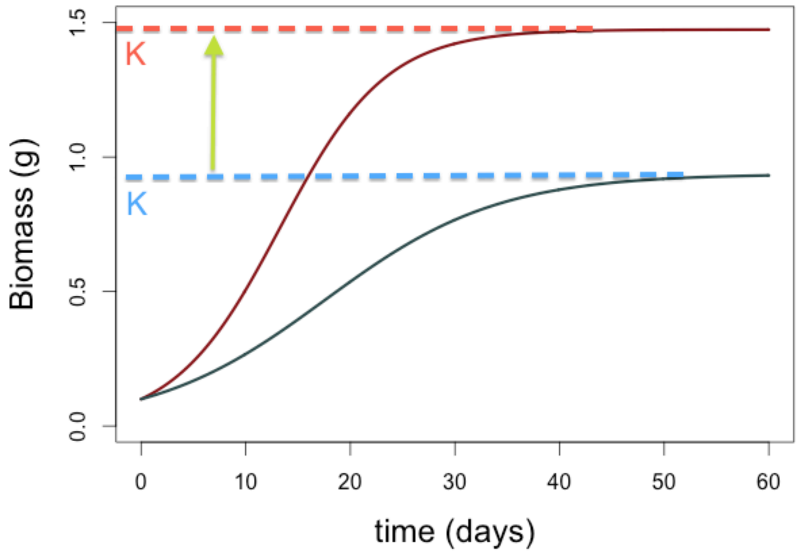


Figure 2.7 Theoretical effect of an increase in both biomass and growth rate with warming. Warming causes the carrying capacity (K) of density dependent growth to increase (green arrow).

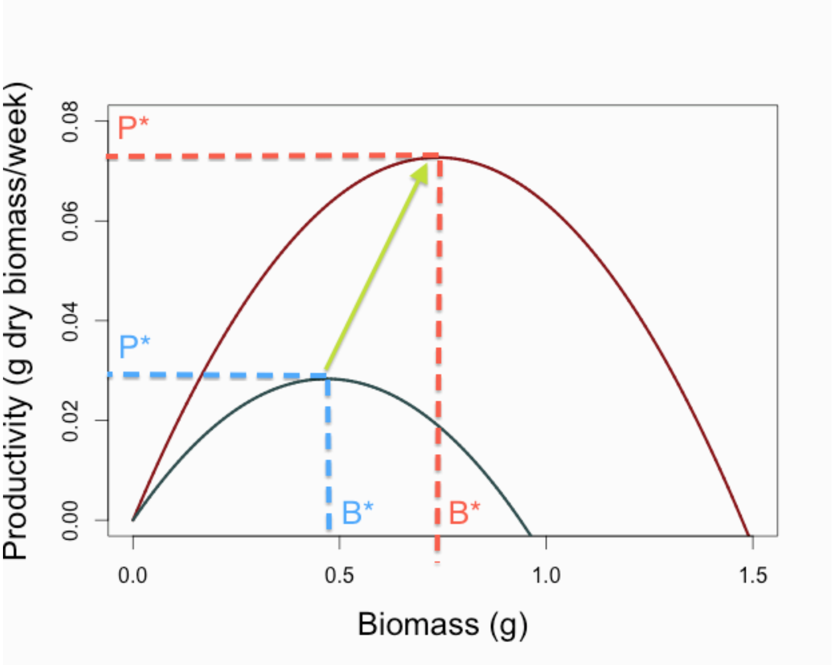


Figure 2.8 Effects of an increase in biomass upon the relationship between biomass and growth rate. Warming causes both the maximum growth rate (P*) and the biomass at which this occurs (B*) to increase (green arrow). This causes rates of productivity to be higher in warmer environments at all levels of biomass.

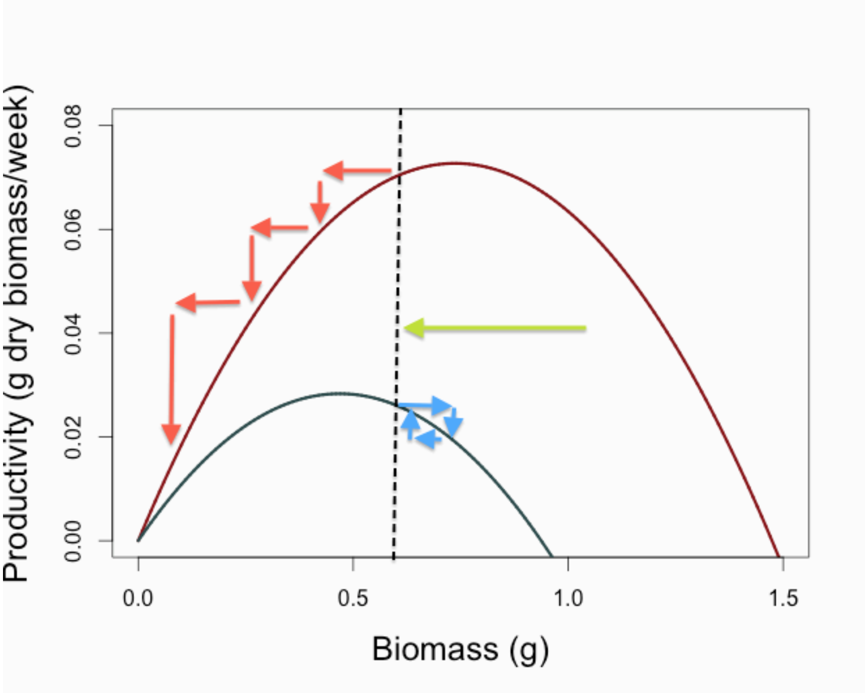


Figure 2.9 Compensatory response determined by temperature. Consumption causes producer biomass to decrease to an equal level in both environments (green arrow, black dashed line)) but because producer biomass is below that at which growth is optimal in warmer environments, growth rate decreases (red arrows) and this in turn causes biomass to decrease. In cooler environments, producer biomass is above that at which growth is optimal such that an effective compensatory response occurs (blue arrows).

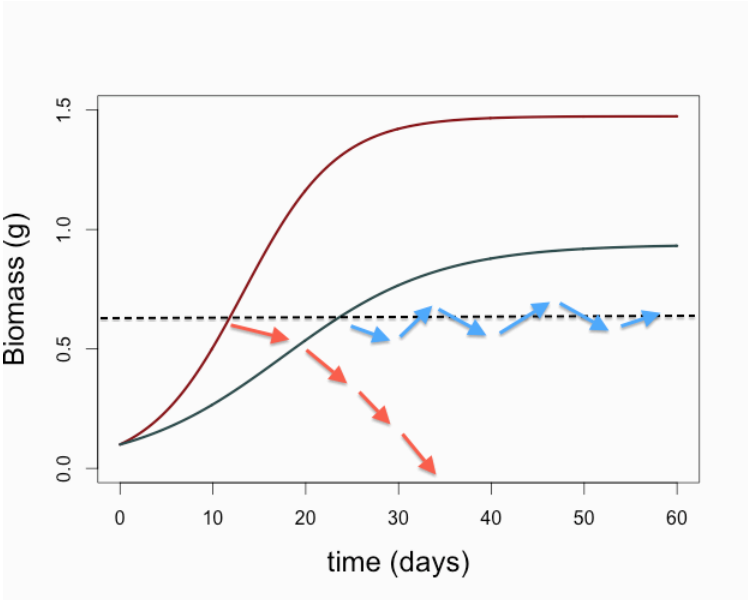


Figure 2.10 Effect of temperature dependent compensatory response on biomass through time. Following consumption (black dashed line), producer biomass in warmer environments (red arrows) declines to extinction whilst in cooler environments (blue arrows) arrives at equilibrium via damped oscillations.

2.1.5 INDIVIDUAL COMPENSATORY RESPONSE AS A DETERMINANT OF PRODUCER BODY SIZE

Individual rates of growth and consumption are expected to scale with individual body size and temperature at a constant rate for all organisms (Gillooly *et al.,* 2001). This means that where increases in temperature do not coincide with increases in growth rates, the body size of all organisms decreases with warming (Brown *et al.,* 2004). For primary producers, this means that unless the growth rate of individuals increases in response to warming, producer body size will decrease. In trophic interactions between individual organisms, a decrease in the body size of producers represents a decrease in the quantity of resources available to the consumer. Thus either consumer growth rate will be constrained by lack of producer biomass available as a resource to the consumer, or where consumer growth rate is maintained, that is expected to drive a decrease in producer body size due to increases in consumption (O'Connor *et al.,* 2009).

These predictions explain, from the basis of individuals, how the ratio of consumer to producer biomass can shift in response to warming. However, these predictions are challenged by compensatory responses of primary producer individuals. This is because a compensatory response by primary producer individuals causes individual producer body size and growth to be dependent not only upon producer body size and temperature, but also consumer body size. As a consequence, individual producers are capable of adapting, within certain bounds, to change in consumer body size. This means that the rate of change in producer body size relative to the rate of change in consumer body size is determined by the adaptive capacity of the producer individual to the effects of temperature upon consumer body size. Thus the resources available to a consumer are not prescribed by the universal scaling of temperature and producer body size, but instead adaptation by producers to those effects.

2.1.5 AIMS AND HYPOTHESES

The aim of this chapter is to investigate whether primary producer individuals adapt to the increases in consumption rate that are caused by temperature, and to thereby investigate whether changes in the ratio of consumer to producer biomass can be predicted from temperature and body size alone. This aim is achieved by first examining the temperature dependence of the relationship between individual body size and growth rates in the macroalgae, *Ulva lactuca.* The effects of temperature dependent consumption by the generalist intertidal herbivore, *Idotea granulosa*, upon this relationship are then examined.

The response by *Ulva lactuca* individuals to increases in consumption is examined under two scenarios: Firstly, it is examined over the period of a week, a timescale sufficiently short for consumers not to grow, and this enables the response of a primary producer to constant rates of temperature dependent consumption to be understood. Secondly, the trophic interaction is examined over the period of four weeks, a timescale sufficient for consumer growth. This enables the response of a modular primary producer to temperature-dependent increases in consumption to be understood.

The week-long observations enable testing of the hypotheses that individual modular primary producers in warmer environments compensate for greater levels of consumption due to higher rates of individual growth. The month-long observations enable testing of the hypothesis that warming increases the rate of increase in consumption rates, and thereby determines the timescale over which the compensatory response is effective. This investigation thereby examines the effects of temperature upon changes in the relationship between consumer and producer body size over time. This is achieved by observing the temperature dependence of interactions between the macroalgae, *Ulva lactuca*, and the generalist herbivore, *Idotea granulosa* under laboratory conditions. This producer-consumer interaction was used as a model for this study because of its adaptability to laboratory conditions and potential relevance regarding observations of the rocky shore ecosystem (see section 1.5).

2.2 MATERIALS AND METHODS

The first objective of this study was to investigate whether the size dependent growth of *Ulva lactuca* individuals was sigmoidal and whether this pattern of indidual growth was affected by temperature. This was achieved by observing *U. lactuca* individual growth, in the absence of consumption, at different temperatures. In order to establish whether individual growth was sigmoidal, a logistic model was fitted to observations of size dependent growth. The effect of temperature upon this individual growth pattern was then examined by incorporating temperature dependence into logistic parameter estimates for *U. lactuca* individual growth. This enabled the growth rate of *U. lactuca* individuals to be estimated from measurements of body size and the temperature of their environment.

The second objective of this study was to investigate the effects of temperature upon size dependent consumption by *Idotea granulosa*. In order to accurately measure the effect of temperature upon the relationship between *I. granulosa* body size and the rate at which individuals consume *U. lactuca,* it was essential that the producer did not grow whilst being consumed. This was achieved by measuring consumption under conditions where photosynthesis by *U. lactuca* was light limited to be equal to the *U. lactuca* respiration rate. Thus changes in *U. lactuca* biomass were entirely explained by consumption by *I. granulosa.* Linear models were then fitted to these observations of *I. granulosa* consumption rate to describe the effects of individual body size and temperature upon consumption. This enabled the consumption rate of *I. granulosa* individuals to also be estimated from their body size and the temperature of their environment.

Establishing accurate estimates of the temperature dependence of relationships between individual body size and rates of consumption and growth meant that the rates of consumption relative to growth (R_c/R_p) could be estimated for any two individuals interacting at any point in time, from observations of the body size of each individual. This enabled comparison of R_c/R_p at any point in time to the ratio of consumer body size relative to producer body size (B_c/B_p) at that same point in time. This enabled an examination of how changes in the ratio of processes (R_c/R_p) corresponded with changes in ratio of biomass (B_c/B_p) over time. This protocol was necessary in order to detect a compensatory response in *U. lactuca* individual growth rates, and to assess the effects of temperature dependent *I. granulosa* growth upon that compensatory response.

2.2.1 MAINTENANCE OF EXPERIMENTAL POPULATIONS AND EXPERIMENTAL SET UP

2.2.1.1 SELECTION OF INDIVIDUAL ORGANISMS

From August 2012 until April 2013, a breeding stock of *Idotea granulosa* individuals collected from ten sites around Anglesey, North Wales, was cultured upon *Ulva lactuca* in a large (circa 100 litre) flow-through tank supplied with seawater from the Menai Strait. This breeding stock was kept in the laboratory at ambient air temperature in order to acclimatise individuals to laboratory conditions. Experiments commenced in October 2013 using individual *I. granulosa* that had been drawn at random from the laboratory stock then selected according to body size. During experiments, these individuals were fed on free-living fragments of *Ulva lactuca* cut from individuals attached to basal substrates in the Menai Strait. In all experiments, a single free-living fragment of *U. lactuca* was used, washed in freshwater to remove epifauna and trimmed to the appropriate wet biomass. Fragments were chosen to be as uniform in topology as possible, to minimise any self-shading imposed by convoluted anatomy. This enabled individual primary producer body size to be an accurately controlled variable, with both pilot experiments and published work (Sand-Jensen, 1988), suggesting that such an approach does not significantly affect *U. lactuca* growth or fitness.

2.2.1.2 MESOCOSM DESIGN AND CONSTRUCTION

Experiments were conducted in three purpose built, temperature controlled units (TCU hereafter). Each TCU comprised a 700l reservoir of seawater filtered to 50 microns and UV treated. The volume of the reservoir was regulated with a jobe ball valve, controlling direct supply of water from the Menai Strait. Stored water was constantly cycled through a 2Kw chiller (Aqua Medic, Titan 2000) and 3kw heater (Integrated Aqua, HTI-3-220) by a pump (Aqua Medic, Ocean Runner 6500) at a rate of 6500 litres per hour. Thermostatic control of these components ensured temperature within the reservoir remained constant ±0.1°C throughout the experiments. From each reservoir, water was gravity fed to mesocosm replicates (n=24) through 6mm silicon tubing. Individual in-line taps ensured that flow rate was constant and equal for all mesocosms, at a rate of 10ml/minute. The replicate mesocosms each comprised a 500ml clear polythene beaker, thus the water in each mesocosm was replaced every 50 minutes. In this way 24 half litre mesocosms could be maintained as independent replicates with a temperature controlled flow of seawater in each of the three TCU systems. This design has significant advantages over containing replicates in cages within a shared pool because it eliminates simple pseudoreplication (Hurlbert, 1984) and the possibility of chemical interference between replicates. The three TCU systems were set to maintain temperatures of 9 ^{o}C, 12 ^{o}C and 15^{o}C as these are within the normal annual range of local seawater temperatures and pilot studies indicated that increments of 3°C induced significant effects.

Each TCU contained a timer and 3x (Arcadia T5 39W, 14,000K) bulbs to deliver each replicate with a 12 hours light/ 12hours dark regime of PAR level of 95-100 microE m^{-2} s^{-1} at the water surface during the light period. This PAR level was shown in pilot studies and published work (Sand-Jensen, 1988) to be sufficiuent for *U. lactuca* growth to not be light limited.

2.2.2 MEASURING TEMPERATURE DEPENDENT ULVA LACTUCA GROWTH

The effects of temperature upon size-dependent *Ulva lactuca* growth was determined by growing individual fragments of *U. lactuca* in individual mesocosm replicates during October 2013. So that the size dependence of individual growth rates could be ascertained at each temperature, individual body size was treated as a continuous variable, with 24 replicates of between 0.2g and 13g wet mass cultured in the absence of consumers at each of the respective temperatures, 9 °C, 12 °C, 15°C, for a period of one week. After this period, individuals were re-weighed and measures of wet mass converted to dry mass for accurate analysis. This conversion was achieved using the linear relationship ($R^2=0.726$, $p<0.01$) (figure 2.11) obtained by calibrating the wet biomass of 146 different sized *U. lactuca* fragments, measured to the nearest centigram after gently blotting dry with tissue paper, with their biomass following desiccation at 80°C for 48 hours.

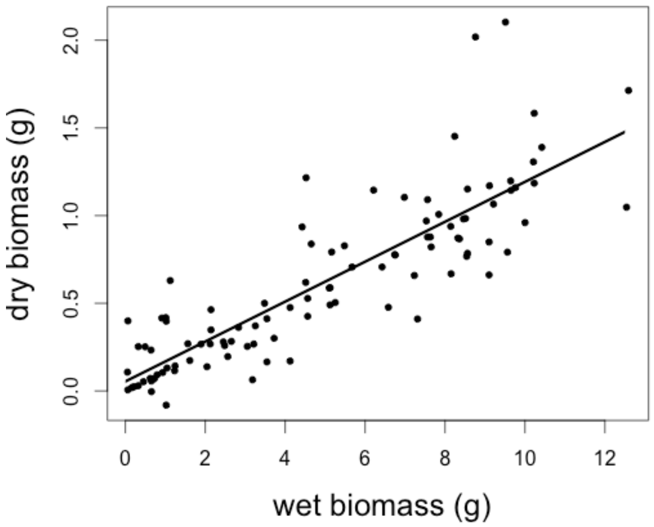


Figure 2.11 Relationship between wet and dry *Ulva lactuca* biomass. A linear model ($y=0.11388x+0.054216$, $R^2=0.73$) describes the relationship.

The growth rate of each replicate, expressed as units of dry biomass per week, was calculated as the calibrated biomass at the end of the experiment (N_{t+1}) divided by the calibrated biomass at the start of the experiment (N_t). From these observations, estimates of parameters for the logistic growth model (Begon *et al.,* 1995) were calculated as follows: The relationship between individual body size and growth rate was determined by plotting a regression of this response variable against the calibrated biomass at the start of the experiment (N_t) as the independent variable. With this relationship being linear, as ascertained by analysis of residuals (figure 2.14), the temperature dependence of the relationship between individual body size and growth rates was then ascertained by performing an ANCOVA using the open source software, R. ANCOVA was performed upon the regression using temperature as a factor, and the minimum adequate model, (ie: that to which the addition of further terms does not describe significantly more data) was selected using the manual protocol described by Crawley (2013). This produced temperature specific estimates for slope (a) and intercept (b) parameters describing the relationship:

$$\frac{N_t}{N_{t+1}} = aN_t + b$$

Equation 2.1

This enabled temperature specific estimates of the maximum body size, K, and the maximal growth rate, R, to be calculated from a and b according to the relationship $R = {}^{1}/_{b}$ and $K = {}^{(1-b)}/_{a}$. This enables the relationship between individual growth rates and body size to be expressed according to the maximum body size and maximal growth rate of individuals according to the difference equation:

$$\frac{N_{t+1}}{N_t} = \left(\frac{1}{\left(1 - \left({}^{1}/_{R}\right)\right)/K}\right)$$

Equation 2.2

Where, according to Euler's identity, the relationship between the maximal growth rate, R, and the intrinsic growth rate, r, is:

$$r = \ln(R)$$

Equation 2.3

Such the relationship between individual body size and rate of change in individual body size is given by the continuous function:

$$\frac{dN_t}{dt} = rN_t\left(\frac{K - N_t}{K}\right)$$

Equation 2.4

Which enabled the growth rate of any individual to be estimated from observations of individual body size and the temperature of the environment in which the individual was observed.

2.2.3 EFFECTS OF TEMPERATURE UPON IDOTEA GRANULOSA CONSUMPTION RATES

In order to accurately measure *Idotea granulosa* consumption rates, it was necessary to culture individuals using live *Ulva lactuca* as a food resource, but without *U. lactuca* simultaneously growing as this would lead to rates of consumption being underestimated. Thus *I. granulosa* individuals were cultured under conditions similar to the light compensation point for growth in *U. lactuca*. (Sand-Jendsen, 1988). The light compensation point is the equilibrium between photosynthesis and respiration at which growth does not occur and is dependent upon light intensity, CO_2 concentration and temperature. It was beyond the scope of this study to accurately control these values across temperature treatments, and therefore the light compensation point was achieved by culturing *U. lactuca* in polyethylene trays, under a 12 hours light/ 12 hours dark regime but shaded from direct light with tinfoil. This resulted in a PAR level of 20-25 microE m^{-2} s^{-1} during light periods at the aperture which caused no growth by *U. lactuca* over the course of one week in six control replicates at each temperature that did not contain consumers.

The relationship between *I. granulosa* body size and consumption rates was determined by treating individual body size as a continuous variable, with single individuals ranging in size from 4mm-20mm placed in 100ml clear polystyrene pots containing filtered seawater and a single 0.25g wet mass fragment of topologically uniform *U. lactuca*. These replicates ($n=48$) were kept in incubators (manufacturer: LMS) at each of the respective temperatures, 9^{o}C, 12^{o}C, 15^{o}C, and filtered seawater in the pots changed every 24 hours to avoid physiological stress. Individuals were cultured for the period of a week and wet biomass of *U. lactuca* measured to the nearest centigram at the end of the week. Such that *I. granulosa* body size could be expressed in units equivalent to those used to measure *U. lactuca* body size, the body length of 200 *I. granulosa* individuals, ranging in size from 1mm to 26mm was calibrated with their dry biomass following desiccation at 80°C for 48 hours. This produced a significant monomial relationship ($R^2=0.881$, $p<0.001$) (figure 2.12) which could then be used to express *I. granulosa* body size, the independent variable, as grams dry biomass, and the response variable, consumption rate, as grams dry *U. lactuca* biomass per week. A regression was performed to determine the relationship between individual body size and consumption rate, and the temperature dependence of this relationship analysed by performing ANCOVA using temperature as a factor and selecting the minimum adequate model using the manual protocol described by Crawley (2013). This produced temperature specific estimates for regression parameters, enabling the consumption rate of *I. granulosa* individuals to be estimated from observations of body size and the temperature of the environment in which they live.

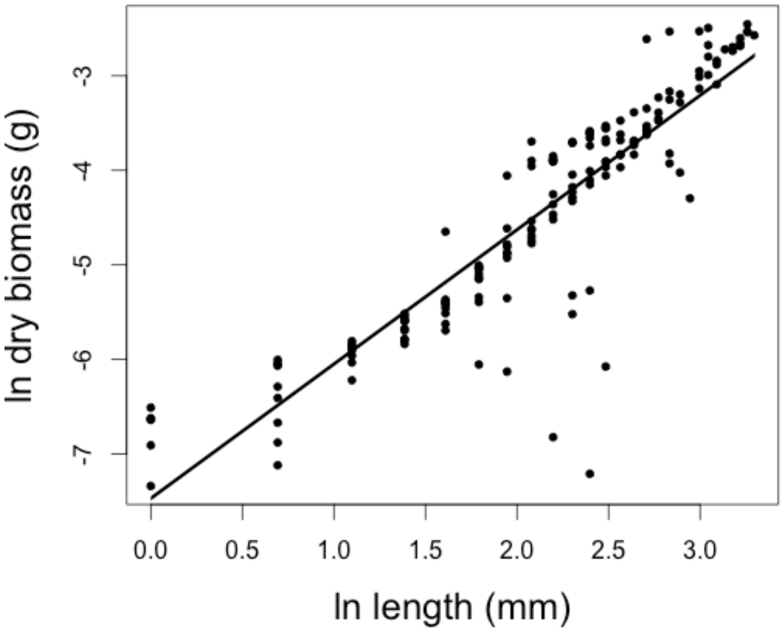


Figure 2.12 Relationship between *Idotea granulosa* length and dry biomass. A log-log model (*$ln(y)= 1.4209(ln(x))-7.469632, R^2=0.80$*) describes the relationship.

2.2.4 EFFECTS OF TEMPERATURE UPON INTERACTIONS IN THE ABSENCE OF CONSUMER GROWTH

In order to test the hypothesis that *U. lactuca* individuals in warmer environments compensate for greater levels of consumption due to higher rates of individual growth, the effect of temperature upon short-term changes in B_c/B_p was observed. This required that the independent variable was the initial B_c/B_p, and the response variable the final B_c/B_p. The period of observation for this experiment was one week, chosen because pilot studies indicated that this period was sufficient for significant growth by *U. lactuca,* yet too short for significant growth by *I. granulosa* and as a consequence, consumption rates were assumed to remain constant for this period of observation.

Initial B_c/B_p was treated as a continuous variable, and four experiments were conducted consecutively using one of four different levels of producer biomass as treatments (0.5, 1, 1.5 and 2g wet biomass) across the three temperatures, 9 °C, 12 °C, 15°C. Results from the four consecutive experiments were pooled for analysis. Whilst a better approach may have been to randomise producer biomass levels within each of the consecutive experiments, temporal pseudo replication was eliminated because producer biomass was not investigated explicitly as a factor.

This is because in all experiments, *I. granulosa* body size was also treated as a continuous variable, with each of the 24 replicates containing a single individual ranging in length from 4mm to 24mm. This ensured that the greatest possible range of values, and the greatest possible range of causes, of the initial ratio of consumer to producer biomass were covered in this study.

After the period of one week, *U. lactuca* fragments were re-weighed to the nearest centigram and *I. granulosa* individual body lengths re-measured. This gave a measure of how individual *U. lactuca* body size had changed, and ensured that *I. granulosa* individuals had not grown. Accurate measures of initial and final B_c/B_p were obtained by conversion of live measurements to those of dry biomass using the calibrations previously described and this enabled the corresponding rates of individual *I. granulosa* consumption and *U. lactuca* growth to be estimated at both the start and end of the experiment such that corresponding change in R_c/R_p could be estimated.

The analysis of change in both B_c/B_p and R_c/R_p followed an identical protocol, with a regression describing the relationship between the independent initial values, and the dependent final values. Performing an ANCOVA using temperature as a factor then determined the effects of temperature upon this relationship, giving temperature specific estimates for regression parameters. Equilibrium values of both B_c/B_p and R_c/R_p were then identified for each temperature by calculating the intersect between temperature-specific models and the line, $y=x$, which describing the situation of unity, enabled identification of the conditions necessary for *U. lactuca* to exhibit a compensatory response to consumption at each temperature.

2.2.5 EFFECTS OF TEMPERATURE DEPENDENT CONSUMER GROWTH UPON INTERACTIONS

In order to test the hypothesis that the efficacy of compensation by *U. lactuca* decreases with warming as a consequence of increases in the rate of increase in consumption rates, change in B_c/B_p was observed over four weeks, a period of time over which pilot studies indicated that *I. granulosa* individuals increased significantly in size at all temperatures. Conditions were identical to those of the week-long experiments, except only one experiment was performed, with temperature the only factor and 24 replicates of 1g initial *U. lactuca* body size.

Correspondingly, analysis of the results from the month long experiment was identical to those of the week long experiment, enabling the effect of consumer growth upon the response of *U. lactuca* to consumption to be identified at each temperature. In order to demonstrate the relative contributions of changes in producer body size and changes in consumer body size towards causing changes in B_c/B_p, and to ascertain the role of temperature in affecting this over the four week period, a further analysis was required. With regard changes in *U. lactuca* body size, an ANOVA was performed upon the change in producer biomass using temperature as a factor because all replicates had the same initial *U. lactuca* body size. This was in contrast to *I. granulosa*, where initial body size was a continuous variable, and as such the relationship between initial body size and final body size was determined by fitting a regression, and the effects of temperature ascertained by performing an ANCOVA using temperature as a factor. The minimum adequate model, (ie: that to which the addition of further terms does not describe significantly more data) was selected using the manual protocol described by Crawley (2013).

2.3 RESULTS

2.3.1 SIGMOIDAL GROWTH IN *ULVA LACTUCA* INDIVIDUALS

A significant linear relationship ($F_{2,97}$=10.43, p<0.001) was observed between the biomass of *Ulva lactuca* individuals and their growth rate over the period of one week, indicating that *Ulva lactuca* individual growth was sigmoidal (figure 2.13). This result was confirmed by analysis of residuals (figure 2.14). Here, a linear error was observed about the logistic model, indicating that the logistic model sufficed in describing the relationship between *U. lactuca* body size and individual growth rates.

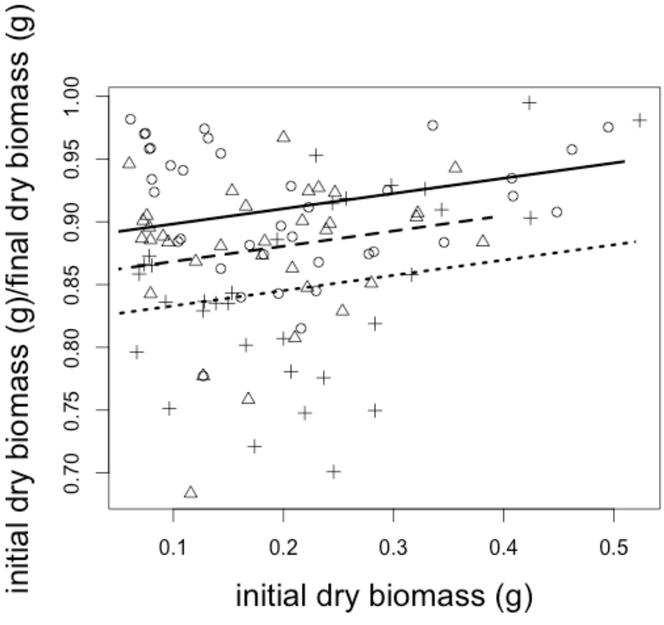


Figure 2.13 Relationship between *Ulva lactuca* biomass and mass specific growth rate. Warming causes the mass specific growth rate to increase at all body sizes and there is no interaction between temperature and body size in determining the mass specific growth rate at any temperature: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line).

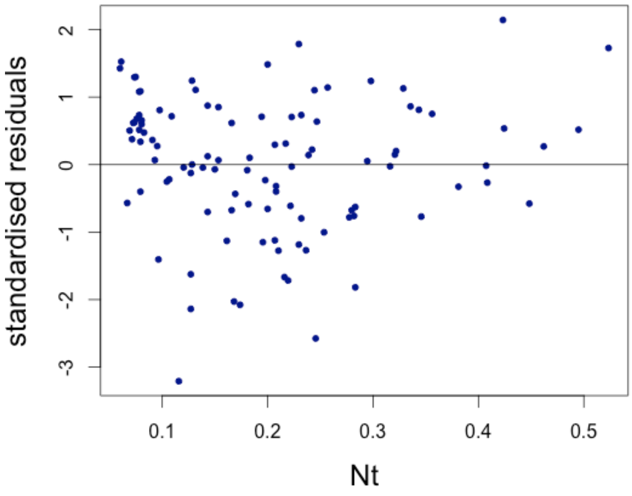


Figure 2.14 Standardised residuals of the ANCOVA model illustrated in figure 2.13. Initial dry body size (Nt) is plotted on the x-axis. Although variation between predicted and fitted values is high, this variation is linear.

2.3.2 EFFECTS OF TEMPERATURE UPON *ULVA LACTUCA* INDIVIDUAL GROWTH

Temperature had significant effects upon the relationship between *U. lactuca* individual body size and growth rate over the period of one week (figure 2.13). Specifically, warming caused a significant increase in the intercept parameter of these relationships ($F_{2,99}$=5.752, p<0.001) but had no significant effect upon the slope parameter ($F_{2,99}$=0.932, p<0.001) (figure 2.13). This means that warming caused the growth rate of *U. lactuca* individuals to increase significantly ($F_{2,97}$=10.43, p<0.001) at all body sizes and that the effects of temperature upon *U. lactuca* growth rate are non-interactive with body size. Because of this, warming had three effects upon the relationship between individual body size and growth rate in *U. lactuca* individuals: the maximum body size of *U. lactuca* increased with warming, the body size at which growth rates were optimal increased with warming, and the maximum growth rate of *U. lactuca* individuals increased with warming (figure 2.15).

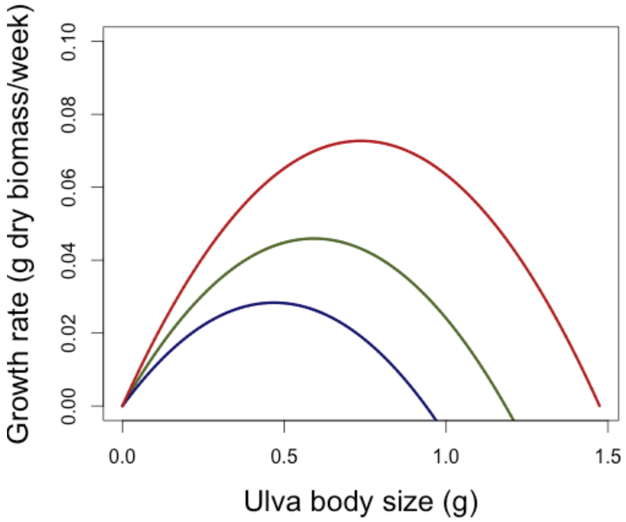


Figure 2.15 Temperature dependence of predicted relationships between *Ulva lactuca* body size and growth rates. Predicted relationships between Ulva lactuca body size and growth rates were calculated at 9°C (blue trendline), 12°C (green trendline) and 15°C (red trendline) from fitting the logistic model to the observed relationships between *Ulva lactuca* body size and growth rates (figure 2.13). Warming causes the maximum growth rate, maximum body size and body size at which growth rate is maximal to increase.

2.3.3 EFFECTS OF TEMPERATURE UPON IDOTEA GRANULOSA CONSUMPTION RATES

The relationship between *Idotea granulosa* body size and consumption rate was significantly affected by warming and these effects were the result of an interaction between body size and temperature ($F_{2,138}=13.48$, $p<0.001$). Specifically, warming caused an increase in the rate at which individual consumption rate increased with body size. This meant that although warming did not always cause the consumption rate of small individuals to increase, the consumption rate of larger individuals was always greater in warmer environments (figure 2.16).

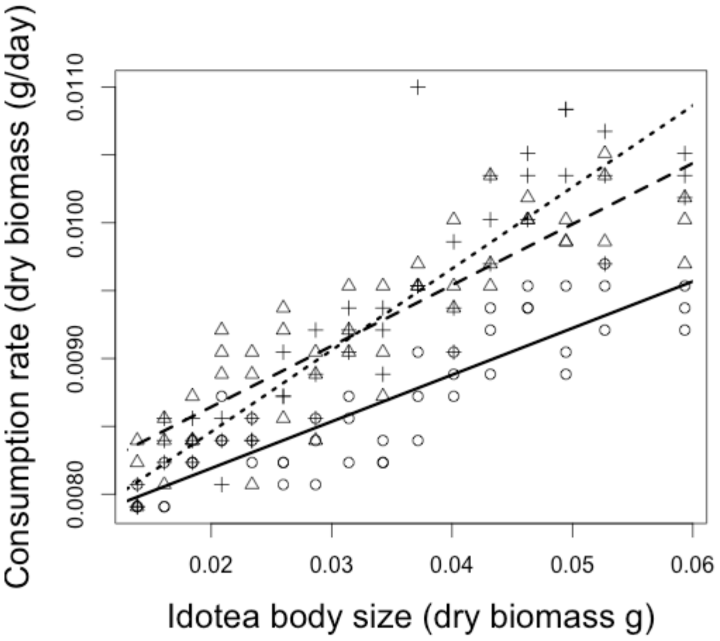


Figure 2.16 Temperature dependence of the relationship between body size and consumption rates for *Idotea granulosa*. Consumption rates increase with body size at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). Temperature and body size have interactive effects and therefore warming increases the rate at which consumption increases with body size.

2.3.4 INTERACTIONS IN THE ABSENCE OF CONSUMER GROWTH

2.3.4.1 EFFECTS OF TEMPERATURE UPON THE RATIO OF CONSUMER TO PRODUCER BODY SIZE

Temperature had significant effects ($F_{2,282}=6.903$, $p<0.05$) upon change in the ratio of consumer to producer body size (Bc/Bp) over the duration of one week (figure 2.17). Over this duration, a significant relationship was observed between the initial ratio of consumer to producer biomass and the final ratio of consumer to producer biomass ($F_{1,282}=4683.592$, $p<0.001$). This means that change in the ratio between consumer and producer body size is dependent upon the initial ratio of consumer to producer biomass. This relationship between initial and final Bc/Bp is significantly affected by temperature, which has significant qualitative effects upon change in Bc/Bp. Specifically, Bc/Bp decreased at the two warmer temperatures, 12°C and 15°C, but increased at the cooler temperature, 9°C. Because consumers did not grow over the duration of one week, changes in Bc/Bp observed in this experiment could be attributed solely to changes in producer body size. This means that producer body size increased at both 12°C and 15°C, but decreased at the cooler temperature, 9°C.

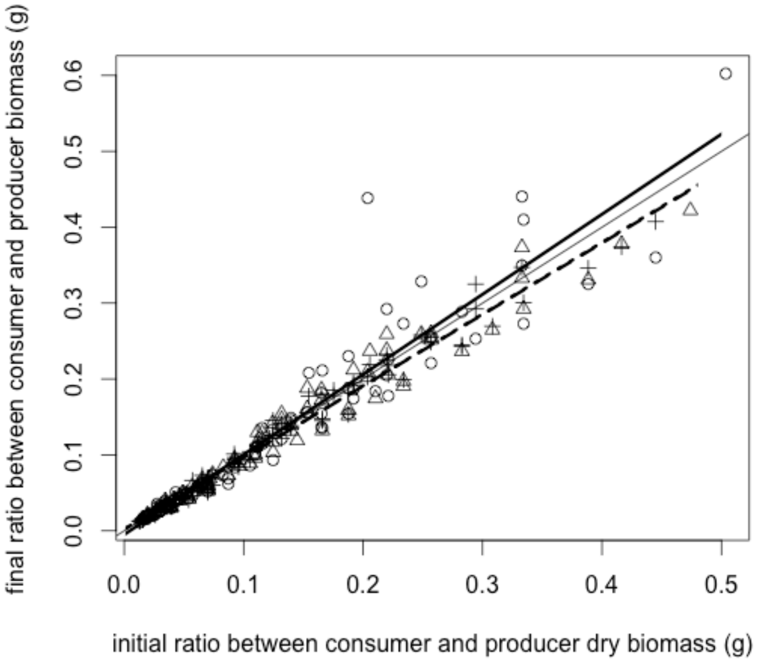


Figure 2.17 Temperature dependence of change in the ratio of consumer to producer biomass over one week. The thin black line illustrates unity, the situation that would arise with no change. Therefore at 9°C (circles, solid line) the ratio of consumer to producer biomass increased, whilst at 12°C (triangles, dashed line) and 15°C (crosses, dotted line) (disguised by similarity with result for 15°C), the ratio of consumer to producer biomass increased. Because consumers did not grow over one week, this means that *Ulva* biomass decreased at 9°C but increased at both 12°C 15°C.

2.3.4.2 EFFECTS OF TEMPERATURE UPON THE RATIO OF CONSUMPTION RELATIVE TO GROWTH

In the short-term experiments, where *I. granulosa* did not grow and consumption rates therefore remained constant, changes observed in Rc/Rp could be attributed solely to changes in producer growth rates and during this period of observation, Rc/Rp consistently increased when initial Rc/Rp was low and consistently decreased when initial Rc/Rp was high (figure 2.18). This result indicates that at all temperatures, low initial Rc/Rp causes growth rates to decrease whilst high initial Rc/Rp causes growth rates to increase (figure 2.18), a result underpinned by size dependent *U. lactuca* growth (figure 2.15): When *U. lactuca* biomass exceeds that of maximum growth, decreases in producer body size cause producer growth rates to increase and therefore high rates of consumption relative to growth have a positive effect upon growth rates. Reciprocally, low rates of consumption relative to growth have a negative effect upon growth rates and the transition between these qualitative effects arises at an initial Rc/Rp specific to the relationships between producer body size and growth rates, and consumer body size and consumption rates, processes which are all governed by temperature. Correspondingly, temperature had significant effects upon both the slope ($F_{2,282}=4.392$, $p<0.05$) and intercept ($F_{2,282}=17.419$, $p<0.001$) parameters describing relationships between initial and final Rc/Rp in the short term experiments. This caused a general decrease in Rc/Rp at all temperatures, but the initial Rc/Rp at which this decrease started to occur decreased with warming. This means that a lower rate of consumption relative to production can be sustained in warmer environments without producer growth rates increasing. This effect is accounted for by increases in *U. lactuca* body size at both 12°C and 15°C, yet decrease at 9°C (figure 2.17) because this result demonstrates that equilibrium Rc/Rp decreasing with warming because *U. lactuca* growth exceeds consumption by *I. granulosa* in warmer environments.

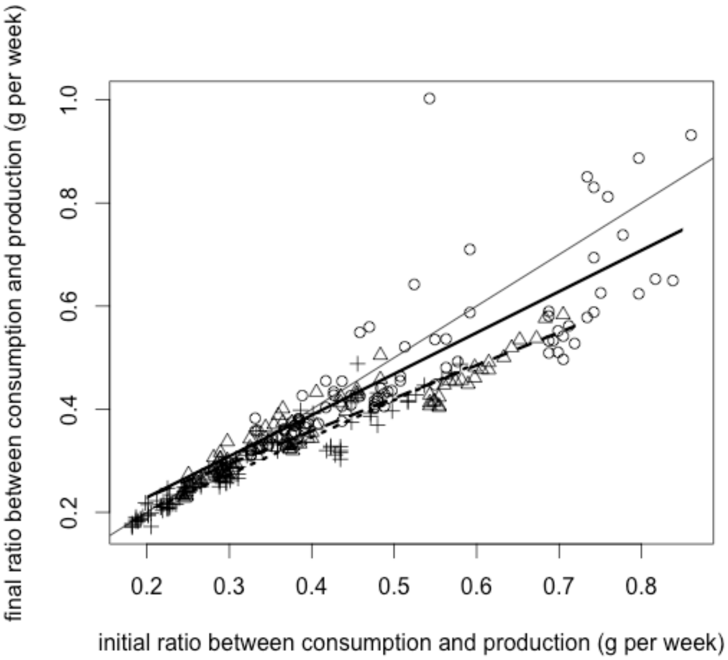


Figure 2.18 Temperature dependence in the change in the ratio of consumption to production rates over one week. The thin black line illustrates unity, the situation that would arise with no change and intersections with this line are equilibrium points. Therefore the ratio of consumption to production increased when initial Rc/Rp was low and decreased when Rc/Rp was high at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). Because temperature interacted with initial Rc/Rp to determine final Rc/Rp, this caused the initial Rc/Rp at which equilibrium occurred too decrease with warming. Because consumption rates remained constant over one week, this means that rates of production began to increase at a lower initial Rc/Rp in warmer environments.

2.3.5 EFFECTS OF TEMPERATURE DEPENDENT CONSUMER GROWTH UPON INTERACTIONS

2.3.5.1 EFFECTS OF TEMPERATURE UPON THE RATIO OF CONSUMER TO PRODUCER BODY SIZE

During the month long experiments, all *I. granulosa* individuals significantly increased in body size ($F_{1,68}$=2972.5, p<0.001) and temperature had significant effects upon these rates of individual growth ($F_{2,68}$=12.66, p<0.001) (figure 2.19). The growth rate of *I. granulosa* individuals increased with warming at all body sizes and there was no significant interaction between body size and temperature ($F_{2,68}$=0.587, p>0.05). This means that the effects of temperature upon change in *I. granulosa* body size were independent of initial *I. granulosa* body size.

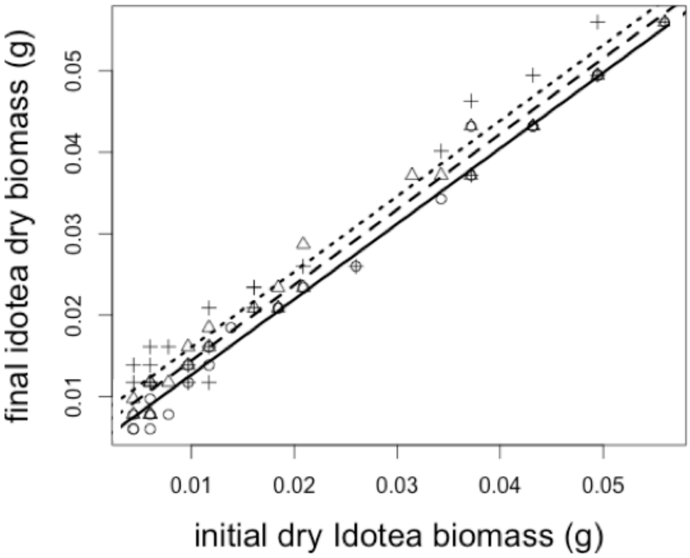


Figure 2.19 Temperature dependence in the change in *Idotea granulosa* body size over one month. The growth rate of *I. granulosa* individuals increased with body size at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). Because temperature and body size did not interact in determining individual growth rate, warming increased the growth rate of individuals at all body sizes.

Although temperature and *I. granulosa* body size did not interact to determine individual growth rates, temperature interacted with the initial ratio of consumer to producer biomass to determine the final ratio of consumer to producer biomass. Here, the final biomass of consumers relative to producers increased with the initial ratio of consumer to producer biomass. The effect of warming upon this relationship was an increase in the rate of change in Bc/Bp over one month ($F_{2,66}=6.06$, $p<0.05$) (figure 2.20).

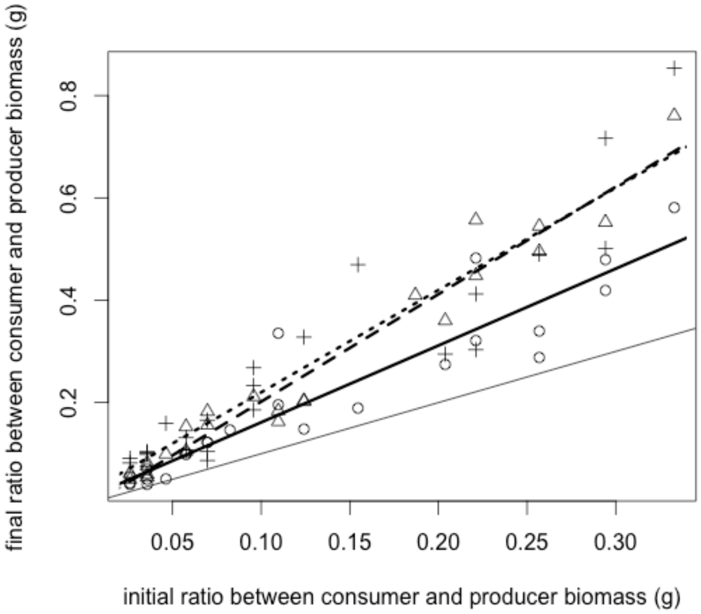


Figure 2.20 Temperature dependence of change in the ratio of consumer to producer biomass over one month. The thin black line illustrates unity, the situation that would arise with no change. Therefore the ratio of consumer to producer biomass increased over one month at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). Temperature interacted with initial Bc/Bp to determine the final Bc/Bp and this meant that the rate at which Bc/Bp increased was greater in warmer environments.

However, although change in Bc/Bp was driven by an increase in consumer body size coinciding with a decrease in producer body size, it was initial consumer body size and not temperature that caused this effect. This is because decreases in *U. lactuca* body size per unit of consumer biomass were not significantly affected by warming ($F_{2,66}$=2.04, p>0.05) (figure 2.21). This means that whilst change in the body size of consumers relative to producers is dependent upon temperature, change in the body size of producers per unit of consumer biomass is independent of temperature.

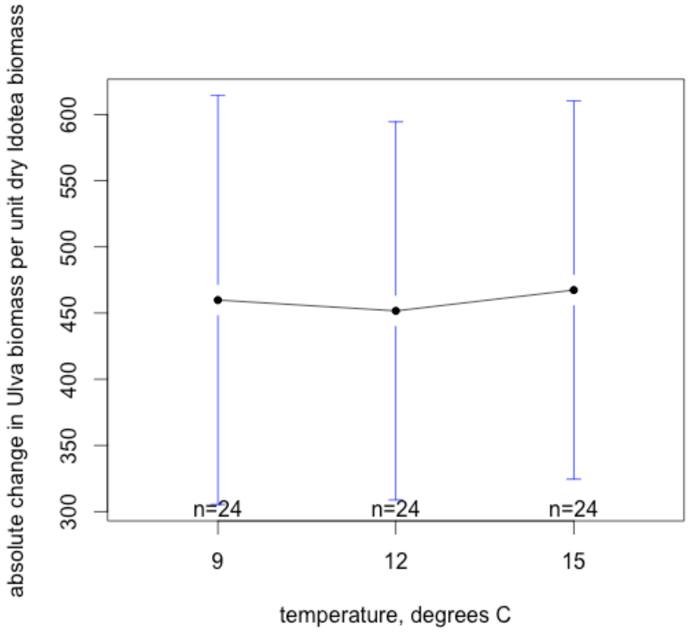


Figure 2.21 **Temperature dependence of the absolute change in *Ulva lactuca* biomass relative to *I. granulosa* biomass over one month.** Relative to *Idotea* body size, absolute change in *U. lactuca* biomass did not significantly differ according to temperature. Thus the initial ratio between producer and consumer biomass is more determinant of change in producer biomass than temperature.Points represent the mean and bars the 95% confidence interval.

2.3.5.2 EFFECTS OF TEMPERATURE UPON CONSUMPTION RELATIVE TO GROWTH

In contrast with the short term experiments, Rc/Rp was observed to significantly increase in all instances in the month long experiment ($F_{2,66}$=2.61, p=0.08) (figure 2.22) and coincide with a consistent increase in Bc/Bp at all temperatures ($F_{2,66}$=6.06, p<0.05) (figure 2.20). This result demonstrates that the temperature dependence of *I. granulosa* growth (figure 2.19) causes consumption rates to increase at a rate that is temperature dependent, and proportional to the effects of temperature upon *U. lactuca* growth rates. Over time therefore, the effects of warming and consumer body size upon consumption rates overrides the positive effects of warming upon *U. lactuca* growth rates (figure 2.21).

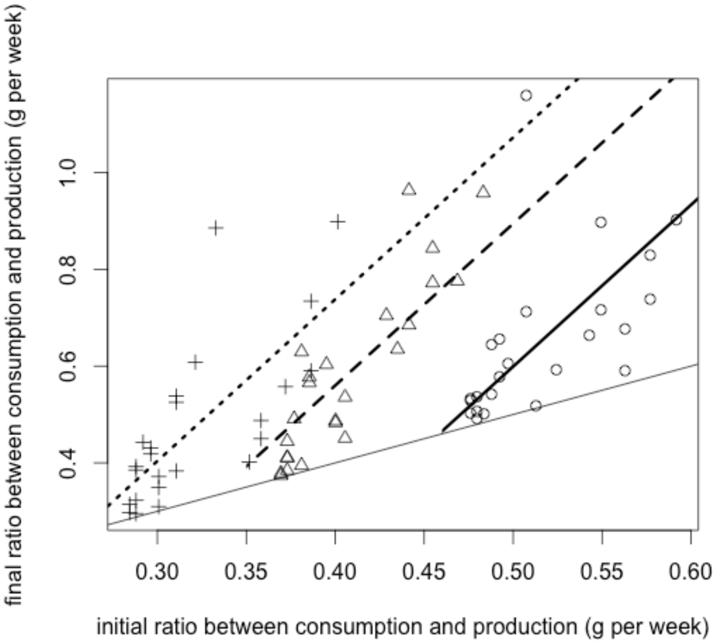


Figure 2.22 Temperature dependence of change in the ratio between consumption to production rates over one month. The thin black line illustrates unity, the situation that would arise with no change and intersections with this line are equilibrium points. Therefore the ratio between consumption and production increased over one month at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). Warming increased the final ratio between consumption and production rates but did not increase the rate at which the final ratio between consumption and production increased. This caused the initial rc/rp at which no change occurs to decrease with warming.

2.3.6 DURATION OF THE COMPENSATORY RESPONSE BY PRODUCERS

Warming had significant effects upon the ratio between consumption and production (Rc/Rp) that could be sustained over time. The initial Rc/Rp at which Rc/Rp remained constant significantly decreased in both the week ($F_{2,66}=4.39$, $p<0.05$) (figure 2.18) and month long ($F_{2,66}=2.61$, $p=0.08$) (figure 2.22) experiments. This means that in warmer environments, a lower ratio of consumption relative to production can be sustained over either duration. However, during the week-long experiments, a high initial Rc/Rp corresponded to a lower final Rc/Rp (figure 2.18) and in the month long experiments, a high initial Rc/Rp corresponded with a greater final Rc/Rp (figure 2.22). This means that during the week-long experiments, a high rate of consumption relative to production caused rates of production to increase relative to consumption and in the month long experiments, a high rate of consumption relative to production caused rates of production to decrease relative to consumption. These results are explained by consumption having a positive effect upon production in the absence of consumer growth and consumer growth eliminating that positive effect. In relation to warming driving a consistent decrease in the Rc/Rp that was stable for the duration of the experiment, this means that the positive effects of consumption upon producer growth are increased by warming, but so too are the negative effects of consumer growth. As a consequence, temperature has no significant effect upon change in producer body size relative to consumer body size (figure 2.21)

2.4 DISCUSSION

The positive effects that grazing has upon productivity (Hilbert *et al.,* 1981, Williamson *et al.,* 1989, Belsky *et al.,* 1993, deMazancourt *et al.,* 1998, Wise & Abrahamson, 2008, Lebon *et al.,* 2014,) appear in this study, to be enhanced by warming. This is because individual producers were able to compensate for increases in consumption and thereby prolong the supply of resources necessary for rapid consumer growth. However, consumer growth caused consumption rates to increase and therefore within the duration of a month, consumption rates began to outstrip rates of producer growth. This caused decreases in producer body size. However, relative to consumer body size, those decreases in producer body size were not affected by temperature (figure 2.21).

The main implication of these results is that warming will not affect food web structure because a degree of equivalence exists in the effects of temperature upon both producers and consumers: The more effective the compensatory response, the more rapidly consumers consume it. It makes sense that consumers should make the best of what they've got, and therefore they may respond to increases in production by increasing rates of consumption to their best advantage. However, the issue arises as to whether consumers have no control over the compensatory response by producers, and therefore just happen to benefit from it, or whether consumers actively tailor their rate of consumption to "optimize" the producers they consume.

If consumers do not control the compensatory response by producers, but just happen to benefit from it, then the compensatory response must be explained from attributes of the producer alone. In this study, the compensatory response by *U. lactuca* to consumption is fundamentally explained by both individual growth rates and maximum body size increasing with warming in the absence of consumption (figure 2.15). This means that in order to understand the causes of the compensatory response we need to explain the mechanisms by which warming caused individual *U. lactuca* growth rates and maximum body size to increase. From the perspective of metabolic theory (Brown *et al.,* 2004, Gillooly *et al.,* 2001), this is complicated because whilst individual growth rates are predicted to increase with warming (Ohlberger, 2013), the maximum body size of ectotherms is expected to decrease with warming (Sheridan, 2011). Thus it is necessary to explain why warming caused the maximum body size of *U. lactuca* to increase. This can be achieved by assuming that warming increased the resource supply levels at which photosynthesis was saturated (saturation point), such that the physiological response of *U. lactuca* to warming effectively increased the carrying capacity of the environment. This is in accordance with observations of warming increasing the saturation point of both light and CO2 at (Idso *et al.,* 1987, Long, 2006, Marsh *et al.,* 1986). However, according to Blackman's (1905) law of limiting factors, the most limiting factor is the only limiting factor. This means that where warming increases the saturation point for any resource, there will still be a factor that is limiting. Thus even if warming increases the saturation point of light and CO_2, then other resources such as nitrogen (N), phosphorous (P), or potassium (K) eventually limit the assimilation of carbon, and therefore primary producer body size. In this study, that is unlikely to be the case. This is because mesocosms were of flow through design and supplied fresh seawater during the winter, a time when phytoplankton levels are low, and therefore nutrient levels high (Hayward & Ryland, 1995, Shammon Hartnoll, 2002). Furthermore, pilot experiments, where mesocosms were enriched with nutrients, also indicated that enrichment with NPK fertilizer had no effect upon *U. lactuca* growth. Thus it can be assumed that the maximum body size of *U. lactuca* in this study was not resource limited.

Returning to Blackman's (1905) law of limiting factors, temperature is now the most limiting factor of *U. lactuca* body size. Thus instead of the compensatory response by producers being explained by metabolic theory, it can be explained by thermal performance curves. This explanation requires that the maximum test temperature used in this study (15°C) is at or below the thermal optimum for *U. lactuca* and indeed it is, with Fortes and Luning (1980) reporting a broad thermal optimum of 10°C -15°C for *U. lactuca* in the North Sea. Thus the compensatory response observed in this study by *U. lactuca* to consumption can be explained very simply: In the range of test temperatures, temperature limited individual body size and growth rate. Mechanisms that cause the compensatory response by producers can thus be explained by observations of producers in the absence of consumption (figure 2.15). However, this explanation requires that equivalence in the responses of *U. lactuca* and *I. granulosa* to warming occurs because warming has similar effects upon rates of consumption as it does upon rates of producer growth. This explanation is again contra to the predictions of metabolic theory (Brown *et al.,* 2004, Gillooly *et al.,* 2001) and contra to the empirical observations of warming having disproportionately greater effects at higher trophic levels (Petchey *et al.,* 1999). Thus as opposed to assuming that consumption rates merely increase as a mechanistic outcome of warming, it is necessary to assume that to some degree, consumption rates are adapted to optimize production. In effect, consumers adapting rates of consumption in response to the body size of producers, and the environment in which they live can achieve this (Belsky, 1986, Paige & Whitham, 1987). However, as opposed to this being a behavioral response by individual consumers in the short term (which would be tantamount to agriculture!) this response by consumers is hypothesized to occur at the species level, as a consequence of evolutionary adaptation by consumers. This hypothesis (Vail, 1992, Agrawal, 2000, deMazancourt *et al.,* 2005) predicts that consumers are adapted to optimize the productivity of the producers they consume as an evolutionary response to the carrying capacity of their shared environment (Agrawal, 2000). This demonstrates that consumers may be adapted to optimize production, and the observations of this study demonstrate that production is optimized when the producer lives at sub-optimal temperatures. Thus consumers may be adapted to consume producers living at sub optimal temperatures and if this is the case, increases in production may compensate for the effects of warming upon consumption.

CONCLUSION

Because the test temperatures used in this study were at or below the thermal optimum for *U. lactuca,* warming increased the growth rate and individual body size of *U. lactuca* in the absence of consumption. This provided the conditions under which increases in consumption by *I. granulosa* due to warming were compensated for by increases in primary producer growth. As a consequence, warming induced increases in consumption may not shift the ratio of consumer to producer biomass if primary producers exist at sub-optimal temperatures.

CHAPTER 3: VARIATION IN INDIVIDUAL RESPONSES TO WARMING: EFFECTS ON POPULATIONS

Abstract

Warming is predicted to cause the ratio of consumer relative to producer biomass to increase as a consequence of increases in consumption relative to production. Simultaneously, warming is expected to drive a universal reduction in the body size of consumer individuals because of fundamental changes in the relative rates of resource acquisition and individual growth. In this chapter, I investigate the effects of variation in consumer body size and temperature upon the ratio between consumer and producer biomass. I achieve this using the interaction between the intertidal herbivore, *I. granulosa,* and the intertidal macroalgae, *U. lactuca* as a model. I found that the mean body size of individual consumers explained change in consumer biomass relative to change in producer biomass whilst temperature did not and this occurred in both individual and population level interactions. This was explained by the gross growth efficiency (E_C) of consumer individuals (the rate at which consumer individuals increase in size relative to the quantity of biomass consumed) because *Ec* decreased with consumer body size yet increased with warming at all body sizes. Thus relative to the rate at which producer biomass was consumed, smaller consumers grew at a faster rate than larger ones, and warming increased this effect. This means that change in consumer biomass relative to change in producer biomass can be equal at different temperatures if mean consumer body size is adjusted accordingly. This result was confirmed by a further experiment where I compared populations containing both juveniles and adults with those containing only adults. In this experiment, populations consisted of a random assortment of individuals within each size class such that whilst population structure was a controlled variable, mean individual body size was not. Here again, the size structure of individuals within a population was a better predictor of change in consumer biomass relative to change in producer biomass than temperature. Overall, these findings indicate that consumer body size may be more important than temperature in determining community structure.

3.1 INTRODUCTION

A fundamental attribute of any individual organism is its body size and in response to warming, this is widely observed to decrease (Gardner *et al.,* 2011, Ohlberger 2013). There are several explanations for how this occurs, either as a response by individuals to their immediate environment, or as a multigenerational adaptive response by populations. However, all of these explanations are fundamentally the same in that they depend upon temperature having variable effects upon the rates of two concurrent processes. For example, as an immediate response by individuals to their environment, the body size of individuals can decrease because temperature can cause rates of individual development to increase at a faster rate than rates of individual growth (Forster *et al.,* 2011, Forster & Hirst, 2012). This causes the size of organisms at maturity to decrease (Atkinson, 1994, Ohlberger, 2013). Alternatively, the rates of processes requiring energy (metabolism) may increase with warming faster than the rate with which individuals acquire energy by foraging or digestion (Atkinson & Silby, 1997). Furthermore, in aquatic organisms, even if individuals are able to forage sufficient food resources, body size may be limited because rates of oxygen uptake are insufficient for metabolism (Portner & Knust, 2011). As an adaptive population level response, the body size of individuals may decrease because warming increases interaction strengths (Kordas *et al.*, 2011) and shifts the fundamental balance between top-down rates of consumption and bottom-up rates of production (Vucic-Pestic *et al.,* 2011, Yvon-Durocher *et al.,* 2011). In both cases, where individual body size decreases either as an immediate response by individuals, or as an adaptive response by populations, it is because the fundamental outcome of two concurrent processes being affected differently by temperature is a decrease in the amount of energy that can be allocated to growth.

Generally and very crudely, the amount of energy that can be allocated to individual growth is described by the relative proportions of individual metabolic rate allocated to maintenance (catabolism) and growth (anabolism) (see section 1.1.4 for more detail). Catabolism increases with temperature, and that increase is disproportionately greater for larger individuals than smaller ones (Brown *et al.,* 2004) and this means that the proportion of metabolic rate that can be allocated to growth is determined by the interaction between body size and temperature (Gillooly *et al.,* 2001). Specifically, the effects of the interaction between body size and temperature upon catabolic rate may be either continuous, increasing exponentially with body size according to a fixed exponent (Perrin, 1995, Brown *et al.,* 2004), or ontogenetic, increasing at certain fixed points in an individuals' life history (Angilletta & Dunham, 2003). According to either mechanism, catabolism increases as individuals get larger, and the proportion of an individuals' metabolism that can be allocated to growth declines. Consequently, individual growth rates decline as individuals get larger and because temperature increases that rate of decrease, individuals in warmer environments attain a smaller maximum body size and at a younger age (Atkinson, 1994).

Closely linked to catabolism is the concept of individual growth efficiency, (Welch, 1968, Kooijman, 2000). For the purposes of this study, I define individual gross growth efficiency, *Ec,* as the relationship between the quantity of resources consumed by an individual, *C*, and the amount by which an individual grows, *G* (Box 3.1). As the catabolic costs of individuals increase, a smaller proportion of metabolism can be allocated to growth, and therefore relative to the quantity of resources consumed, the growth rate of an individual decreases (Angiletta et al., 2004). As a consequence, *Ec* decreases according to the interaction between temperature and body size that determines catabolism, and in warmer environments larger individuals have a lower *Ec* than smaller ones.

BOX 3.1 DEFINING *EC*: RELATIONSHIPS BETWEEN INDIVIDUAL GROWTH AND CONSUMPTION

According to dynamic energy budget models (Kooijman, 2000) then of the quantity of resources consumed by an individual (C), a proportion is lost as faeces (F) and the remainder is assimilated as biomass (A). Therefore, the total resources assimilated by an individual can be expressed as:

$$\textit{Assimilation} = A = C - F$$

Assimilated resources can be incorporated into individual biomass either as somatic growth (S) or gonads (G). Thus the total body mass of an individual can be expressed as:

$$\textit{Body mass} = S + G = B$$

However, the process of incorporating assimilated resources (A) into body mass (B) causes energy to be lost via respiration (R) and excretion (E). Thus in terms of assimilated energy, body mass can be expressed as:

$$\textit{Body Mass} = B = A - (R + E)$$

This means that in terms of the quantity of resources consumed, body mass can be expressed as:

$$\textit{Body Mass} = B = (C - F) - (R + E)$$

This means that as individuals grow over time (G), the efficiency with which that occurs can be expressed either as relative to the quantity of resources assimilated (G/A) or the quantity of resources consumed (G/C). In the latter case, this is the gross growth efficiency of individuals, the rate of growth relative to the quantity of resources consumed (G/C). In this thesis I describe this by the parameter *Ec*. Thus:

$$Ec = G/C$$

The functions that contribute to individual fitness, such as foraging, locomotion, growth etc. are affected by temperature (Kingsolver & Huey, 2008) and thermal performance curves (Angiletta, 2009) describe these general effects of temperature upon individual fitness (figure 3.1). In the context of *Ec* and catabolism, performance increases when fewer resources are allocated to maintenance.

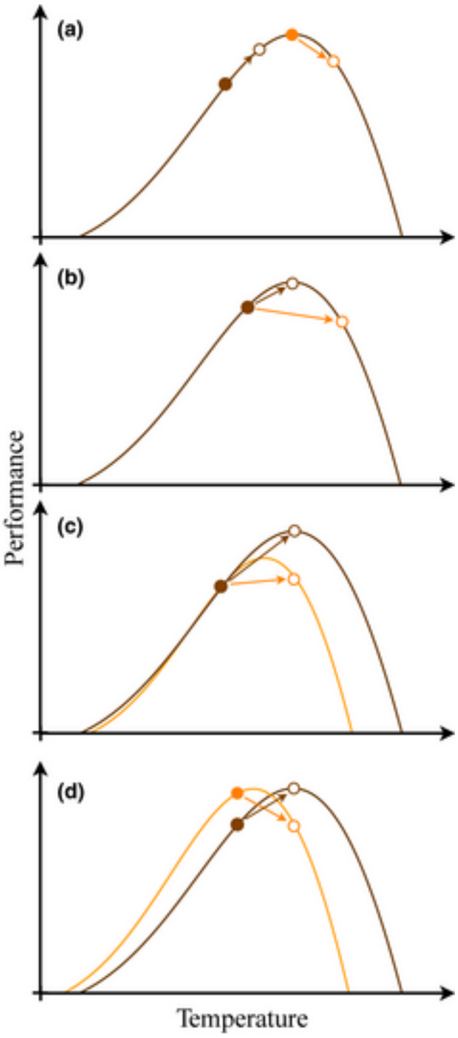


Figure 3.1 The ways in which thermal performance curves can be affected by warming (Ohlberger, 2013): (a) warming increases performance of individuals currently experiencing lower than optimal temperatures (brown dot), but decreases performance of those experiencing close to optimal temperatures (orange dot); **(b)** moderate warming may increase performance (brown arrow), but severe temperature increases lead to a reduction in performance in the absence of adaptation (orange arrow); **(c)** optimal temperatures are lower when food is limiting (orange curve), and therefore positive effects of warming on performance may be compromised by reduced food availability; **(d)** thermal optima differ between life stages and therefore different responses in performance may occur in response to warming at different stages in the individuals' life history.

Because catabolism is determined by the interaction between temperature and body size, reductions in body size that occur either as an individual response, or population level adaptation in response warming, can result in decreased catabolism and therefore increased thermal performance (Kingsolver *et al.,* 2004) (figure 3.2a). However, such decreases in body size may decrease the relative performance of smaller individuals in cooler environments (figure 3.2b) and this means that a horizontal shift in the thermal performance curve occurs with shifts in body size (figure 3.2). As catabolism is minimised by shifts in body size, multidimensional variation in thermal performance curves occurs with body size determining both the temperature at which performance is optimal and the optimal level of performance (Jonsonn *et al.,* 2001, Kingsolver *et al.,* 2004). Over several generations, organisms become adapted to a range of temperatures. This range may be highly specific, where organisms are specialists with high levels of performance limited to within a narrow range of temperatures, or less specific, where organisms are generalists, with lower levels of performance but attainable across a range of temperatures (figure 3.2c) (Stintchcombe & Kirkpatrick, 2012). With specific reference to body size, this variation in thermal performance curves describes the extent to which performance is affected by adaptation in individual body size: The extent to which catabolism is minimised, and therefore performance increased, by adaptation in body size is greater for specialists than generalists (figure 3.2c).

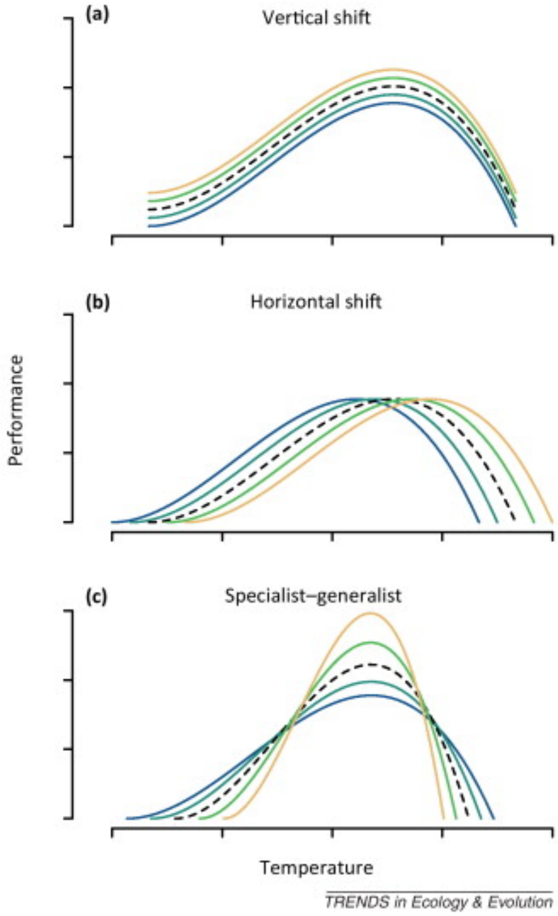


Figure 3.2 Effects of changes in body size upon thermal performance curves (Stintchcombe & Kirkpatrick, 2012). (a) Individuals of smaller body size (orange) have higher performance at any given temperature than those of larger body size (blue) due to lower catabolic costs associated with smaller body size. **(b)** Individuals of smaller individual body size (orange) have thermal optima at higher temperature than those of larger body size (blue) due to lower catabolic costs associated with smaller body size. **(c)** Organisms with less phenotypic plasticity in body size are specialists (orange), and have a higher thermal performance, but within a narrower range of temperatures than generalists (blue), which have high plasticity in body size.

Within an individual's life span, body size increases due to growth and therefore the thermal performance curve of an individual changes through time. A single thermal performance curve for an individual therefore describes the average relationship between temperature and performance for that individual over its entire lifespan. Equally, the thermal performance curve of a population describes the average relationship between temperature and performance for all individuals over the duration of observation. This has important consequences because the effects of horizontal and specialist-generalist shifts in thermal performance curves are non-linear (Izem & Kingsolver 2005) (figure 3.3). With specific reference to changes in body size, this means that average thermal performance is only explained by the average under certain circumstances. Specifically, changes in body size must increase optimal performance, not the temperature at which performance is optimal (figure 3.3).

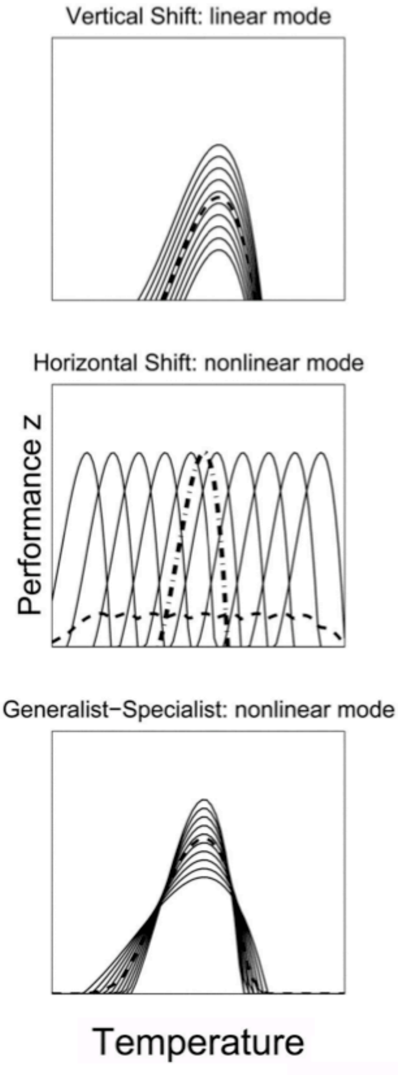


Figure 3.3 Effects of changes in body size through time upon average thermal performance curves (Izem & Kingsolver, 2005). These show the effects of change upon differences in point wise means (dashed lines) and Fréchet means (dashed-dot lines). **(Top panel)** Changes in body size over time cause changes in performance at a specific temperature with the pointwise average performance over time (dashed line) occurring at the same temperature (left). **(middle panels):** Changes occur in the

temperature at which performance is optimal; hence the pointwise average performance over time (dashed line; estimated from the arithmetic mean) occurs across a range of temperatures and performances; however, the Fréchet mean, defined as the mean which falls in the middle of the variation (Izem &Marron, 2007) (dashed and dotted line), describes the average of all points in all the curves, and therefore occurs at a specific temperature and follows the pattern of the curves. **(bottom):** Changes in thermal tolerance over time cause changes in temperature at which performance is optimal and change in optimal performance: Average performance over time (dashed line) occurs across a range of temperatures and performances but does roughly follow the pattern of the curves.

The gross growth efficiency, *Ec*, of individual consumers may play a role in determining the ratio of consumer relative to producer biomass (*I/U)* (Yodzis & Innes, 1992). This is because interactions between consumers and producers cause producer biomass to decrease (ΔU) as a consequence of consumption and consumer biomass to increase (ΔI) as a consequence of individual growth. Because the assimilation efficiency, *Ec,* describes the rate at which consumers grow relative to the amount of consumed biomass, changes in consumer biomass, ΔI, relative to changes in producer biomass, ΔU, may depend upon individual body size and temperature. As a means of investigating this, the ratio between simultaneous changes in consumer relative to producer biomass can be described by the index, $\Delta I/\Delta U$. Where gross growth efficiency is 100%, such that all producer biomass consumed is assimilated as producer biomass, ΔI would be equal to ΔU such that $\Delta I/\Delta U$ equals one. As assimilation efficiency decreases, change in ΔI decreases relative to ΔU, thus causing $\Delta I/\Delta U$ to decrease.

With regards to shifts in community structure in response to warming, consumer body size may therefore play a critical role. This is because models that predict shifts in community structure with warming do so by predicting increases in consumption as a consequence of warming, thus driving decreases in producer biomass that are simultaneous, and in direct proportion with increases in consumer biomass (O'Connor *et al.,* 2011, Iles, 2014). Yet the dependence of *Ec* upon the interaction between body size and temperature illustrates that despite warming causing consumption to consistently increase, the effects of that consumption upon consumer growth are dependent upon body size. As a consequence, the proportional decrease in producer biomass relative to increase in consumer biomass is a non-linear function of both body size and temperature (figure 3.3) (Perrin, 1995).

At the population level, non-linearity in the effects of warming upon $\Delta I/\Delta U$ may be further enhanced. This is because an increase in the body size of individuals due to growth affects attributes of the populations they comprise. In the absence of mortality, population biomass will increase linearly with the growth of individuals but where density dependence limits population biomass, mortality will occur, limiting the number of individuals. This relationship between mortality and individual growth leads to changes in the distribution of body sizes within a population over time. As illustrated by thermal performance curves (figure 3.2), this will in turn affect the rate at which the interaction between consumers and producers causes relative change in consumer and producer biomass. Most frequently observed in natural populations is size dependent mortality (Lefort *et al.,* 2015), where individual mortality rates decrease as body size increases. By selectively removing smaller individuals from the population, this increases the mean body size of individuals even in the absence of individual growth. Incorporating individual growth, the effect is magnified, with the mean body size of individuals further increasing. As a consequence, at the individual level $\Delta I/\Delta U$ is subject to constant change as individual consumers grow and at the population level $\Delta I/\Delta U$ is subject to constant change as the mortality and individual growth interact to determine the size distribution of individuals within a population. This may limit the extent to which shifts in community structure can be predicted in response to warming.

The aim of this chapter is to investigate whether individual consumer body size determines $\Delta I/\Delta U$ and to test whether changes in assimilation efficiency, Ec, explain the result. This is achieved by first examining whether body size and temperature interact to determine individual Ec. The effects of consumer body size upon $\Delta I/\Delta U$ are then investigated using individual and population level experiments. At both levels of observation, these test the general hypothesis that change in consumer biomass per unit change in producer biomass, $\Delta I/\Delta U,$ increases with temperature yet decreases with the body size of individual consumers. In the individual level experiment, this is achieved by observing the effects of individual body size upon $\Delta I/\Delta U$. The effects of consumer body size upon $\Delta I/\Delta U$ at the population level are investigated by conducting two experiments. In the first experiment, mean individual body size is manipulated to investigate the effects that individual body size has upon $\Delta I/\Delta U$. In the second experiment, a comparison is made between populations containing only adults with those containing both adults and juveniles.

In the individual level experiment where individual body size is manipulated, and in the population level experiment where mean individual body size is manipulated, estimates of Ec are made according to body size and temperature. These estimates are calculated using the model developed in this study from observations of *I. granulosa* operating in isolation and are then correlated with observations of $\Delta I/\Delta U$. The aim of this is to investigate whether the combined effects of temperature and body size upon Ec explain variation in $\Delta I/\Delta U$ that occurs with temperature.

3.2 METHODS

In order to achieve the objectives, I first determined the relationships between consumer body size and consumption rate and consumer body size and growth rate. These relationships were studied at three temperatures and described using fitted models as shown in figure 3.6. Secondly, I combined these relationships to describe the relationship between consumer body size and gross growth efficiency (E_C) at the test temperatures. Thirdly, I investigated the individual level effects of consumer body size upon change in isopod biomass per unit change in *U. lactuca* biomass by observing single isopods interacting with *U. lactuca* at the three test temperatures. Fourthly, I investigated the population level effects of consumer body size upon change in isopod biomass per unit change in algae biomass in two separate experiments by observing populations of isopods interacting with *U. lactuca* at the three test temperatures. In both experiments an equal population biomass was established across treatments. In the first experiment mean body size of isopods was varied and in the second two distinct population structures were compared, one with adults only and one combining adults and juveniles.

3.2.1 MAINTENANCE OF EXPERIMENTAL POPULATIONS AND EXPERIMENTAL SET UP

Stocks of *Idotea granulosa* and free-floating fragments of *Ulva lactuca* were maintained in the laboratory between August 2012 and July 2013 and individuals were drawn at random from these stocks for use in experiments.

Between January 2013 and March 2013, the relationships between individual *I. granulosa* body size and consumption rates, and *I. granulosa* body size and growth rates were measured by observing individuals cultured in isolation in incubators (manufacturer: LMS). From these observations, the conversion efficiency of individual isopods, E_c, and the mass specific conversion efficiency of isopods, E_c/I, was estimated (see details below)

Between March 2013 and July 2013, the effects of individual consumer body size, the mean body size of consumer populations, and population structure upon change in isopod biomass relative to change in *Ulva* biomass were measured. In each experiment, isopods were cultured together with *Ulva* in the temperature controlled units (TCU) described in chapter 2 of this PhD thesis. Each experiment was conducted over the duration of four weeks and live measurements of biomass (length in *I. granulosa*, wet biomass in *U. lactuca*) were used throughout, with dry biomass calculated according to the calibrations described in Chapter 2 for the purposes of analysis.

3.2.2 DEPENDENCE OF GROWTH AND CONSUMPTION UPON BODY SIZE AND TEMPERATURE

3.2.2.1MEASURING THE RELATIONSHIP BETWEEN IDOTEA BODY SIZE AND CONSUMPTION RATES

The relationship between *I. granulosa* body size and consumption rate was measured at the three test temperatures (9°C, 12°C, 15°C). This was done according to the protocol described in chapter 2 of this PhD thesis where individuals were cultured using live *Ulva lactuca* as a food resource, but without *U. lactuca* simultaneously growing. Individual body size was treated as a continuous variable, with single individuals ranging in size from 4mm-20mm placed in 100ml clear polystyrene pots containing filtered seawater and a single 0.25g wet mass fragment of topologically uniform *U. lactuca*. These replicates (n=48) were kept in incubators (manufacturer: LMS) at each of the respective temperatures, 9^{o}C, 12^{o}C, 15^{o}C, and filtered seawater in the pots changed every 24 hours to avoid physiological stress. Individuals were cultured for a period of one week, after which wet biomass of *U. lactuca was* measured to the nearest centigram

3.2.2.2 MEASURING THE RELATIONSHIP BETWEEN IDOTEA BODY SIZE AND GROWTH RATES

The relationship between *Idotea granulosa* body size and growth rate was measured by culturing isolated individuals at the three test temperatures exactly as according to the protocol for measuring consumption rates except individuals were fed an unlimited food supply. This was achieved by feeding 22mm diameter, topologically uniform discs of *U. lactuca* every 48 hours. Algae discs were punched from *U. lactuca* fragments using sharpened 22mm diameter copper pipe. At each test temperature, 48 isopod individuals were cultured, spanning a range of body sizes from 1 to 24mm.

Individual isopod growth rates were measured by commencing observations immediately after moulting. At this stage, individual body size was measured to the nearest millimetre and the time until each individual's subsequent moult was measured in days. The body size of individuals following this subsequent moult was then measured again to the nearest millimetre. This method was employed to counter the significant physiological, behavioural and integumentary variation that can occur during crustacean moulting (Chang & Mykles, 2011).

3.2.3 ESTIMATING GROSS GROWTH EFFICIENCY

3.2.3.1 INDIVIDUAL GROSS GROWTH EFFICIENCY

The gross growth efficiency of individual isopods, E_C, was defined as the ratio between growth rate, G_C, per unit biomass, B_C, and consumption rate, R_C, per unit biomass, B_C, of individual isopods.

Thus for individual isopods, E_c could be expressed as:

$$E_c = \frac{G_C/B_C}{R_C/B_C}$$

Equation 3.1

The effect of temperature upon *I. granulosa* consumption and growth rates was analysed by performing ANCOVA using temperature as a factor, individual biomass as the covariate and consumption and growth rates as dependent variables. The minimum adequate model was selected using the manual protocol described by Crawley (2013). Thus for each temperature, different estimates were made for parameters describing the linear relationship between individual consumer body size and consumption rate and the monomial relationship between individual consumer body size and the mass-dependent individual growth rate. With *a, b, c* and *d* as constants:

$$\ln\left(G_C/B_C\right) = \mathrm{a}\,B_C + b$$

Equation 3.2

Therefore:

$$G_C/B_C = e^{(a \ln B_C + b)}$$

Equation 3.3

and:

$$R_C = cB_C + d$$

Equation 3.4

therefore:

$$R_C/_{B_C} = c + {}^{d}/_{B}$$

Equation 3.5

Such that:

$$E_c = \frac{e^{(aB_C+b)}}{c + {}^{d}/_{B_C}}$$

Equation 3.6

3.2.3.2 Mass-specific gross growth efficiency

In order to investigate the effects of conversion efficiency upon interactions at both the individual and population level, it was necessary to describe the gross growth efficiency of both individuals and populations according to an equivalent metric.

This was achieved by estimating the gross growth efficiency per unit biomass per individual, $E_C/I/N$, as:

$$\frac{E_C}{I/N} = \frac{\sum_{i=1}^{N} Ec_i}{(\sum_{i=1}^{N} Bc_i)/N}$$

Equation 3.7

Which for individuals, where N=1:

$$\frac{E_C}{I/N} = \frac{E_C}{I} = \frac{Ec}{Bc}$$

Equation 3.8

3.2.4 OBSERVATIONS OF INTERACTIONS

The effects of individual body size upon the temperature dependence of change in isopod biomass relative to change in *Ulva* biomass, ΔI/ΔU, was investigated at both the individual and population level. At the population level, individual consumer body size was manipulated whilst maintaining constant consumer biomass across all treatments, whilst at the individual level, consumer biomass varied according to individual body size. In order to make the results of these experiments comparable therefore, the effects of consumer body size upon ΔI/ΔU needed to be standardised according to both the number of individuals involved in each experiment and the total biomass of all individuals in each experiment.

3.2.4.1 STANDARDISING CHANGE IN ISOPOD BIOMASS RELATIVE TO CHANGE IN ULVA BIOMASS

Change in isopod biomass relative to change in Ulva biomass, ΔI/ΔU, was standardised between individual and population levels by describing this change according to an equivalent metric. This was achieved by expressing the change in both isopod and *Ulva* biomass as change per unit isopod biomass per individual isopod. Thus for populations, change in isopod biomass per unit change in *Ulva* biomass is described by the difference equation:

$$\frac{\left(\frac{\Delta I}{I_t/N}\right)}{\left(\frac{\Delta U}{I_t/N}\right)} = \left(\frac{\sum_{i=1}^{N}\left(B_{C_{i_{t+1}}} - B_{C_{i_t}}\right)}{\left(\sum_{i=1}^{N} B_{C_i}\right)/N}\right) \Bigg/ \left(\frac{\sum_{i=1}^{N}\left(B_{P_{i_t}} - B_{P_{i_{t+1}}}\right)}{\left(\sum_{i=1}^{N} B_{C_i}\right)/N}\right)$$

Equation 3.9

Which for individuals, where N=1 becomes:

$$\frac{\left(\frac{\Delta I}{I_t/N}\right)}{\left(\frac{\Delta U}{I_t/N}\right)} = \frac{\left(\frac{\Delta I}{I_t}\right)}{\left(\frac{\Delta U}{I_t}\right)} = \frac{\left(\frac{\left(B_{C_{t+1}} - B_{C_t}\right)}{B_{C_t}}\right)}{\left(\frac{\left(B_{P_t} - B_{P_{t+1}}\right)}{B_{C_t}}\right)}$$

Equation 3.10

3.2.4.2 MEASURING *CHANGE IN ISOPOD BIOMASS RELATIVE TO CHANGE IN ULVA BIOMASS*

3.2.4.2.1 INDIVIDUAL LEVEL INTERACTIONS

The effects of individual isopod body size upon temperature dependent ΔI/ΔU were investigated in individual-level interactions by observing the interaction between *U. lactuca* and *I. granulosa* over four weeks. This was according to the protocol of the medium-term experiment in Chapter2 where for each test temperature, 24 replicates of a single *I. granulosa* individual ranging in length from 4 to 24mm were cultured with a 1g free floating fragment of *U. lactuca*. Replicates were cultured in 500ml clear polystyrene cups within the TCUs and fed a constant flow of filtered seawater at each of the test temperatures (9°C, 12°C, 15°C). After four weeks, *Ulva lactuca* was re-weighed and isopods measured to the nearest millimetre. These measures of wet biomass were used to estimate dry biomass according to the calibrations in chapter 2 and ΔI/ΔU, standardised according to individual biomass calculated. Using ANCOVA, with temperature as a factor and the individual body size as a covariate, the effects of isopod body size and temperature upon ΔI/ΔU were then investigated. I then investigated whether temperature dependence in ΔI/ΔU is explained by the gross growth efficiency of individuals by using ANCOVA again, with temperature as a factor and the predicted mass-specific *Ec* of individuals as a covariate. In both analyses, ANCOVA was performed using the open source software, R and the minimum adequate model was selected using the manual protocol described by Crawley (2013).

3.2.4.2.2 POPULATION LEVEL INTERACTIONS

The effects of individual isopod body size upon temperature dependent ΔI/ΔU was investigated in population-level interactions by observing the interaction between *U. lactuca* and *I. granulosa* over four weeks in two experiments. In the first experiment the mean body size of consumer populations was manipulated whilst maintaining constant population biomass between replicates and in the second experiment, the structure of consumer populations was manipulated whilst maintaining constant population biomass across replicates. This protocol was intended to examine and compare i) the effects of individual body size upon the temperature dependence of ΔI/ΔU when population biomass remains constant and ii) the effects of population structure upon the temperature dependence of ΔI/ΔU when population biomass remains constant.

In the first population experiment, where mean individual body size was manipulated, I investigated whether the temperature dependence of ΔI/ΔU is explained by the gross growth efficiency of individuals by using ANCOVA. Here, temperature was treated as a factor and the predicted mass-specific *Ec* of the population as a covariate. The most parsimonious model was selected using the manual protocol described by Crawley (2013).

In a second population level experiment, the effect of population structure upon ΔI/ΔU was investigated by comparing populations containing both adult and juvenile isopods with populations containing only adult isopods. Analysis was conducted using ANOVA with population structure and temperature as factors.

Both of the population level experiments were conducted in the same purpose built TCUs as the individual level experiment. In order to accommodate the increased number of individuals in each replicate, mesocosms in the population level experiment were 5 litres in volume instead of the 500ml mesocosms used in the individual level experiment. Because of space constraints within the TCU's, the number of replicates correspondingly decreased from 24 to eight per temperature. The 5 litre mesocosms were each fed filtered seawater at a flow rate of 30ml/minute. Thus water in each of the replicates was replaced approximately every three hours. Each population level experiment replicate contained 2g wet biomass of *U. lactuca* as a single free-floating fragment, and

0.0917g +/- 0.0002g dry biomass of *I. granulosa* individuals. I. granulosa dry biomass did not differ significantly between replicates ($F_{1,46}$=0.0108, p=0.92) and therefore the initial ratio between consumer and producer biomass, B_C/B_P, was roughly constant, at 2.42+/-0.008.

For both of the population level experiments, and across all replicates, a roughly constant initial isopod population biomass was attained whilst manipulating mean body size (first population level experiment) and population structure (second population level experiment) by constructing populations from individuals of 11mm, 9mm, 7mm, 5mm and 4mm. These body sizes were chosen because biomass calibration demonstrated the biomass of larger individuals could be approximated with integer quantities of several smaller ones, such that populations of different body size distributions yet roughly equal overall biomass could be constructed. For example, the dry biomass of an 11mm individual (0.018g) corresponds to the biomass of either a single 9mm individual (0.014g) plus a single 4mm individual (0.004g), a single 7mm individual (0.01g) plus two 4mm individuals (0.008g), or a single 5mm individual (0.006g) plus three 4mm individuals (0.012g) etc.

3.4.2.2.1 EFFECT OF MEAN CONSUMER BODY SIZE UPON ΔI/ΔU

Mean consumer body size was manipulated whilst maintaining constant population biomass across replicates by constructing populations orderly across the eight replicate mesocosms at each temperature. This meant that mean individual body size was a continuous variable, ranging between 0.01g and 0.07g dry biomass for each temperature. The population with highest mean body size was constructed of six individuals (2 x 11mm, 2 x 9mm, 2x7mm), and populations of successively lower mean individual biomass were constructed by replacing larger individuals with multiples of smaller individuals such that the population of lowest mean individual body size contained thirteen individuals (1 x 11mm, 1 x 9mm, 1x7mm, 5x5mm, 5x4mm) (table 3.1).

After four weeks, *Ulva lactuca* was re-weighed and isopods measured to the nearest millimetre. According to the calibrations in chapter 2, dry biomass and ΔI/ΔU was calculated. I then used ANCOVA, with temperature as a factor and the mean body size of individuals as a covariate, to investigate the effects of mean isopod body size and temperature upon ΔI/ΔU. I then investigated whether temperature dependence in ΔI/ΔU is explained by the conversion efficiency of individuals by using ANCOVA again, with temperature as a factor and the predicted mass-specific *Ec* of populations as a covariate. In both instances, themost parsimonious model was selected using the manual protocol described by Crawley (2013).

REPLICATE	*Mean Biomass (g)*	*N*		*LENGTH (mm)*				
				11	**9**	**7**	**5**	**4**
1	0.0138	6	Frequency	3	2	1	0	0
2	0.0132	7		2	3	1	0	1
3	0.0113	8		1	1	6	0	0
4	0.0101	9		1	1	5	1	1
5	0.0092	10		1	1	4	2	2
6	0.0084	11		1	1	3	3	3
7	0.0077	12		1	1	2	4	4
8	0.0072	13		1	1	1	5	5

Table 3.1 Frequency distributions of individuals according to body size comprising replicates in the population level experiment where mean individual body size was manipulated

3.4.2.2.2 Effect of population structure upon temperature dependence of ΔI/ΔU

The effect of population structure upon the temperature dependence of ΔI/ΔU was investigated by comparing two different population structures at each temperature: Complete populations (comprising both juveniles and adults) were compared with adult populations (comprising only adults). Four replicate populations of each category were constructed at each temperature. Juveniles were categorised as individuals below 7mm in length as this is the body size at which *I. granulosa* are reported to reach sexual maturity (Healy & O'Neill, 1984).

The aim of this experiment was to test between two population categories and therefore it was necessary to ensure that within those categories, population size structure was completely random. This was achieved as follows: A laboratory stock containing only adults was cultured. From this stock, 12 populations were constructed by collecting individuals at random and assigning them to one of 12 mesocosms. This procedure was repeated across all 12 mesocosms until the estimated population biomass of a mesocosm was either equal to, or exceeded, 0.092g. At this point no further individuals were added to that mesocosm. Once all 12 mesocosms for each stock contained either 0.092g or more biomass, population biomass was made constant across all mesocosms according to an iterative process: An individual was selected at random from within each mesocosm that contained over 0.092g biomass, and these individuals were returned to the laboratory stock. A replacement individual was then randomly selected from the laboratory stock and the process repeated until the population biomass was estimated to be 0.092g for each mesocosm. This entire procedure was then repeated only drawing individuals from a laboratory stock containing both adults and juveniles in order to create 12 replicate complete populations. Within the two population categories of 12 mesocosms, each mesocosm was then randomly assigned one of the three temperature treatments and placed in the appropriate TCU.

After four weeks, *Ulva lactuca* was re-weighed and isopods measured to the nearest millimetre. According to the calibrations of chapter 2, estimates of dry biomass were used to calculate ΔI and ΔU. Using temperature and population structure as factors, three 2-way ANOVA tests were used to identify the effects of populations structure and temperature upon ΔI, ΔU and $\Delta I/\Delta U$. Post-hoc power analysis was performed on these results using the open source software G-power.

3.3 RESULTS

3.3.1 CONSUMPTION AND GROWTH RATES

3.3.1.1 CONSUMPTION RATES

Consumption rates increased linearly with body size ($F_{2,138}$=8.713, p=0.03

, R^2=0.83, figure 3.4) but the rate of change depended on temperature. This was indicated by slope parameters differing between temperature treatments ($F_{2,138}$=13.48, p<0.001), so that higher slopes were found at higher temperatures.

3.3.1.2 GROWTH RATES

The mass specific individual growth rate decreased log-linearly with body size, high temperature led to increased mass specific growth rates at all body sizes ($F_{2,138}$=50.785, p<0.001, figure 3.5). This was indicated by significantly different intercept parameters for each treatment ($F_{2,138}$=431.64, p<0.001). However, temperature had no significant effect upon the rate of decrease in growth rate with body size, as indicated by a slope parameter that did not differ significantly between temperature treatments ($F_{2,138}$=0.055, p=0.95) (figure 3.5).

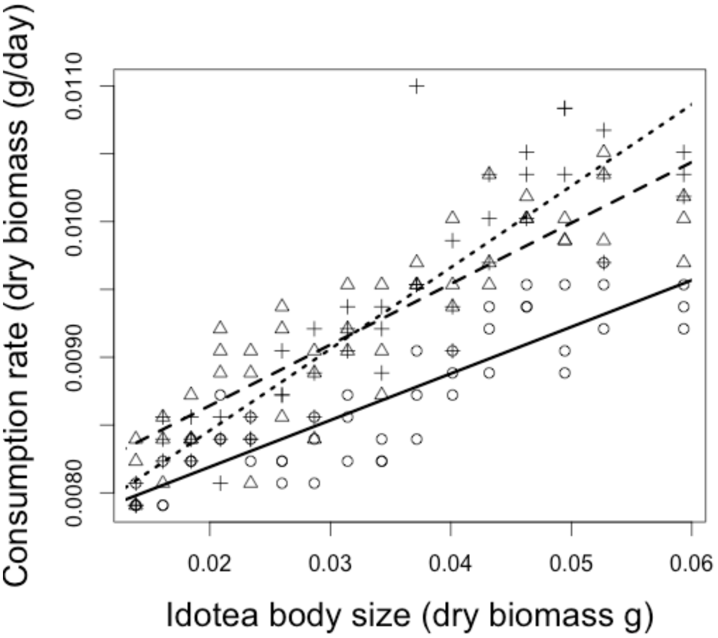


Figure 3.4 Effects of temperature upon the relationship between body size and consumption in *I. granulosa.* The consumption rate of *I. granulosa* increased with body size at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). The interactive effects of temperature and body size meant that the rate at which consumption increased with body size increased with warming.

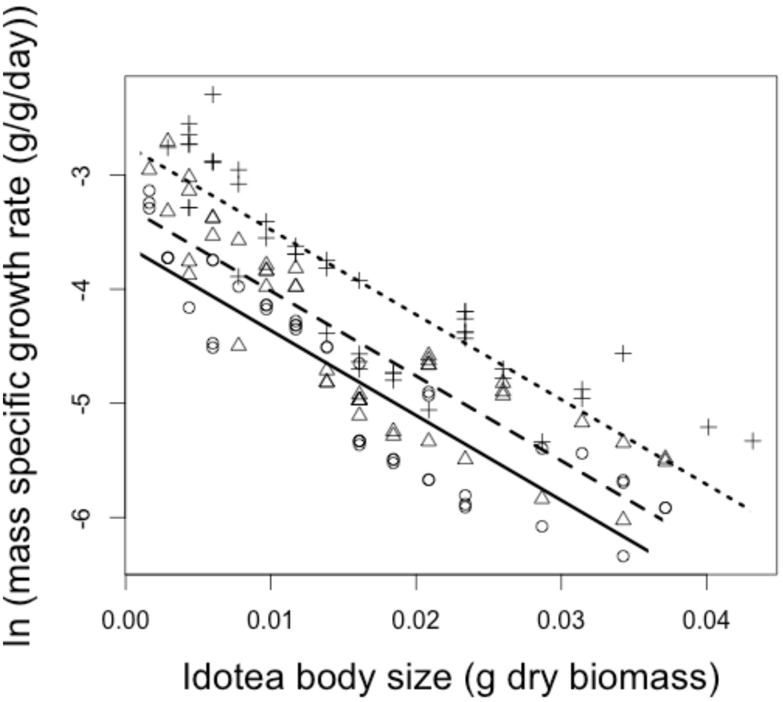


Figure 3.5 Effects of temperature upon the relationship between body size and mass specific growth in *I. granulosa.* The mass specific growth rate of *I. granulosa* decreased with body size at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). The effects of temperature and body size in determining the mass specific growth rate were non-interactive and therefore warming increased the mass specific growth rate of *I. granulosa* at all body sizes.

3.3.2 GROWTH EFFICIENCY

The observed effects of body size and temperature upon individual consumer growth and consumption rates were incorporated into equation 3.6 in order to predict individual growth efficiency. This model predicted a humped-shape relationship between individual body size and E_C at all temperatures (figure 3.6). The optimum body size occurred at the same body size for all temperature treatments. However, higher temperature resulted in increased growth efficiency especially around the optimum body size (figure 3.6).

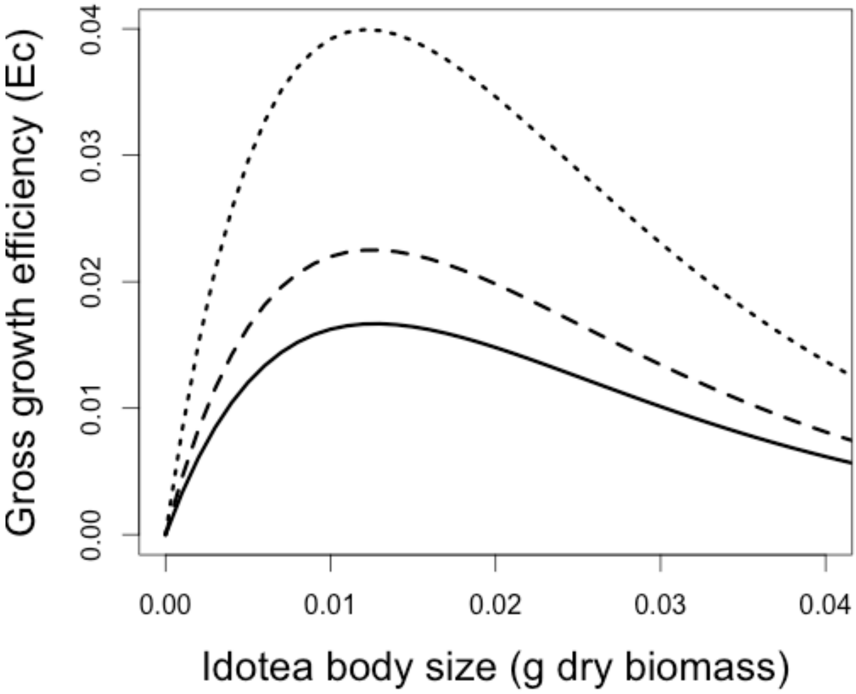


Figure 3.6 Effects of temperature upon the relationship between *Idotea body size* and gross growth efficiency, *Ec*. The relationship between body size and gross growth efficiency is the same for individuals at 9°C (solid line), 12°C (dashed line) and 15°C (dotted line). However, warming increases the gross growth efficiency of individuals at all body sizes.

3.3.3 EFFECTS OF CONSUMER BODY SIZE IN INDIVIDUAL INTERACTIONS

In the individual level interactions, change in isopod biomass relative to change in *Ulva* biomass, $\Delta I/\Delta U$, significantly decreased with individual body size at all temperatures ($F_{1,68}$= 23.408, p<0.001) (figure 3.7) and temperature dependence in these relationships was described better by linear than exponential models (linear model: R^2=0.31, $F_{3,68}$=8.89, p<0.001, exponential model: R^2=0.28, $F_{3,68}$=10.32, p<0.001). This means that relative to the rate at which isopods grow, smaller isopods have a lesser effect upon *Ulva* biomass than larger isopods. Temperature significantly increased this effect ($F_{2,68}$= 3.783, p=0.028), causing $\Delta I/\Delta U$ to significantly increase at all body sizes, but without a significant interactive effect between temperature and body size ($F_{2,66}$= 1.36, p=0.26).

Because of this, isopods in warmer environments had a lesser effect upon Ulva biomass than those in cooler environments (figure 3.7). Because ΔI/ΔU is therefore dependent upon both body size and temperature, ΔI/ΔU can be equal in environments of different temperature provided variation in isopod body size exists. The effects of gross growth efficiency, *Ec*, upon ΔI/ΔU explain this observation (figure 3.8). A significant positive relationship ($F_{1,68}$= 23.61, $p<0.001$) between *Ec* and ΔI/ΔU (figure 3.8) indicates that as *Ec* increases, the effect of consumption upon *Ulva* biomass decreases relative to consumer growth. Upon this general relationship, temperature had no significant effect ($F_{2,68}$= 1.953, $p=0.15$), thus indicating that *Ec* has consistent effects upon ΔI/ΔU across all temperatures. *Ec* is therefore a good predictor of ΔI/ΔU because being determined by temperature and individual body size (figure 3.6), it describes the rate of isopod growth relative to consumption and the consequent increase in isopod biomass relative to decrease in Ulva biomass at all temperatures.

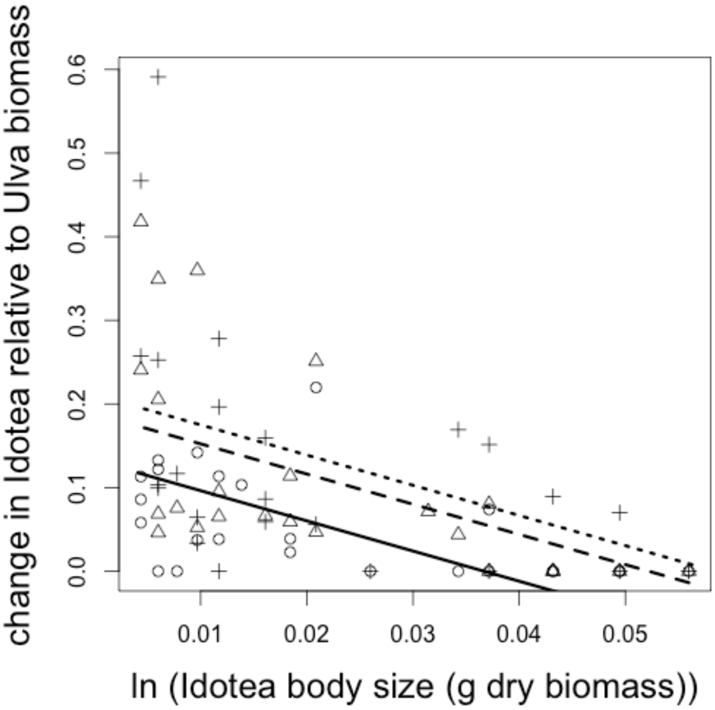


Figure 3.7 Effects of temperature upon the relationship between individual body size and Δ*I*/Δ*U* in individual level interactions. A linear model fitted the data marginally better than an exponential model at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). Temperature and *Idotea* body size did not interact in determining the change in *Idotea* relative to *Ulva* biomass. This meant that change in *Idotea* relative to *Ulva* biomass increased with warming at all body sizes. Thus relative changes in biomass can be equal in environments of different temperature if consumer body size is adjusted accordingly.

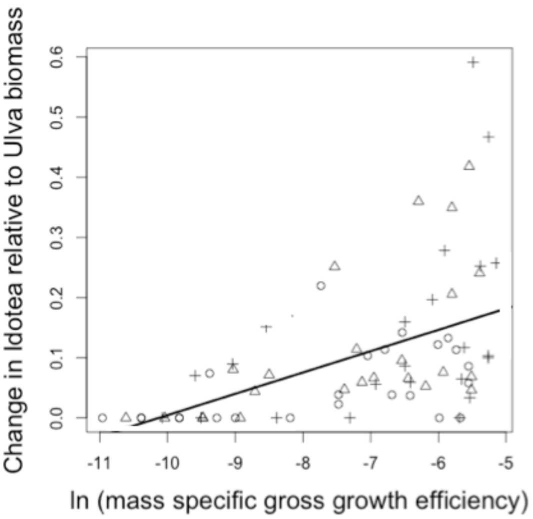


Figure 3.8 Effects of temperature upon the relationship between mass specific assimilation efficiency and *ΔI/ΔU* in individual level interactions. A linear model fitted the data marginally better than an exponential model and the relationship between gross growth efficiency and relative change in *Idotea* and *Ulva* biomass is the same at all temperatures: 9°C (circles), 12°C (triangles) and 15°C (crosses), black trendline describes the common relationship. This means that temperature dependence in the gross growth efficiency of individuals explains the relative change in *Idotea* and *Ulva* biomass.

3.3.4 EFFECTS OF MEAN CONSUMER BODY SIZE IN POPULATION LEVEL INTERACTIONS

At the population level, increases in mean individual body size caused a significant decrease ($F_{1,20} = 42.33$, $p<0.001$), in ΔI/ΔU, meaning that populations of smaller isopods have a lesser effect upon Ulva biomass than populations containing larger isopods. This effect was consistent across all temperatures because the interaction between temperature and body size was not significant ($F_{2,18} = 0.47$, $p=0.63$) (Figure 3.9) and therefore increases in temperature caused a significant increase ($F_{2,20} = 8.89$, $p=0.002$) in ΔI/ΔU at all body sizes (fig 3.9). This means that ΔI/ΔU can be equal for a population of large isopods in a warm environment and a population of smaller isopods in a cooler environment and therefore relative to the rate of increase in population biomass, the effect of a population of smaller isopods upon *Ulva* biomass in a cool environment is equal to the effect of a population of larger isopods in a warmer environment. This result is explained by the observation that temperature did not significantly affect ($F_{2,18}$ = 0.83, p=0.45) the relationship between Ec and ΔI/ΔU (figure 3.10), a result which indicates that Ec has consistent effects upon ΔI/ΔU across all temperatures.

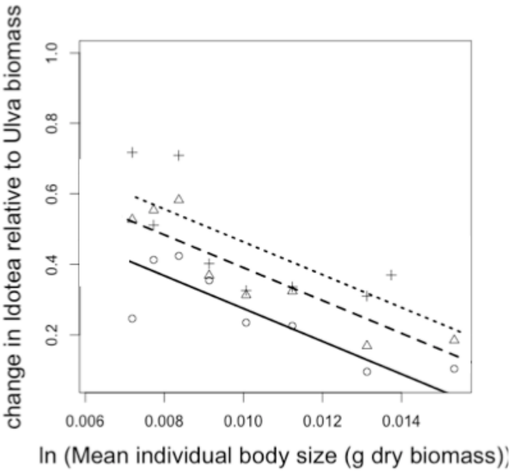


Figure 3.9 Effects of temperature upon the relationship between mean body size and Δ*I*/Δ*U* in population level interactions. Change in *Idotea* relative to *Ulva* biomass decreased with mean individual body size at all temperatures: 9°C (circles, solid line), 12°C (triangles, dashed line) and 15°C (crosses, dotted line). The effects of temperature and mean individual body size were non interactive and warming increased change in *Idotea* relative to *Ulva* biomass at all mean individual body sizes.

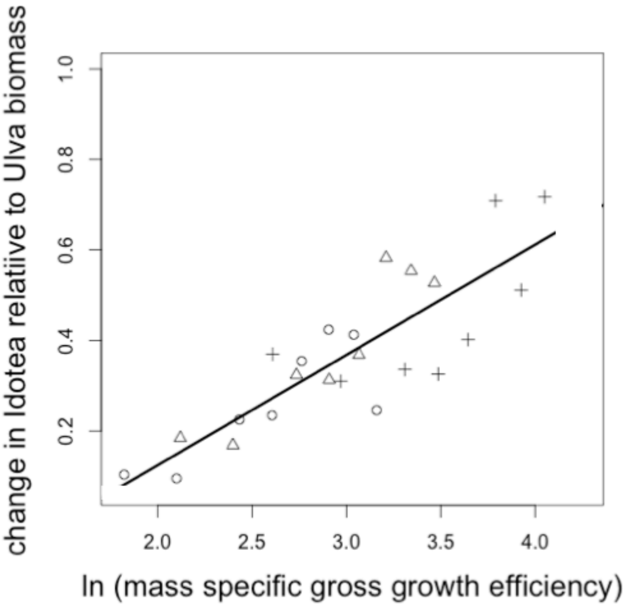


Figure 3.10 Effects of temperature upon the relationship between mass specific E_C and $\Delta I/\Delta U$ in population level interactions. The relationship between gross growth efficiency and relative change in *Idotea* and *Ulva* biomass is the same at all temperatures: 9°C (circles), 12°C (triangles) and 15°C (crosses), black trend line describes the common relationship. This means that temperature dependence in the gross growth efficiency of populations explains the relative change in *Idotea* and *Ulva* biomass.

3.3.5 EFFECTS OF POPULATION STRUCTURE

Population structure had significant effects ($F_{1,18}$ = 6.47, p=0.02, λ=753.49 power=1) upon ΔI/ΔU, with populations consisting of both adults and juveniles causing greater ΔI/ΔU than those containing only adults (figure 3.13). However, temperature did not affect ΔI/ΔU and there was no significant interaction ($F_{1,18}$ =0.11, p=0.89, λ=0.218, Power=0.907) between population structure and temperature in determining ΔI/ΔU (figure 3.12). This result occurred despite temperature having significant effects ($F_{2,18}$ = 6.86, p=0.006, λ=847.07, power=1) upon ΔU (figure 3.11) and population structure having a significant effect ($F_{1,18}$ = 6.81, p=0.02, λ=834.77 power =1) upon ΔI (figure 3.12). That is because whilst temperature significantly affects ΔU, population structure has no effect on ΔU, and whilst population structure has significant effects upon ΔI, temperature has no effect upon ΔI. These reciprocal results are interpreted as follows: Irrespective of population structure, warming significantly increases ΔU (figure 3.11), because consumption rates are higher in warmer environments. Irrespective of temperature, populations of mixed cohorts cause greater ΔI than adult populations (figure 3.12), because juvenile consumers have a higher rate of growth than adults. Combined, the effect of population structure upon ΔI/ΔU is non interactive with temperature because relative to the increase in consumer population biomass (ΔI), change in producer population biomass (ΔU) decreases with at lower temperature (figure 3.13). Therefore, the positive effects of warming upon ΔU are cancelled out. Thus where populations differ according to the size structure of individuals but mean individual body size is not a controlled variable, population structure, rather than temperature, is a better predictor of ΔU.

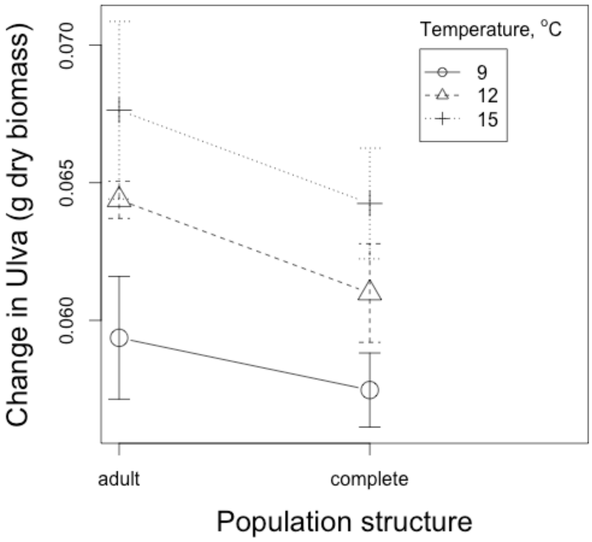


Figure 3.11 Effects of temperature and population size structure upon absolute change in *U. lactuca* biomass. *Ulva* biomass decreased in all experiments. However, whilst warming significantly increased the magnitude of decrease, population structure had no significant effects. Points represent means and bars the 95% confidence interval.

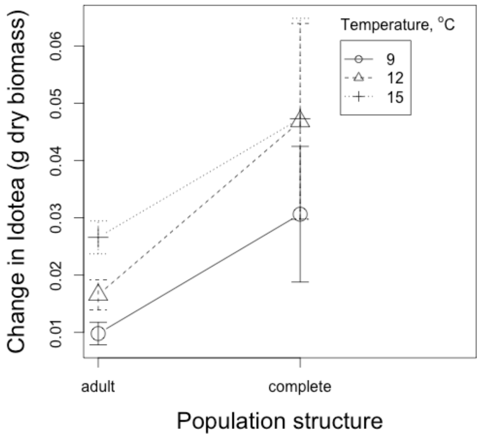


Figure 3.12 Effects of temperature and population size structure upon absolute change in *I. granulosa* biomass. *Idotea* biomass increased in all experiments. The magnitude of increase was significantly greater in complete populations than in juvenile populations. However, temperature had no significant effect. Points represent means and bars the 95% confidence interval.

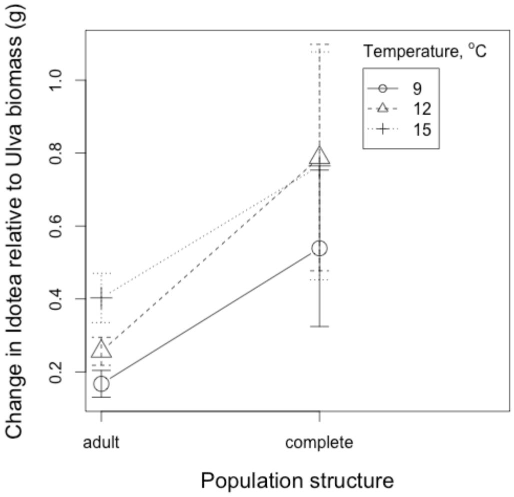


Figure 3.13 Effects of temperature and population size structure upon relative change in *I. granulosa* and *U. lactuca* biomass. Population size structure did not interact with temperature to determine the magnitude of relative change in *Idotea* and *Ulva* biomass. As a consequence, relative change in *Idotea* and *Ulva* biomass was greater in complete populations than adult populations. Points represent means and bars the 95% confidence interval.

DISCUSSION

3.4.1 SYNTHESIS OF RESULTS

The main finding of this study is that change in consumer biomass relative to change in producer biomass, ΔI/ΔU, can be equal between consumer populations existing at different temperatures depending upon variation in the body size of consumer individuals. This is demonstrated by the results of the population level experiments. In the first experiment, mean individual body size was manipulated but total population biomass kept constant. Here, ΔI/ΔU was observed to decrease as mean individual body size increased, and to increase with temperature (figure 3.9). This caused two effects. Firstly, populations in warmer environments increase in biomass faster than those in cooler environments. Secondly, populations with lower mean individual body size grow faster than those of larger mean individual body size. These two effects are non-interactive and therefore a common slope describes the effects of mean individual body size upon ΔI/ΔU whilst different intercept parameters describe the effects of temperature upon ΔI/ΔU (figure 3.9). It is this common slope describing the relationship between mean individual body size and ΔI/ΔU (figure 3.9) that illustrates how ΔI/ΔU can be equal across temperatures when variation occurs in the mean individual body size. This result is a clear indication that in natural communities, the effects of warming upon community structure may be limited by adaptation of consumer body size in response to temperature.

In the second population level experiment, consumer population biomass was kept constant and the effects upon ΔI/ΔU of populations containing only adults were compared with the effects of those containing both adults and juveniles. Within each category, populations were constructed randomly and as a consequence the mean body size of individuals was not controlled. Here, temperature did not interact with population category to determine ΔI/ΔU (figure 3.13). This was despite temperature having significant effects upon ΔU (figure 3.11) and population category having significant effects upon ΔI (figure 3.12). These results demonstrate that it is the effects of individual body size upon ΔI rather than the effects of temperature upon ΔU that determine ΔI/ΔU.

Thus the effects of temperature and consumer body size are mixed, but do not interact in determining the overall change in consumer relative to producer biomass: Temperature determines the extent to which consumers cause producer biomass to decrease, and consumer body size determines the extent to which consumer population biomass increases. Overall, in randomly constructed populations, consumer body size masks the temperature dependence of $\Delta I/\Delta U$.

The individual level experiments demonstrate the mechanism by which variation in the body size of consumers can cause $\Delta I/\Delta U$ to be equal for consumer populations existing at different temperatures. From observations of the effects of temperature and body size upon individual rates of consumption and growth, the gross growth efficiency, Ec, of individuals was estimated. E_C was found to increase with temperature yet decrease with consumer body size (figure 3.6), explaining the results of the individual level experiment where individuals of different body sizes interacted with *Ulva lactuca*. In this experiment, $\Delta I/\Delta U$ decreased with individual body size and increased with warming (figure 3.7) and at all temperatures, a common relationship between Ec and $\Delta I/\Delta U$ was observed (figure 3.8). This indicates that at all temperatures, Ec explains the amount to which individual consumers grow relative to the effect they have upon producer biomass.

An equal metric of Ec (see equations 3.7 & 3.8) also explained the outcome of the population level experiment where mean individual body size was manipulated and producer population biomass kept constant. In this experiment, $\Delta I/\Delta U$ decreased with mean individual body size and increased with warming (figure 3.9) yet a common relationship between Ec and $\Delta I/\Delta U$ was observed at all temperatures (figure 3.10). In this experiment population biomass was kept constant yet in the individual level experiment consumer biomass varied with body size. This was accounted for by expressing conversion efficiency at both levels of observation as Ec per unit biomass per individual. By explaining $\Delta I/\Delta U$ at both levels of observation, this metric has two implications: Firstly, the conversion efficiency of any unit of consumer biomass is determined by the size of the individual of which it is part. Secondly the average conversion efficiency of all units of consumer biomass in a population determines change in consumer relative to producer biomass. Combined, this means that the body size of individuals determines both the behaviour of biomass within that body, and the behaviour of the system that body is part of.

3.4.2 IMPLICATIONS OF THIS STUDY

This study indicates that shifts in consumer relative to producer biomass are determined by consumer body size. This result at first appears to be in accordance with other studies (Woodward *et al.,* 2011, Kordas *et al.,* 2011, Atkins *et al.,* 2015) that demonstrate the importance of body size in determining community structure. However, the effects of consumer body size upon the ratio of consumer to producer biomass are explained by metabolism scaling according to both body size and temperature (Brown et al., 2004). According to this explanation, the expected result of this study would be parity in ΔI/ΔU to occur at different temperatures when consumer body size is smaller in warmer environments. This however, is not observed. Instead, ΔI/ΔU is equal across temperatures both when individual body size is greater in warmer environments (figure 3.7) and when mean individual body size is greater in warmer environments (figure 3.9). This contradiction and its implications are explained by analysis of thermal performance curves.

Thermal performance curves describe the performance of organisms as having a thermal optimum at which maximum fitness is attained (Kingsolver & Huey, 2008). At temperatures below optimum, performance is limited by temperature being too low (cold limitation), and at temperatures above the optimum performance is limited by temperature being too high (warm limitation) (Angiletta, 2009).

Under warm limitation catabolic demands limit performance as a consequence of the interaction between body size and temperature whereas under cold limitation, warming increases the performance of individuals at all body sizes(Angiletta, 2009, Miller & Stillman, 2012). In this study, no significant interaction was observed between temperature and body size in determining the mass specific growth rate of individuals (figure 3.5) and warming had a positive effect upon *Ec* (figure 3.6) at all body sizes. This indicates that in this study individual performance was cold limited and therefore the parity across temperatures observed in ΔI/ΔU when individuals were larger in warmer environments occurred because warming had positive effects upon individual consumer performance. In order for this mechanism to have operated, two conditions must have been satisfied: Firstly test temperatures must have been sub-optimal such that the growth rate of consumers could increase with warming, and secondly, the body size of consumers must have been below maximum such that individuals could increase in size with warming. Thus in effect, individuals used in this study must have been both at a body size and in an environment below their thermal optimum. Whilst this may be interpreted as a downfall of this study, because it means that this study cannot explain how warming induced decreases in body size affect food web structure (Woodward *et al.,* 2011, Kordas *et al.,* 2011, Atkins *et al.,* 2015), it also provides the exception to prove the rule: The test temperatures and body sizes of individuals used in this study were apparently suboptimal. However, these test temperatures and body sizes were those observed in a natural ecosystem and this leads to the question. Why would a consumer exist at a body size and temperature that is suboptimal?

Over the range of sub optimal temperatures used in this study, the effects of temperature upon the performance of individuals was independent of body size. Because of this, no link was observed between the effects of body size upon the performance of individuals and temperature, and therefore it can be assumed that at suboptimal temperatures, individual body size is a trait determined by factors other than temperature alone. Thus contrary to the predictions of metabolic theory (Brown *et al.,* 2004, Gilloly *et al.,* 2001), individual body size may not always be optimised according to the temperature of the environment in which an individual lives. This can be explained simply by the fact that individuals grow. As a consequence, unless temperature changes at a rate proportional to the rate of individual growth, the body size of an individual, most of the time, will not be optimal relative to the temperature of the environment. Thus an alternative “optimum” is a longer term one, whereby the body size of an individual is not optimal at a single point in time, but instead optimal on average, over time. This scenario was observed in this study: Because the body size of individuals were not optimised according to temperature, and individuals were living at sub-optimal temperatures, individuals could respond to warming with an increase in gross growth efficiency at all body sizes, all of the time. This conjecture is rationalised by Martin & Huey's (2008) hypothesis of "*Why sub optimal is optimal*". According to this hypothesis, because individual performance increases steadily with rising sub-optimal temperatures, yet then decreases very rapidly with rising post-optimal temperatures, ectotherms benefit from being adapted to temperatures just below optimal: being adapted to suboptimal temperatures means that instead of warming always imposing fitness costs, warming often increases the fitness of individuals. This means that in a stochastic world, instead of individual fitness being determined by the specific genotype that encodes for the optimum temperature, fitness may be determined by phenotypic adaptation of individuals around that specific genotype (Kingsolver and Huey, 2008). This illustrates that in a changing world, alternative evolutionary strategies may be hedged: Organisms may be adapted to a specific temperature at which their performance is optimal if they attain the optimal size at the right time, or organisms may be adapted to a range of temperatures at which their performance is suboptimal, but over time leads to greater performance. Thus the results of this study point towards *I. granulosa* existing around Anglesey optimised according not to a specific temperature, but fluctuations in temperature within a specific range.

In an intertidal organism such as *I. granulosa* this makes sense because with submersion and emersion, the temperature of the intertidal environment can be highly variable (Raffaelli & Hawkins, 1996). Furthermore this variability in temperature can change in any one location daily due to variation in the timing of low and high tides relative to diurnal fluctuations in air temperature, and can simultaneously be highly variable over narrow geographic ranges due to regional variation in tide times (Denny *et al.,* 2011). As a consequence of this local temperature variation, "hot spots" and "cold spots" may occur within very narrow geographic ranges of intertidal environments (Helmuth *et al.,* 2006) such that populations within close proximity may experience variable selection pressures with regard to temperature. Thus it is plausible that the response of *Idotea granulosa* to warming that was observed in this study may be general to organisms that exist in highly variable thermal regimes and in those environments, the ratio of consumer to producer biomass may be more dependent upon consumer body size than on temperature.

3.5 CONCLUSION

The gross growth efficiency of *I. granulosa* was observed to increase with warming at all body sizes in this study, indicating that the range of test temperatures, and range of body sizes examined were below the thermal optimum for this species. This response of gross growth efficiency to warming meant that shifts in consumer relative to producer biomass were more dependent upon consumer body size than upon temperature. Thus it is expected that where consumers exist in environments where temperature is suboptimal, warming will not shift the ratio of consumer to producer biomass.

CHAPTER 4: WAVE EXPOSURE DETERMINES THE INTERACTIONS BETWEEN CONSUMERS AND PRODUCERS

Abstract

Laboratory studies predict that because warming increases the maintenance costs of individuals, the mass specific consumption rate of consumers increases. This mechanism is expected to cause warming to drive a strengthening of trophic interactions and an increase in the top-down control of producer populations. However, abiotic factors other than temperature may determine relationships between the top-down and bottom-up control of community structure and therefore warming may have unpredictable effects upon natural ecosystems. In this chapter I test the hypothesis that wave exposure increases the maintenance costs of individuals and thereby strengthens the trophic interaction between *Idotea granulosa* populations and their food resource. I achieve this by observing the *Idotea* populations and the macroalgae community over thirteen months on four shores around Anglesey. Shores were divided into two localities (Cemlyn and Aberffraw) and within each locality, a shore representing each of the two extremes in wave exposure studied. Using the Granger test of causality, I investigated whether Idotea populations were subject to bottom up control by the macroalgae community, and whether wave exposure affected this. I found that on exposed shores, macroalgae community biomass determined *Idotea* population biomass whilst on sheltered shores it did not. It is expected that this relationship occurs because macroalgae provides both the food resource and habitat for *Idotea* populations and therefore pruning and dislodgement of macroalgae by wave action causes simultaneous losses in both macroalgae community biomass and *Idotea* population biomass. Despite this, there was no significant difference between the macroalgae community biomass of exposed and sheltered shores over the 13 month period and this result is explained by variation in the mass-dependence of macroalgae community growth rates between shore: On exposed shores, the growth rate of low standing biomass is greater than on sheltered shores whilst on sheltered shores the growth rate of high standing biomass is greater than on exposed shores. This result indicates that the macroalgae community present on sheltered and exposed shores is adapted to local conditions such that the negative effects of wave action upon macroalgae community biomass are compensated for increases in growth at low standing biomass. Over the 13 month period, no significant effects of wave exposure were observed upon the mean body size of *Idotea* individuals, thus indicating that any dislodgement of individuals is independent of body size. However, the relative contribution of larger individuals to population growth was smaller for *Idotea* in exposed locations. This result is explained by the hypothesis that the energetic costs associated with not being dislodged are greater for larger individuals in more exposed environments. Overall, these results indicate that whilst an abiotic factor

such as wave exposure can be determinant of community structure, it has highly variable, and not necessarily coupled effects upon interactions between consumers and producers.

4.1 INTRODUCTION

Warming is predicted to drive shifts in food web structure by altering the relative effects of top-down and bottom up control (Shurin *et al.,* 2012, Kishi *et al.,* 2005). The supply of nutrients determines bottom up control (Masterson *et al.,* 2008) and where that does not increase simultaneously with temperature, warming causes rates of consumption to increase faster than rates of production (O'Connor *et al.,* 2009) such that the top-down control of food webs increases (Petchey *et al.,* 1999). This shift in the control of food webs is explained by warming increasing the maintenance costs of individuals (Brown *et al.,* 2004) such that the rate at which consumers grow, relative to the rate at which they consume resources decreases (O'Connor *et al.,* 2009, O'Connor *et al.,* 2011, Kratina *et al.,* 2012, Shurin *et al.,* 2012, Seifert *et al.,* 2014). In reality however, abiotic factors other than temperature, such as the disturbance regimes of fire, drought, flooding or wave exposure may affect the maintenance costs of individuals (Parminter, 1998). Because of this, the ratio of consumer to producer biomass observed in a food web, and the relative roles of top-down and bottom-up control, may not be determined by temperature alone, but also by other abiotic factors which affect the maintenance costs of individuals.

4.1.1 WAVE EXPOSURE AS A DISTURBANCE REGIME

The structure of rocky shore ecosystems is generally dominated by wave exposure (Dayton, 1971, Lobban & Harrison, 1994, Raffaelli & Hawkins 1996), with geography, local geology and topography affecting the degree to which certain habitats are affected (Burrows *et al.,* 2008, Hartnoll *et al.,* 1985, Hartnoll & Hawkins, 1985). Within habitats, the action of waves can have various consequences for organisms depending upon local geology because in addition to the direct effects of hydrodynamic forces dislodging and shearing organisms, wave action can move particles of sand, gravel and rocks that damage organisms by scouring (Lobban & Harrison, 1994). Thus although rocky shore ecosystems are generally dominated by wave action, the extent and nature of this is heavily dependent upon local context.

In addition to wave action being a highly variable factor, it has variable effects upon different organisms in the rocky shore community. For example, whilst increases in hydrodynamic forces may negatively affect some algae species due to shearing, scouring or dislodgement, it may positively affect others by moving tissues, and thereby increasing the distribution of resources and minimising self-shading (Raven, 1988, Pederson *et al.,* 2012). Thus wave action determines the relative fitness of individuals within any community depending upon the identity of species and the suitability of the habitat to those species. However, although wave action determines the relative fitness of different species in a specific habitat, this does not necessarily mean that the relative abundance of each species is determined by exposure. That is because removal of individuals by wave action can minimise competition for space between individuals, such that competition between species becomes a weak force in the structuring of communities (Tamelan, 1996). Trophic interactions cause further variation in the effects of wave action upon community structure. This is because either the effects of consumers upon producers are altered by wave exposure or wave exposure directly affects consumer behaviour. For example, grazing by the limpet *Patella vulgata* weakens macroalgae fronds and thereby increases the susceptibility of algae to be dislodged or sheared by hydrodynamic forces. As a consequence, the relationship between limpet grazing intensity and algae biomass is affected by wave exposure (Jonsson et al., 2006) without limpet behaviour being affected. Alternatively, wave exposure can affect the habitat requirements, and feeding preferences of consumers. For example, in the Baltic Sea, the isopod *Idotea baltica* feeds preferentially upon *Fucus vesiculosis* instead of *Fucus serratus* in high flow conditions, and this has been proposed as a potential mechanism by which wave exposure indirectly affects algae community structure (Engkvist *et al.,* 2004).

4.1.2 EFFECTS OF WAVE EXPOSURE ON INDIVIDUAL MAINTENANCE COSTS

Whilst the shearing, dislodging and scouring of organisms in exposed environments is likely to increase the maintenance costs of some individuals, it is not possible to predict what the general effects of exposure will be upon the maintenance costs of all individuals. This is because individuals may alter their behaviour or physiology in response to their environment (as observed in *I. baltica* (Engkvist *et al.,* 2004) and the algae *Lamineria hyperborea* (Pederson *et al.,* 2012)), and whilst that adaptation may incur energetic costs, they may be outweighed by energetic gains. Equally, the species composition of communities may be adapted to the environmental conditions such that whilst the negative effects of wave exposure upon individuals are minimised, this has associated energetic costs. Thus in order to assess the general energetic costs associated with increases in wave exposure, it is necessary to observe the effects of wave exposure upon community and population level relationships between biomass and productivity. This approach is validated by assuming that any adaptation in behaviour, physiology, species composition etc. has occurred to optimise individual fitness, and therefore the maintenance costs incurred by the community as a whole are the lowest possible. This means that irrespective of species identity, behaviour or physiology, we can assume that the proportion of metabolism allocated to growth by any community is maximal. Thus the relative and general maintenance costs associated with wave exposure can be inferred from community level observations of relationships between biomass and productivity.

4.1.1 EFFECTS OF WAVE EXPOSURE ON TOP DOWN AND BOTTOM-UP CONTROL

Rocky shore communities are comprised of a multitude of connected interactions between species (Wootton, 1993, Menge, 1995) and the precise spectrum of these interactions, which all vary in relative strength, determines community structure (Menge, 2000). Specifically, the relative strength and interconnectedness of interactions determines the relative biomass of each species (Menge, 2000) and the stability of the food web (O'Gormon & Emmerson, 2009). In some instances, keystone species (Mills *et al.,* 1993) and ecosystem engineers (Jones *et al.,* 1996) engage in interactions that are more deterministic of ecosystem attributes than the multitude of other interactions at play (Menge *et al.,* 1994). For example, limpets are considered a keystone species of the rocky shore because their grazing determines overall algae biomass and community stability (Coleman *et al.,* 2006). In turn, the canopy forming fucoid algae which limpets control recruitment of (Jenkins & Hartnoll, 2001), operate as ecosystem engineers. This is because fucoid canopies modify the environment, providing shade, dissipating wave energy and preventing desiccation during emersion that contributes to provide suitable habitat for a diverse understory community (Mangialajo *et al.,* 2012).

The key determinant of community structure is thus variation in interaction strengths, and variation in the connectedness of interactions (Emmerson & Raffaelli, 2004), and this means that the mechanisms by which wave exposure affects community structure are complex and contextual (Crowe et al., 2011). As a consequence, it is difficult to predict the general effects of wave exposure upon broad patterns of top-down and bottom up control in ecosystems (Menge, 1995). However, if the general effect of wave exposure is a scouring, dislodging or shearing of biomass, then it may be expected that in more exposed environments, a smaller quantity of production is available for consumption by consumers. As a consequence, increases in wave exposure may be expected to have the general effect of increasing the bottom up control of consumer populations.

4.1.2 DETECTING TOP-DOWN AND BOTTOM-UP CONTROL IN TWO FLUCTUATING MEASUREMENTS OF BIOMASS ON THE ROCKY SHORE.

Complex relationships exist between the biomass of organisms and the rates of change in their biomass. Because of this, correlations between the relative biomass of interacting organisms are of limited use in predicting which species determines the biomass of the other. Specifically, a correlation between two interacting organisms can only imply that a causal relationship between them exists and it cannot explain which organism causes the other to take effect. Thus in order to ascertain whether wave exposure increases the bottom-up control of consumer biomass, it is necessary to detect the causal relationships between producer and consumer biomass. This is achieved in this study by first developing a null hypothesis: The interaction between *I. granulosa* and the macroalgae community does not determine the biomass of either component. With random variation due to stochastic processes, this would be indicated by both *Idotea* biomass and macroalgae biomass randomly fluctuating through time independently of each other. From this Null hypothesis, three alternative hypotheses can be generated:

a) Macroalgae biomass fluctuates randomly but determines *Idotea* biomass
b) *Idotea* biomass fluctuates randomly but determines macroalgae biomass
c) Macroalgae biomass determines *Idotea* biomass and *Idotea* biomass determines macroalgae biomass.

Of these alternative hypotheses, c) is distinct from the others. This is because in a) macroalgae biomass is determined by stochastic processes and *Idotea* biomass is determined by macroalgae biomass such that *Idotea* biomass follows the same stochastic drift as macroalgae. In b) stochastic processes determine *Idotea* biomass and macroalgae biomass is determined by *Idotea* biomass thus macroalgae biomass follows the same stochastic drift as *Idotea* biomass. In c) however, both variables are better explained by the other than by stochastic processes and therefore stochastic processes operating on macroalgae biomass are (at least partially) over-ridden by *Idotea* biomass and stochastic processes operating on *Idotea* biomass are (at least partially) over-ridden by macroalgae biomass. Thus only in c) does the biomass of both components begin to deviate from stochastic drift and instead be determined by the interaction between the two components. Causality can thus be detected by objectively analyzing the relative stochastic drift of two simultaneous measurements (Kaufman *et al.,* 2004).

4.1.2.1 GRANGER CAUSALITY

The relative stochastic drift of two simultaneous measurements is analysed by the Granger test (Granger, 1986). This statistic detects whether variation in one time series causes variation in another based on the principal assumption that cause must precede effect (Southwick, 1997). Because of autocorrelation, the values of any variable Y at any point in time (Y_t, Y_{t+1}, Y_{t+2}, etc…) are in part dependent upon previous values of Y. However, an interaction may exist between Y and another variable X, which also varies through time (X_t, X_{t+1}, X_{t+2}, etc…) such that Y_{t+1} is determined both by Y_t and X_t. The Granger test detects the statistical significance of X_t "*Granger causing*" Y_{t+1}. The term "*Granger causing*" is used to formally describe this type of causality as distinct from other philosophical definitions of causality. This is because of the major limitations of the Granger test: It cannot test for the effects of other confounding variables that may simultaneously affect X and Y, and it cannot test for the latent, cumulative effects of *X* upon *Y*. Thus the formal causal relationship is defined as *X* "Granger causes" *Y* when Y_{t+1} is better predicted from Y_t and X_t combined than Y_t alone. This means that instead of testing for correlation between two variables, the Granger test detects the statistical significance of co-integration, which is the statistical significance of two variables sharing the same stochastic drift. This stochastic drift over a variable time lag can be used to test for Granger causality such that the statistical significance of X_t in Granger causing Y_{t+1}, Y_{t+2}, Y_{t+3} etc… can be tested. However, in this study the statistical significance of macroalgae biomass in Granger causing *Idotea* biomass and statistical significance of *Idotea* biomass in Granger causing macroalgae biomass is only tested using a time lag of one month. This is to accommodate for two pitfalls of the Granger test: Firstly, the Granger test will not detect instantaneous causality and will not detect non-linear effects of *X* upon *Y*. Secondly, the Granger test may detect (one type of) causality, but does not identify the mechanism of that causality. These pitfalls are overcome by performing Granger tests using the same time lag as that over which growth rates are calculated (monthly). This is because any non-linearity is expected to arise as a consequence of relationships between biomass and growth rates. Thus by comparing results of Granger tests (which test for linearity) with correlations in growth rates (which identify non-linearity), the true linearity of causal effects detected between macroalgae community biomass and *Idotea* population biomass can be evaluated. Furthermore, this method enables the mechanisms underlying Granger causality between macroalgae community biomass and *Idotea* population biomass to be inferred.

4.1.5 AIMS AND HYPOTHESES

The overall aim of this chapter is to test two hypotheses: Firstly, wave exposure increases the maintenance costs of individual consumers. Secondly, that this increases the bottom-up control of consumer biomass. In order to achieve this aim, I measured macroalgae community biomass and *I. granulosa* abundance, population biomass and population size structure over a 13-month period across four sites on Anglesey. These sites were split into two localities (Cemlyn and

Aberffraw), and within each locality, shores representing the extremes of wave exposure (ie: exposed and sheltered) were studied at each locality as individual sites.

4.1.5.1 WAVE EXPOSURE AFFECTS TOP-DOWN VS. BOTTOM UP CONTROL OF CONSUMERS

The first step in achieving the overall aim was to investigate whether wave exposure affected the relationship between bottom-up control of consumer biomass and top-down control of macroalgae biomass by consumers. This was achieved by testing for Granger causality between *I. granulosa* population biomass and macroalgae community biomass. In the context of Granger causality, top-down and bottom up processes can be identified as follows: Top-down control of macroalgae community biomass by *I. granulosa* population biomass is indicated by *Idotea granulosa* population biomass randomly fluctuating through time but determining macroalgae community biomass. Reciprocally, Bottom up control of *Idotea* population biomass by macroalgae community biomass is indicated by macroalgae community biomass randomly fluctuating through time but determining *Idotea* population biomass.

4.1.5.2 WAVE EXPOSURE INCREASES THE MAINTENANCE COSTS OF INDIVIDUALS

The second step in achieving the overall aim was to investigate whether wave exposure affected the maintenance costs of individuals. The proportion of individual metabolism that is allocated to catabolic maintenance and anabolic growth is determined by a complex array of cellular processes and to accurately measure those processes under natural conditions would have been beyond the scope of this study. Furthermore a complex network of species interactions determines the effects of wave exposure upon the relative fitness of individuals and to measure all of those interactions was beyond the scope of this study. As a consequence, the maintenance costs of individuals living in exposed versus sheltered environments were inferred from broader scale observations. This was achieved by observing general relationships between biomass and growth rates in sheltered and exposed environments.

4.2 METHODS

In order to test the hypotheses, I conducted a programme of fieldwork where macroalgae biomass and Idotea biomass were sampled monthly over the course of thirteen months between August 2012 and August 2013. Sampling occurred as close to Spring tides as weather permitted at each of four study sites on Anglesey, North Wales, and specimens were returned to the laboratory in Menai Bridge for analysis.

4.2.1. STUDY SITES

Two localities Aberffraw and Cemlyn, on the southwest and northerly shorelines of Anglesey, North Wales respectively, were chosen. Within each locality, two study sites were chosen, one on an exposed rocky shore, and one on a sheltered rocky shore. The relative exposure of each shore was ascertained using the Ballantine scale (Ballantine, 1961) with sheltered shores having a score of around 7.5 exposure units and exposed shores having a score of around 4.5 exposure units. In total, this meant that four study sites were chosen across the region of Anglesey, representing extremes of variation between localities and extremes of variation in wave exposure within localities. Within each locality study sites were chosen to be as far apart as possible (at least 0.5km of shore) to ensure independence from each other. At each study site a 10m x 10m area of rocky shore dominated by (>80%) *Fucus serratus* canopy was chosen between 1.5 and 3m above LAT. This community was chosen for study on two counts: Firstly, pilot studies indicated that this algal community was that in which *I. granulosa* were of greatest abundance, and secondly, during the summer when the observations began, this community appeared to be similar across the range of environments chosen.

4.2.2 SAMPLING

4.2.2.1 FIELDWORK

Between August 2012 and August 2013, each site was visited on a date as close to low spring tide as weather conditions and daylight hours permitted. At each site, ten replicate samples were collected each month. Replicates were sampled by throwing a $0.1m^2$ quadrat at random within the $100m^2$ study site. From each replicate quadrat, the biomass of canopy algae was sampled by cutting the basal stipe of any macroalgae over 15cm tall within that quadrat using a sharp knife. Cut algae was removed and sealed in labelled plastic bags. This method meant that 1% of each study site was sampled each month and therefore over the thirteen month period, a maximum of 13% of the 100m^2 site was sampled. Some quadrats, which at first appeared to have a dense algal cover, actually yielded little canopy biomass because basal stipes occurred outside of the area of the replicate quadrat. However, this method was chosen because it was assumed that observed canopy cover during emersion was not representative of canopy cover during immersion, because during periods of immersion algae are structured vertically throughout the water column. Following removal of the canopy, a 0.01m^2 quadrat was placed centrally in the larger, 0.1m^2 quadrat. From within this smaller quadrat, all algae was removed to measure understory biomass and samples were sealed in labelled plastic bags.

A total of 13% of each shore was destructively sampled over thirteen months. Although no control measures were put in place to ensure the same quadrats were sampled more than once, no visual evidence of previous sampling was observed in quadrats. This is unsurprising because the probability of not sampling new territory with each quadrat increased by just 0.01% with each replicate. This means that when the final quadrat was thrown, the probability of not sampling new territory was just 1 x 0.999 x 0.998 x 0.997…. 0.872 x 0.0871 = 0.759 which approximates to 76%. This means that for the 130th quadrat there was less than 24% chance of that quadrat containing any territory that had previously been sampled, but a much smaller probability of that replicate quadrat being entirely composed of previously sampled territory.

4.2.2.2 LABORATORY ANALYSIS

4.2.2.2.1 SEPARATING *IDOTEA GRANULOSA* FROM ALGAE

Samples of canopy and understory biomass were returned to the laboratory in Menai Bridge for analysis. For canopy samples, this was achieved by cutting fronds from the basal stipe so as to ensure all surfaces from within the complex architecture of individual algae were sampled. *I. granulosa* individuals were removed by hosing algae under pressure with fresh tap water. Pressure was applied by attaching a length of 8mm diameter silicon tubing to a tap and squeezing to create a sufficient jet of water. Algae was simultaneously shaken by hand and the resulting run-off from this process was passed through a 0.5mm mesh, to collect epifaunal individuals. This process was repeated for each piece of algae until no further epifauna were sampled.

Understorey samples were analysed differently because of the delicate and intricate nature of the algae sampled. Here, replicates were emptied into a 38 x 24cm clear pyrex roasting dish placed atop a sheet of white paper. This enabled the samples to be easily visualised. Tap water was then added to a depth of approx. 4cm which enabled individual fragments of algae and *I. granulosa* to be easily separated. Using tweezers and a 3ml plastic pipette, *I. granulosa* individuals were then separated from the algae.

4.2.2.2.2 MEASURING ALGAE BIOMASS

For each replicate, fragments of algae were blotted with tissue paper before being weighed to the nearest 0.001g. Canopy algae was weighed separately to understorey algae such that for each replicate, total canopy biomass was measured per $0.1m^2$ and total understorey biomass was measured per $0.01m^2$.

4.2.2.2.3 MEASURING IDOTEA BODY SIZE AND BIOMASS

For each replicate, *I. granulosa* individuals were counted and measured to the nearest millimetre using callipers. The wet biomass of individuals was then estimated using the calibration curve shown in figure 2.2 of this thesis. Canopy samples were analysed separately to understorey samples such that for each replicate, total *Idotea* abundance and biomass was measured per $0.1m^2$ for the canopy and per $0.01m^2$ for the understorey.

4.2.3 DATA ANALYSIS

4.2.3.1 ESTIMATES OF BIOMASS

Community level estimates of macroalgae biomass, *Idotea* biomass and *Idotea* abundance were expressed per m^2 each month. At each site, a total of $1m^2$ canopy and $0.1m^2$ understorey was sampled each month. Thus by multiplying the data for each understorey replicate by 10 and then summing the total of all canopy and understorey replicates for each month gave an estimate of total biomass per m^2 for each site each month.

4.2.3.2 ESTIMATES OF MEAN IDOTEA BODY SIZE

Estimates of mean *Idotea* body size were calculated for each site each month as the total observed biomass of Idotea per m^2 divided by the total number of individuals counted per m^2.

4.2.3.3 EFFECTS OF WAVE EXPOSURE ON TOP DOWN VS. BOTTOM UP CONTROL OF CONSUMER BIOMASS

4.2.3.3.1 GRANGER CAUSALITY BETWEEN PRODUCERS AND CONSUMERS

Community level estimates of macroalgae and *Idotea* biomass per m^2 for each month were analysed as a 13 month time series for each study site. In order to account for autocorrelation, Granger's test of causality was used in a series of pairwise comparisons to test for causal relationships. The effects of macroalgae biomass upon *Idotea* biomass, and the effects of *Idotea* biomass upon macroalgae biomass were tested in each pairwise comparison.

4.2.3.3.2 RELATIONSHIPS BETWEEN BIOMASS AND GROWTH RATES

The growth rates of Idotea populations and the macroalgae community were estimated in terms of grams per m^2 according to the following relationship:

$$Growth\ at\ time\ (t) = \frac{Biomass\ at\ time\ (t+1)}{Biomass\ at\ time\ (t)}$$

Equation 4.1

Because growth rate is thus calculated as the rate of change between two points in time, it can be correlated with either of those observations in time without consideration of autocorrelation. As a consequence, the relationship between Idotea biomass and macroalgae growth rates, and the reciprocal relationship between macroalgae biomass and Idotea growth rates was analysed using regression analysis. The effects of locality and exposure upon these relationships were then tested for using ANCOVA with locality and exposure as factors and the most parsimonious models selected according to the manual protocol described by (Crawley 2013). Each month, the same 10m x 10m area of each site was sampled, but using random quadrats. Because of this, estimates of growth rates were not generated from observations of the same quadrats through time. Whilst this increases uncertainty in estimates of growth rates at the quadrat scale, it gives estimates of growth rates general to each site.

4.2.3.4 EFFECTS OF WAVE EXPOSURE ON INDIVIDUAL MAINTENANCE COSTS

Using regression analysis, I tested the hypothesis that macroalgae community growth rates are determined by community biomass. I then tested for significant effects of locality and exposure upon this relationship using ANCOVA with locality and exposure as factors. Similarly, I tested the hypothesis that *Idotea* population growth rates are determined by mean individual body size and then tested for significant effects of locality and exposure upon this relationship using ANCOVA with those variables as factors. Minimum adequate models were selected using the manual protocol described by Crawley (2013).

4.2.3.5 EFFECTS OF WAVE EXPOSURE ON BIOMASS

In order to demonstrate that exposure had significant effects upon the relationships between biomass and growth rates, it was necessary to demonstrate that this was not due to wave exposure affecting biomass. Because of this, the effects of exposure upon macroalgae community biomass and mean *Idotea* body size were analysed using Friedman tests with monthly observations blocked together and exposure being a group (factor). This accounted for autocorrelation whilst testing whether the difference between mean Macroalgae biomass and mean *Idotea* body size over the course of 13 months differed significantly with exposure.

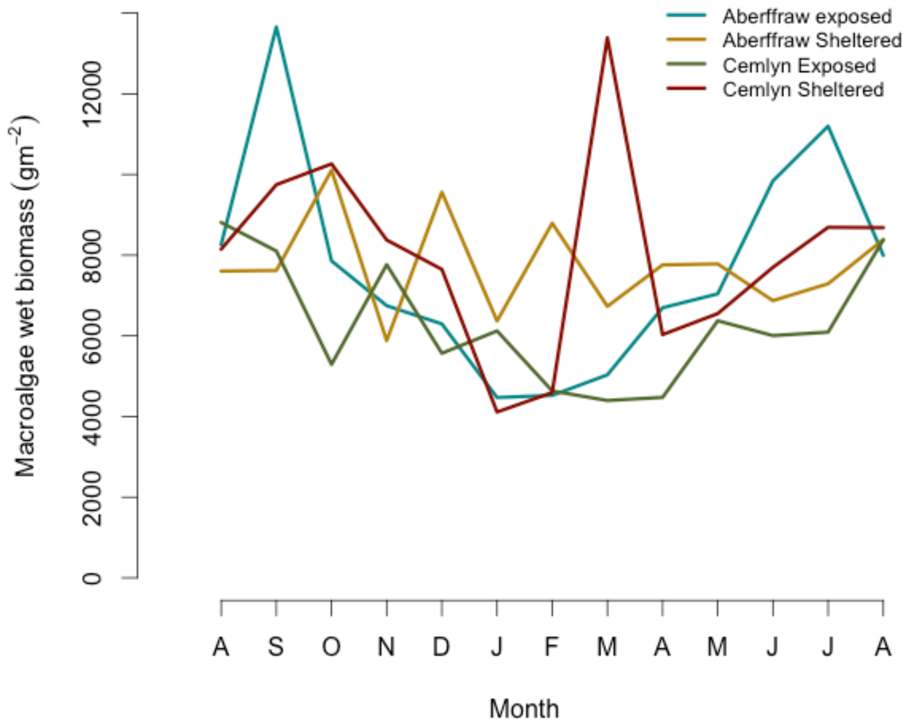
4.3 RESULTS

4.3.1 EFFECTS OF WAVE EXPOSURE UPON TOP-DOWN VS. BOTTOM UP CONTROL OF THE RATIO OF PRODUCER TO CONSUMER BIOMASS

4.3.1.1 GRANGER CAUSALITY BETWEEN PRODUCERS AND CONSUMERS

Monthly variation was observed in both total macroalgae biomass and *I. granulosa* biomass, with the general pattern being peak total biomass of macroalgae occurring between May and September (figure 4.1 (top)) and the peak biomass of *I. granulosa* occurring between April and August (figure 4.1 (bottom)).

Pairwise Granger tests indicated that causal relationships exist between macroalgae biomass and *Idotea* biomass at all study sites except the sheltered shore of Cemlyn. However, the direction of causal relationships was heavily dependent upon both exposure and location. Regarding exposure, temporal variation in *I. granulosa* biomass was significantly explained by variation in total macroalgae biomass on the exposed, but not sheltered shores of both Aberffraw and Cemlyn (table 4.1). This causality was also significant when localities were pooled and a pairwise comparison made between levels of exposure (table 4.1), indicating that *Idotea* are limited by macroalgae biomass on exposed, but not sheltered shores. Regarding location, temporal variation in total macroalgae biomass was significantly explained by temporal variation in *I. granulosa* biomass on both the sheltered and exposed shores of Aberffraw, but neither shore of Cemlyn (table 4.1). This causality was also significant when exposures were pooled and a pairwise comparison made between localities (table 4.1), indicating that *I. granulosa* biomass limits macroalgae biomass at Aberffraw, but not Cemlyn.



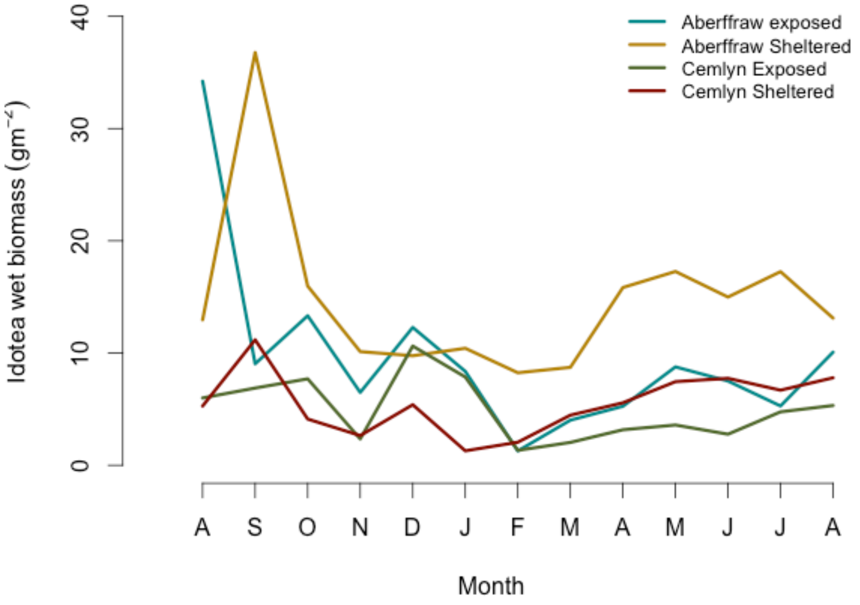


Figure 4.1 Monthly variation in *Idotea* and macroalgae community biomass. (top) Monthly variation in total macroalgae wet biomass between August 2012 and August 2013 for four study sites on Anglesey. **(bottom)** Monthly variation in *Idotea* granulosa wet biomass between August 2012 and August 2013 for four study sites on Anglesey.

SITE	CAUSE	EFFECT	df	F	p
ABERFFRAW EXPOSED	**Macroalgae**	**Idotea**	**10**	**6.86**	**0.03**
	Idotea	**Macroalgae**	**10**	**6.29**	**0.04**
ABERFFRAW SHELTERED	Macroalgae	Idotea	10	0.14	0.72
	Idotea	**Macroalgae**	**10**	**10.43**	**0.01**
CEMLYN EXPOSED	**Macroalgae**	**Idotea**	**10**	**6.38**	**0.03**
	Idotea	Macroalgae	10	0.54	0.48
CEMLYN SHELTERED	Macroalgae	Idotea	10	0.01	0.92
	Idotea	Macroalgae	10	0.4	0.54
ABERFFRAW	Macroalgae	Idotea	10	0.6	0.44
	Idotea	**Macroalgae**	**10**	**5.67**	**0.04**
CEMLYN	Macroalgae	Idotea	10	3.26	0.11
	Idotea	Macroalgae	10	0.04	0.86
EXPOSED	**Macroalgae**	**Idotea**	**10**	**6.97**	**0.03**
	Idotea	Macroalgae	10	2.55	0.15
SHELTERED	Macroalgae	Idotea	10	0.002	0.96
	Idotea	Macroalgae	10	2.38	0.16
ALL	Macroalgae	Idotea	10	0.33	0.58
	Idotea	Macroalgae	10	0.40	0.54

Table 4.1 Results of pairwise Granger tests detecting causality between temporal variation in macroalgae and Idotea biomass. A timelag of 1 month was used and significant results are shown in bold.

4.3.1.2 RELATIONSHIPS BETWEEN BIOMASS AND GROWTH RATES OF MACROALGAE AND I. GRANULOSA

The granger causality observed between macroalgae and *I. granulosa* biomass demonstrated that on exposed shores, total macroalgae biomass each month was significant in causing *I. granulosa* biomass the following month (table 4.1), and on both shores in Aberffraw, *I. granulosa* biomass each month was significant in causing macroalgae biomass the following month. These results indicate therefore, that depending on exposure and location, the biomass of either macroalgae or *I. granulosa* during any given month should determine subsequent change in the other variable. However, no relationships were observed between either total macroalgae biomass and *I. granulosa* population growth rates each month ($F_{1,49}$=0.023, p=0.879, R^2=0) (figure 4.2) nor *Idotea* population biomass and macroalgae biomass each month ($F_{1,49}$=0.038, p=0.846, R^2=0) (figure 4.3). Introducing locality and exposure as factors into these relationships also failed to explain variation. Regarding the relationship between macroalgae biomass and *I. granulosa* population growth rate, this was non significant across all study sites, with both locality ($F_{1,49}$=0.12, p=0.73)and exposure ($F_{1,49}$=0.064, p=0.80) having no significant effect. Thus despite total macroalgae biomass being significant in determining *I. granulosa* biomass the following month on exposed shores (table 4.1), this was not due to macroalgae biomass determining *I. granulosa* growth rates. Regarding the relationship between *I. granulosa* biomass and macroalgae growth rate, there was no correlation (R^2=0) and the relationship was non significant across all study sites, with both locality ($F_{1,49}$=1.11, p=0.29) and exposure ($F_{1,49}$=0.064, p=0.80) having no significant effect. Thus despite *I. granulosa* biomass being significant in determining total macroalgae biomass the following month on both shores at Aberffraw (table 4.1), this was not due to *I. granulosa* biomass determining macroalgae growth rates.

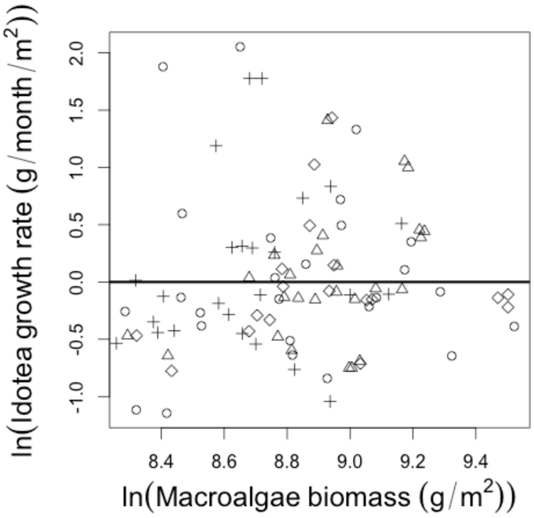


Figure 4.2 Relationship between macroalgae biomass and *Idotea* population growth rate. No significant relationship is observed for any of the four sites across Anglesey: Aberffraw exposed (circles), Aberffraw sheltered (triangles), Cemlyn exposed (crosses), Cemlyn Sheltered (diamonds).

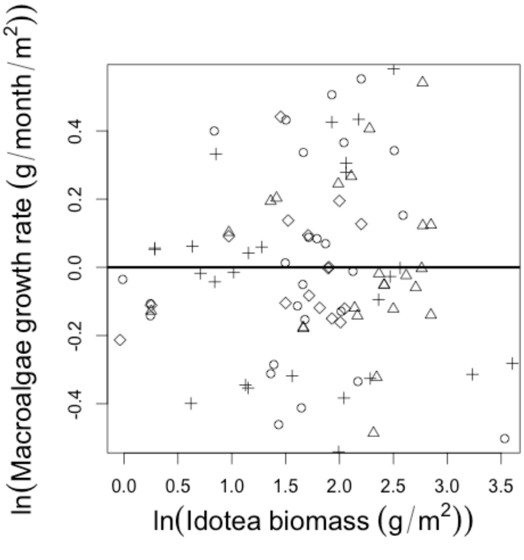


Figure 4.3 Relationship between *Idotea* abundance and macroalgae community growth rate. No significant relationship is observed at any of the for four sites across Anglesey: Aberffraw exposed (circles), Aberffraw sheltered (triangles), Cemlyn exposed (crosses), Cemlyn Sheltered (diamonds).

4.3.5 WAVE EXPOSURE INCREASES THE MAINTENANCE COSTS OF INDIVIDUALS

4.3.5.1 RELATIONSHIP BETWEEN MACROALGAE BIOMASS AND MACROALGAE GROWTH RATES

A significant positive relationship was observed between macroalgae biomass and macroalgae community growth rate ($F_{1,49}$=25.69, p<0.001, R^2=0.35) (figure 4.4). ANCOVA demonstrated that locality had no significant effects upon this relationship ($F_{1,49}$=1.11, p=0.298) yet exposure had significant interactive effects ($F_{1,49}$=3.76, p=0.03). These interactive effects of exposure caused macroalgae growth rate to increase with macroalgae biomass at a significantly greater rate on sheltered shores than on exposed shores ($F_{1,49}$=6.4, p=0.02) (figure 4.4). Despite exposure having interactive effects with macroalgae biomass in determining macroalgae growth rates, intercept parameters were not significantly different for shores of different exposure ($F_{1,49}$=1.13, p=0.29). This result indicates that whilst macroalgae community growth rates are not necessarily lower on exposed shores, they become increasingly lower relative to growth rates on sheltered shores as biomass increases. This would imply that macroalgae community growth rate is limited by wave exposure, and the degree to which wave exposure is limiting increases as biomass increases.

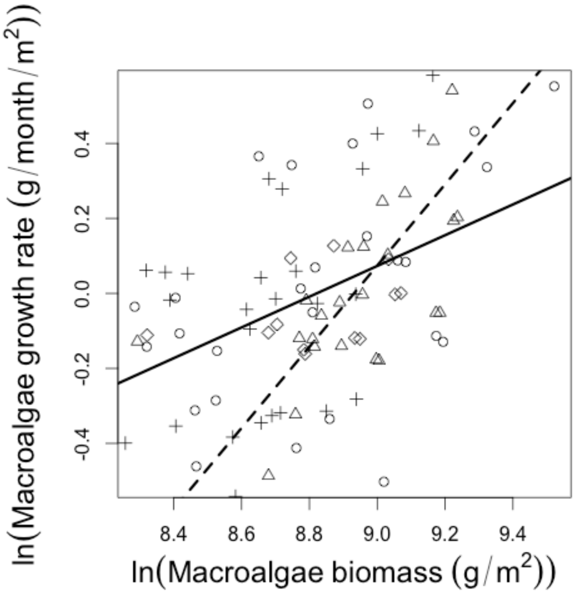


Figure 4.4 Effects of exposure upon the relationship between macroalgae community biomass and growth rate. Macroalgae community growth rate increased with macroalgae biomass on both sheltered (dashed line) and exposed (solid line) shores and growth rates increased with biomass at a faster rate on sheltered shores than exposed shores. Slope parameters are significantly different but intercepts are not. Sheltered locations are Aberffraw sheltered (triangles) and Cemlyn Sheltered (diamonds). Exposed locations are Aberffraw exposed (circles) and Cemlyn exposed (crosses). Locality (Aberffraw vs Cemlyn) had no significant effect upon the relationships.

4.3.5.2 RELATIONSHIP BETWEEN MEAN *IDOTEA* BODY SIZE AND IDOTEA POPULATION GROWTH

When data from all sites were pooled, regression analysis demonstrated that no significant relationship was observed between mean *Idotea* body size and *Idotea* population growth rate ($F_{1,49}$=0.406, p=0.53, R^2=0.09) (figure 4.5). However, performing ANCOVA upon the data categorised according to the factors of exposure and locality demonstrated that significant relationships that are specific to these factors exist (AIC incorporating factors =115.8, excluding factors = 116.4). Whilst locality did not significantly interact with *I. granulosa* body size in determining population growth rate ($F_{1,49}$=0.55, p=0.46), exposure did interact significantly ($F_{1,49}$=4.36, p=0.04). This caused significant relationships between *I. granulosa* body size and population growth rate to exist that were specific to levels of exposure. In sheltered locations, *I. granulosa* population growth rate increased with mean *I. granulosa* body size at a significantly greater rate than in exposed locations ($F_{1,49}$=4.36, p=0.04) (figure 4.5). As with the relationship between macroalgae community biomass and growth rate, intercept parameters were not significantly affected by exposure ($F_{1,49}$=0.033, p=0.86). This result indicates that whilst *Idotea* growth rates are not necessarily lower on exposed shores, they become increasingly lower relative to growth rates on sheltered shores as mean individual body size increases. This would imply that *Idotea* population biomass is limited by wave exposure, and the degree to which wave exposure is limiting increases as mean body size increases.

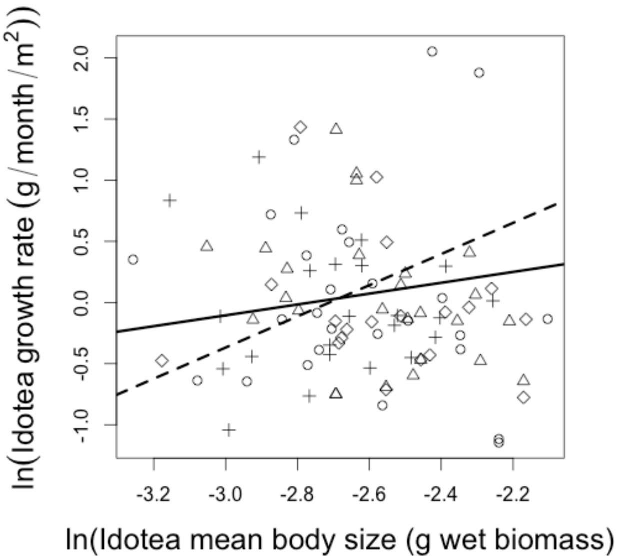


Figure 4.5 Effects of exposure upon the relationship between mean *Idotea* body size and population growth rate. *Idotea* population growth rate increased with mean individual body size on both sheltered (dashed line) and exposed (solid line) shores and growth rates increased with mean body size at a faster rate on sheltered shores than exposed shores. Slope parameters are significantly different but intercepts are not. Sheltered locations are Aberffraw sheltered (triangles) and Cemlyn Sheltered (diamonds). Exposed locations are Aberffraw exposed (circles) and Cemlyn exposed (crosses). Locality (Aberffraw vs Cemlyn) had no significant effect upon the relationships.

4.3.6 EFFECTS OF WAVE EXPOSURE UPON PRODUCER AND CONSUMER BIOMASS

The growth rate of macroalgae and the population growth rate of *I. granulosa* was different for each study site each month, as indicated by the vertical range in data points in figures 4.4 and 4.5. This variation in macroalgae growth rates was explained by a significant interaction between exposure and macroalgae biomass (figure 4.4) and variation in *I. granulosa* population growth rates was explained by a significant interaction between exposure and mean *I. granulosa* body size (figure 4.5). However, throughout the course of the year, the mean macroalgae biomass of study sites was significant (Friedmans test: $t=115.24$, $p<0.001$) but not significantly affected by either exposure ($F_{1,48}=3.371$, $p=0.073$), locality ($F_{1,48}=3.17$, $p=0.081$), or the interaction between locality and exposure ($F_{1,48}=0.547$, $p=0.46$), (figure 4.6). Thus variation in macroalgae growth rates between different study sites is explained by the interaction between macroalgae biomass and exposure without either exposure or locality causing significant variation in macroalgae biomass. Regarding mean individual body size, a similar pattern was observed. Here the mean *I. granulosa* body size of study sites was significant (Friedmans test: $t=37.349$, $p<0.001$) but not significantly affected by either exposure ($F_{1,48}=2.03$, $p=0.16$), locality ($F_{1,48}=0.502$, $p=0.482$), or the interaction between locality and exposure ($F_{1,48}=1.01$, $p=0.32$), (figure 4.7). Thus variation in *I. granulosa* population growth rates between different study sites is explained by the interaction between *I. granulosa* mean body size and exposure without either exposure or locality causing any significant variation in *I. granulosa* mean body size.

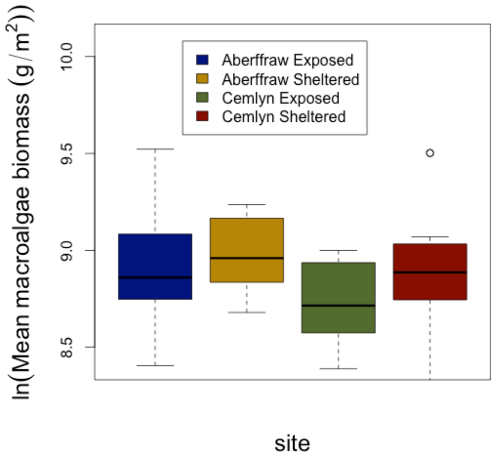


Figure 4.6 Macroalgae community biomass for the four study sites between August 2012 and August 2013. Friedman's tests indicated that macroalgae biomass was unaffected by both locality and exposure. Horizontal black lines show the median with boxes containing 50% of the data. Whiskers show the range of data, excluding outliers. Open circles show outliers.

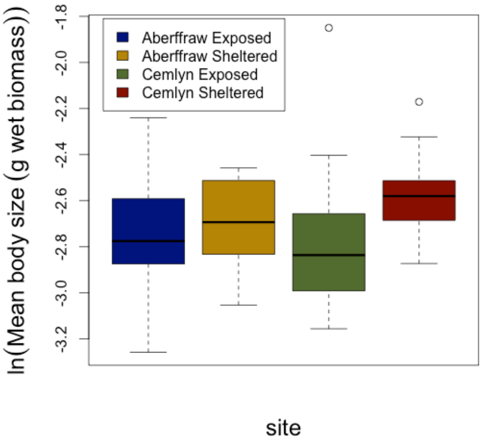


Figure 4.7 Mean Idotea body size for the four study sites between August 2012 and August 2013. Friedman's tests indicated that mean Idotea body size was unaffected by both locality and exposure. Horizontal black lines show the median with boxes containing 50% of the data. Whiskers show the range of data, excluding outliers. Open circles show outliers.

The observation that exposure does not significantly affect either macroalgae community biomass or mean *Idotea* body size over the 13-month duration is explained by analysis of the effects of exposure upon macroalgae biomass (figure 4.8) and *Idotea* body size (figure 4.9) over time.

4.3.6.1 EFFECTS OF EXPOSURE ON VARIATION IN MACROALGAE COMMUNITY BIOMASS

On both exposed and sheltered shores, maximum and minimum macroalgae biomass were similar. However, maximum biomass occurred during September on exposed shores and during October on sheltered shores whilst minimum biomass occurred during February on exposed shores and during January on sheltered shores (figure 4.8). This means that maximum macroalgae biomass occurs earlier, and minimum macroalgae biomass occurs later on exposed shores than sheltered shores. Thus whilst total change in biomass over the course of the thirteen months is similar for both sheltered and exposed shores, the amount of time over which this change occurs, and therefore the rate of change, is different for each level of exposure.

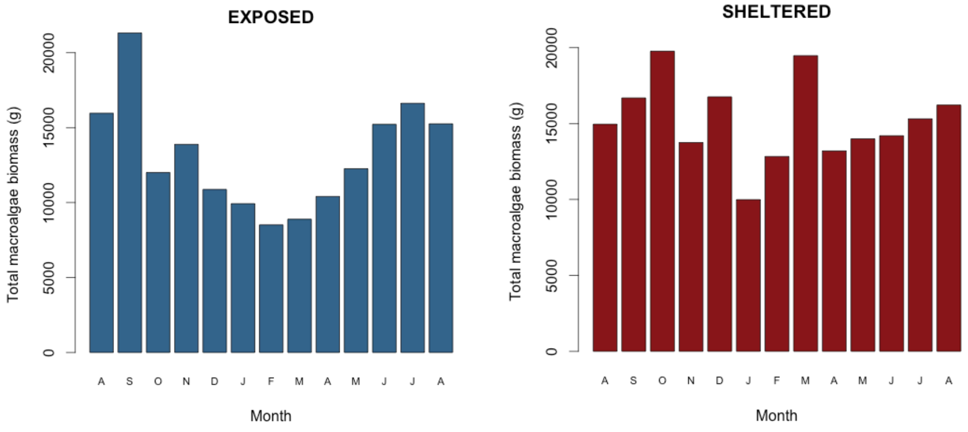
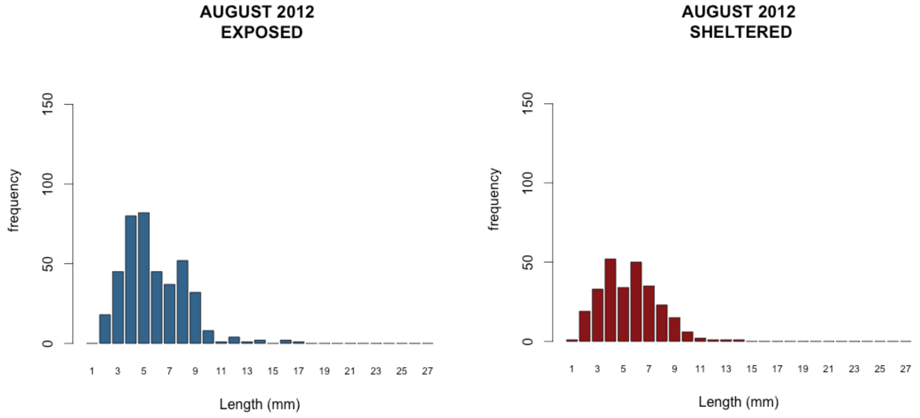


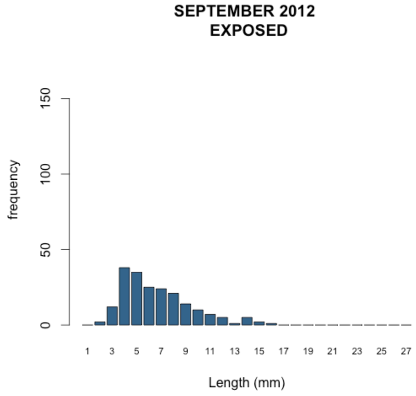
Figure 4.8 Effects of exposure upon monthly variation in total macroalgae biomass. (left) Monthly variation in total macroalgae biomass for exposed study sites between August 2012 and August 2013. **(right)** Monthly variation in total macroalgae biomass for sheltered study sites between August 2012 and August 2013.

4.3.6.2 EFFECTS OF EXPOSURE UPON IDOTEA POPULATION STRUCTURE

Monthly variation in the effects of exposure upon *I. granulosa* body size explains the interactive effects of exposure and mean body size in determining *I. granulosa* population growth rates. On both exposed and sheltered shores, the range of body sizes observed was similar each month. However, in all months except one (August 2012) *I. granulosa* individuals below 4mm in length were more abundant on sheltered than exposed shores (figure 4.9). Because the mass-specific growth rate of *I. granulosa* individuals decreases with body size (Chapters 2 and 3 of this thesis), this means that marginal (and perhaps non significant) increases in the abundance of juvenile individuals can significantly affect population growth rates. Thus whilst exposure may not significantly affect the mean body size of individuals within a population each month, it may determine the rate of change in population biomass.

Figure 4.10 (below and next three pages) Effects of exposure upon monthly variation in *Idotea* population structure. (left) Monthly variation in *Idotea* population structure for exposed study sites between August 2012 and August 2013. **(right)** Monthly variation in Idotea population structure for sheltered study sites between August 2012 and August 2013.

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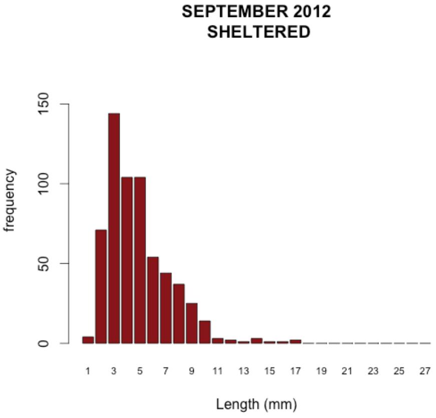
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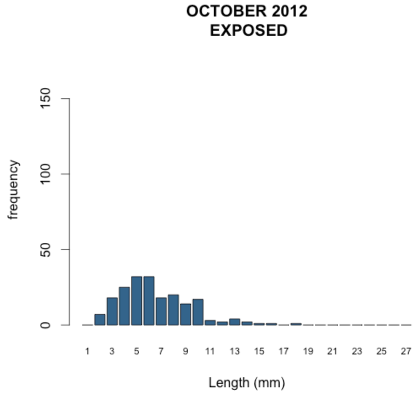
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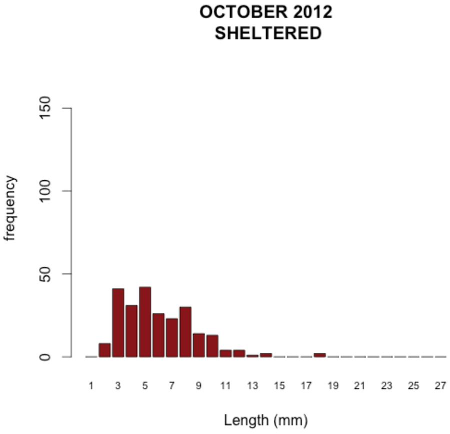
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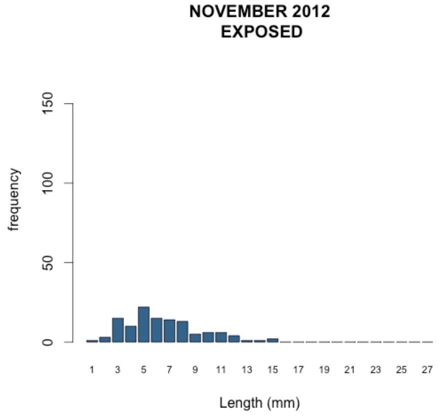
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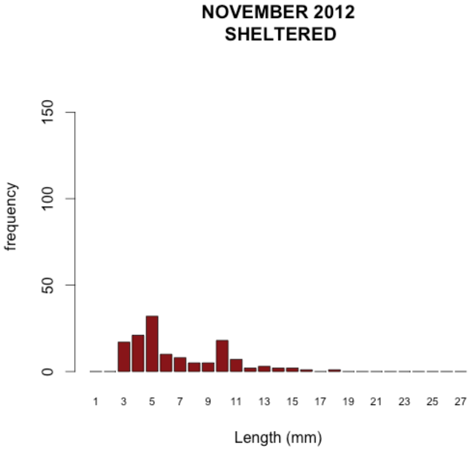
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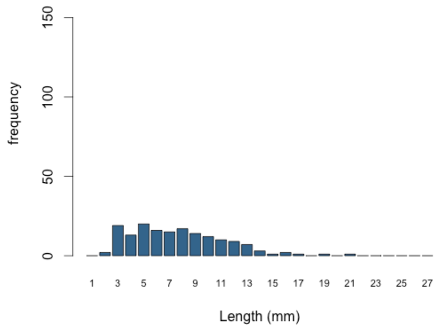

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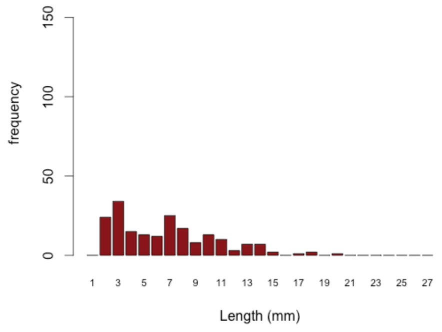

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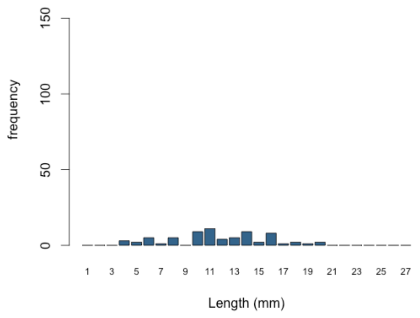

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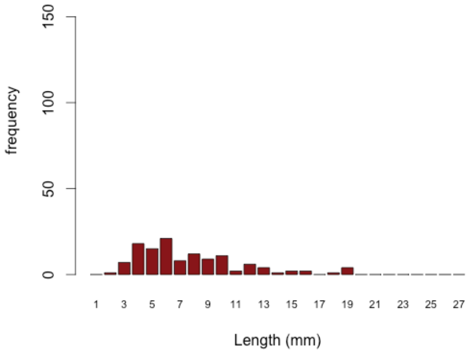

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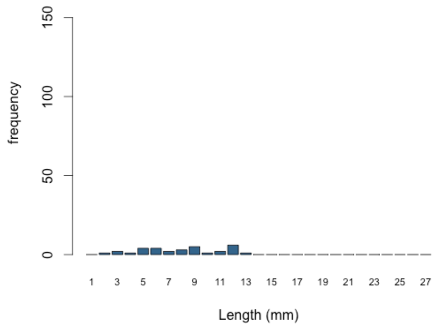

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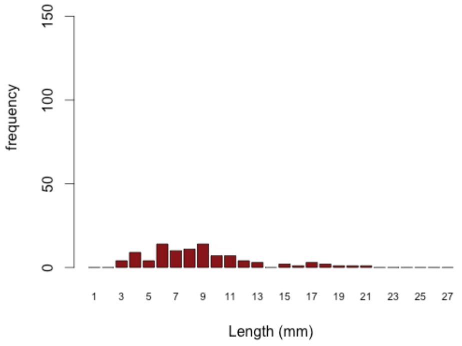

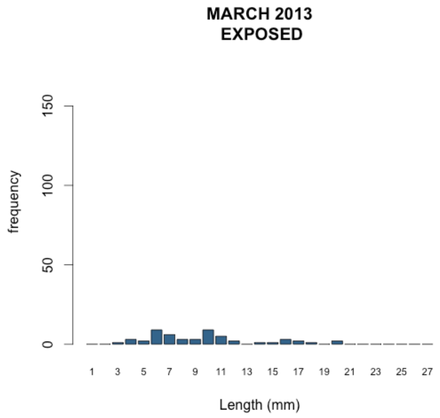
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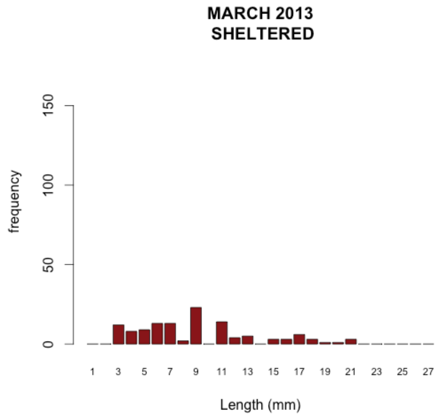
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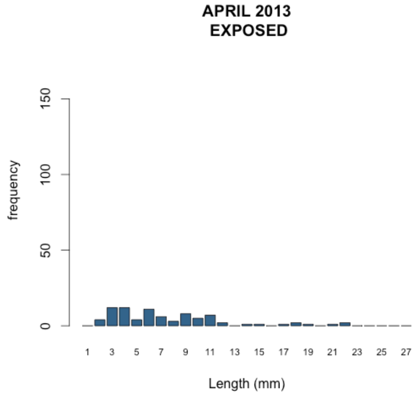
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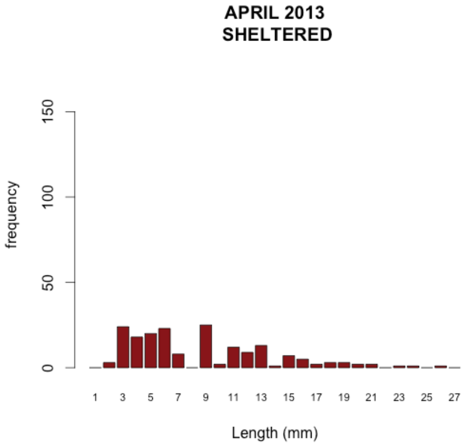
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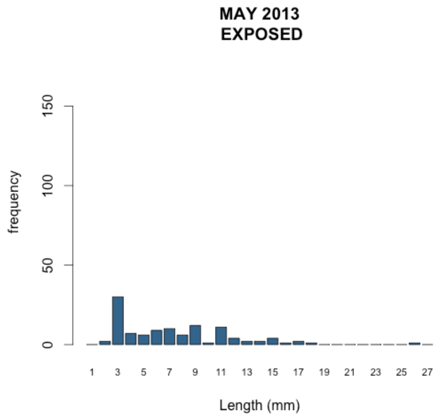
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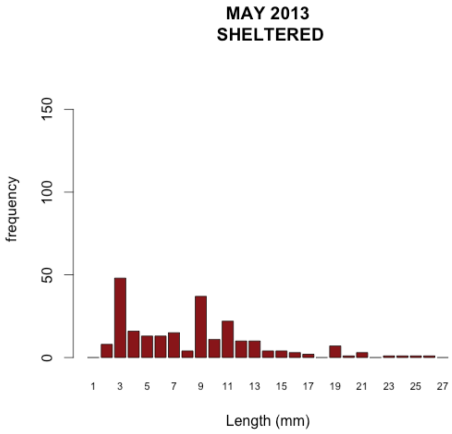
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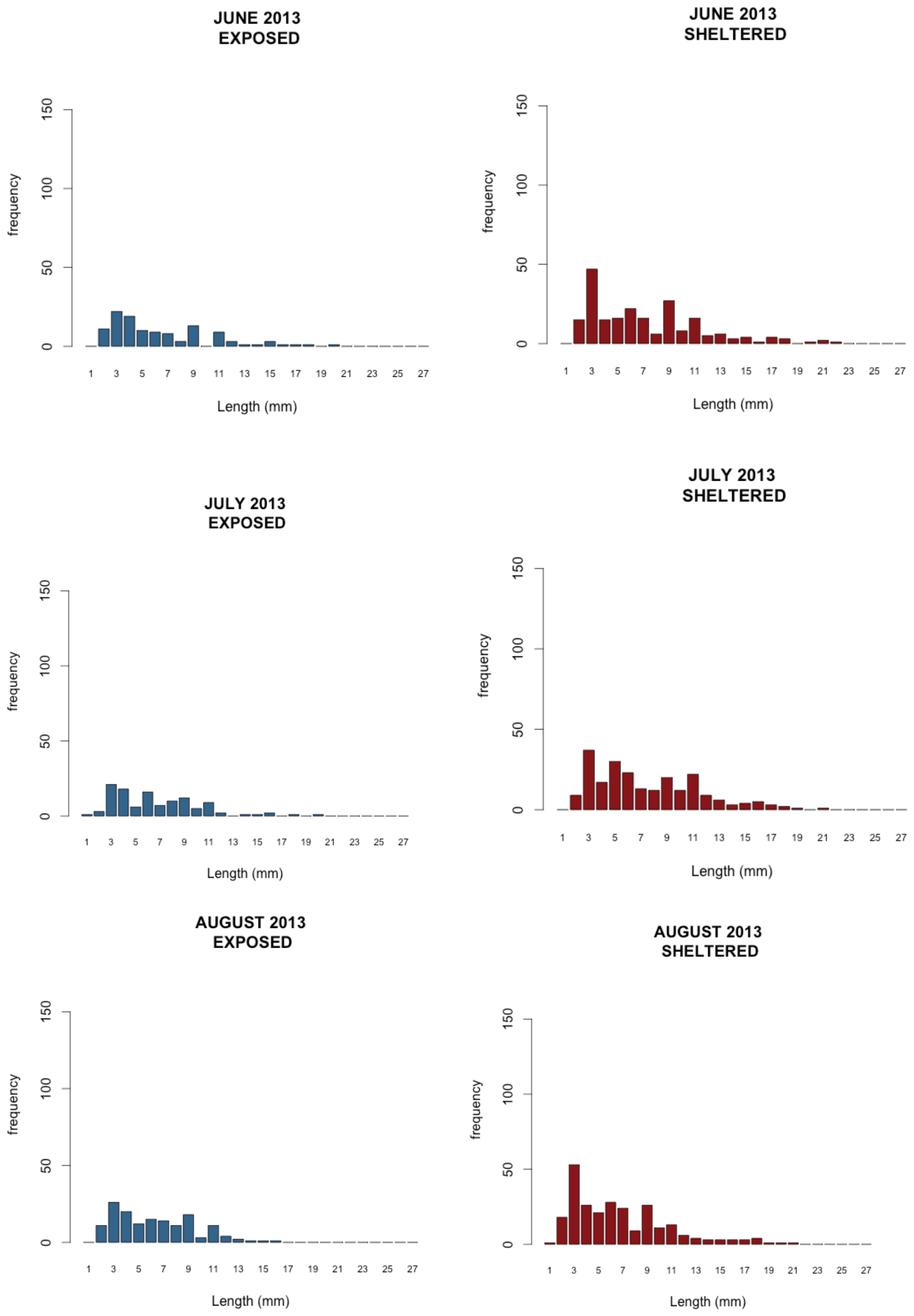


4.4 DISCUSSION

The results of this study indicate that macroalgae community biomass plays a more important role in determining *I. granulosa* population biomass on exposed shores than it does on sheltered shores (table 4.1). This result indicates that on exposed shores, greater bottom-up control of this consumer exists. This is in support of the hypothesis that the scouring, shearing and dislodging of producers by wave action may limit the availability of production to consumers. However, the overall effects of wave action scouring, shearing and dislodging producer biomass was observed to be limited because over the course of 13 months, macroalgae community biomass did not differ significantly between exposed and sheltered shores. This was despite macroalgae community biomass on exposed shores decreasing to a lower winter minimum than macroalgae biomass on sheltered shores. This combination of results is explained by relationships between macroalgae community biomass and growth rates: The macroalgae community on exposed shores grew faster than the macroalgae community on sheltered shores when community biomass was low and the macroalgae community on sheltered shores grew faster than the macroalgae community on exposed shores when community biomass was high. This means that although winter minimum biomass was lower on exposed shores, reductions in biomass were compensated for more quickly than on sheltered shores. Reciprocally, macroalgae growth during the summer, when community biomass was high, was faster on sheltered than exposed shores. Because of this, there was no net effect of exposure upon macroalgae community biomass over the 13-month period. These results indicate that the availability of producer biomass to *Idotea granulosa* is unaffected by wave exposure, and therefore they do not support the hypothesis that bottom-up control of *Idotea granulosa* population biomass increases with wave exposure. Instead, the effects of exposure upon the relationship between mean *Idotea* body size and population growth rates indicate that the interaction between *I. granulosa* and the macroalgae community was strengthened by exposure. This is because population growth rate increased faster with mean individual body size on sheltered shores than it did on exposed shores. However, mean individual body size was not significantly affected by exposure and therefore the relative contribution of individuals to population growth on sheltered shores is higher than on exposed shores. This indicates that individual maintenance costs may be greater on exposed than sheltered shores, strengthening this consumer-producer interaction.

Wave exposure has been previously shown to strengthen trophic interactions. For example Jenkins and Hartnoll (2001) report that the limpet, *Patella vulgata* grazes the microalgal community with greater intensity and has a faster growth rate in exposed locations, indicating that the interaction between this consumer and the microalgae community is strengthened by exposure. However, they also report that *P. vulgata* exists at lower density on exposed shores and that when density is increased to equal with sheltered shores, growth rate decreases. These results therefore indicate that the growth rate of limpets is limited by microalgae on exposed shores, but maintained by reduced limpet density on exposed shores. It is feasible that the hydrodynamic forces operating on exposed shores dislodge limpets and thereby lower density on exposed shores. In this context, the more intense consumption is facilitated by wave exposure reducing intraspecific competition, thereby enabling rapid individual growth as an adaptive response by limpets to increased exposure. With reference to the results of this chapter, the macroalgae community not only represents the food resource for *Idotea granulosa,* but also the substrate upon which individuals live. As a consequence, increases in hydrodynamic forces which increase the rate at which macroalgae are simultaneously dislodged, scoured or sheared will have simultaneous effects upon *Idotea* (Salemaa, 1979). Thus them both being washed away may suffice to explain the causality between macroalgae and Idotea detected by Granger tests. This further explains why different relationships exist between macroalgae community biomass and growth rate on sheltered and exposed shores: A greater standing biomass is more susceptible to pruning. Thus on more exposed shores, a greater standing biomass is pruned more and therefore grows less. However, this alone does not explain why the growth rate of a lower standing biomass is greater on exposed than sheltered shores. This can be explained in general terms by assuming that the growth pattern of all individual macroalgae is sigmoidal because in doing so, it is implicit that the maximum growth rate of all individuals occurs at roughly half the maximum body size. This means that the relative productivity of a community of smaller individuals is greater at a lower standing biomass than the productivity of a community of larger individuals and that a reduction in body size to a lower level will cause an increase in growth rate (figure 2.8). From this model we can explain the greater productivity of a lower standing biomass in exposed shores as arising because the macroalgae community there is comprised of smaller individuals. This result is in accordance with the findings of transplanting experiments (Blanchette, 1997) and laboratory measurements (Gaylord *et al.,* 1994) that demonstrate that wave action constrains the body size of individuals. Thus where smaller individuals have greater fitness in exposed locations, the composition of macroalgae communities in exposed situations will be skewed towards comprising of smaller species. Thus as an adaptive response by the community to the effects of wave action, the growth rate when biomass is low may be increased.

The hypothesis that the causality between macroalgae and *Idotea* is explained by them being simultaneously washed away is supported by the observation that no significant difference was observed in the mean body size of individuals between sheltered and exposed shores. This is based on the assumption that wave exposure has equal effects on *Idotea* of all body sizes. However, this hypothesis of simultaneous dislodgement fails to explain how differences in the relationship between mean *Idotea* body size and population growth rate occur and this observation is still best explained by the hypothesis that larger individuals incur greater maintenance costs in more exposed environments. This makes sense because larger individuals may be more exposed to hydrodynamic forces than smaller ones, and therefore exert greater force to resist being dislodged (Lau & Martinez, 2003). However, despite wave exposure plausibly increasing the energetic demands of consumer individuals, it does not appear in this instance to affect population structure. Instead, the effects of wave exposure upon the macroalgae community cause a decrease in macroalgae minimum biomass and this corresponds with an increase in macroalgae community growth when biomass is low, likely because of adaptation in species composition. This means that overall, patterns of causation between macroalgae and *Idotea* are best explained by them being simultaneously washed away. Further studies, measuring rates of consumption and linking those to detailed measurements of growth and individual body size are necessary to understand whether wave exposure shifts the balance of top down and bottom up control.

4.5 CONCLUSION

Wave exposure has both fundamental and complex effects upon the interaction between *I. granulosa* and the Macroalgae community. Fundamentally, dislodgement of macroalgae by wave exposure means that macroalgae and Idotea are simultaneously washed away and this means that a causal link between macroialgae community biomass and Idotea population biomass exists on exposed shores. However, adaptation by the producer community to wave exposure, and the effects of wave exposure upon the maintenance costs of *Idotea* individuals affect the general relationships between biomass and rates of growth.

CHAPTER 5:EFFECTS OF PRODUCER SPECIES RICHNESS UPON CONSUMERS

Abstract

By strengthening trophic interactions, warming is expected to increase top down control of producer biomass. This mechanism is dependent upon the ratio of consumer to producer biomass being determined by the strength of trophic interactions. However, in reality, producers constitute not only the food resource for consumers but also habitat. This means that variation in producer species richness can affect both the availability of resources, and diversity of habitats suitable for the consumer community. In this chapter I investigate the relative roles of macroalgae species richness and macroalgae community biomass in determining consumer abundance and species richness. Ten locations were studied on the Island of Anglesey during February 2013 (winter) and August 2013 (summer). Macroalgae species richness, macroalgae biomass, consumer abundance and consumer functional group richness were recorded for ten quadrats ($0.1m^2$) in each location during each month. During summer, weak and non significant correlations were observed between the macroalgae and consumer communities. However, during winter, macroalgae biomass was positively correlated with consumer abundance and consumer group richness at the quadrat scale. However, these relationships were interactive with location. This was in contrast to macroalgae species richness which had positive effects upon consumer abundance and group richness during winter that were affected by, but not interactive with location. These results indicate that variation in the macroalgae species richness of quadrats has consistent effects upon the consumer community irrespective of which shore that is on, whilst variation in the macroalgae biomass of quadrats has variable effects upon consumers depending upon location. This result is explained by the relationship between macroalgae community biomass and species richness. Here, ANCOVA indicated that a significant positive relationship between macroalgae biomass and species richness exists within quadrats and that this is common to all shores across Anglesey. However, this relationship is significantly affected by local conditions, and so no significant relationship exists between shore species richness and biomass across Anglesey. This result means that variation in macroalgae community biomass between quadrats within shores has consistent effects upon species richness. Combined, these results imply that the rocky shore community is structured according to within-shore heterogeneity in relationships between producer biomass and producer species richness.

5.1 INTRODUCTION

Warming is expected to cause shifts in food web structure because it increases rates of consumption faster than it increases rates of production. As a consequence, warming is expected to increase the extent to which consumers are resource limited, thereby causing the ratio of consumer relative to producer biomass to shift (O'Connor *et al.,* 2009, O'Connor *et al.,* 2011, Kratina *et al.,* 2012, Shurin *et al.,* 2012, Seifert *et al.,* 2014). However, this effect of warming upon food web structure is dependent upon the assumption that the quantity of producer biomass determines the extent to which consumers are resource-limited and this assumption may be invalid. This is because producer biomass performs two functions: In addition to standing biomass performing the process of production, the existence of standing producer biomass also modifies the environment. Because of this, producer biomass can provide both the food resource and habitat for higher trophic levels (Gamfeldt *et al.,* 2005).

In natural food webs comprising several interacting species, attributes of the primary producer standing biomass thus determine not only the availability of resources, but also the diversity of habitats available to consumers. Most fundamentally, because each of the different producer species in a community may affect the environment in a different way, then as the number of different producer species increases, so too does the number of different habitats. Thus the species richness of primary producers may determine the range of habitats available to consumers. Secondly, relative to the standing biomass of each primary producer species, the productivity may differ depending upon the suitability of the abiotic environment to each producer species. Because of this, the identity of primary producer species in relation to their environment, and the number of primary producer species may determine the availability of resources to consumers.

5.1.1 RELATIONSHIPS BETWEEN PRODUCER BIOMASS AND PRODUCER SPECIES RICHNESS

Producer species identity can affect the quantity of resources available to consumers and producer species richness can affect the suitability of habitat to consumers. Because of this, the relative effects of producer biomass and species richness upon consumers cannot be understood without understanding the relationship between producer biomass and producer species richness, and the contextual role of producer species identity in determining this relationship.

5.1.1.2 THE PRODUCTIVITY-RICHNESS RELATIONSHIP

The productivity-richness relationship (PRR) (Waide *et al.,* 1999) describes the relationship between the biomass and species richness of primary producer communities. In this context, the biomass of primary producer communities is used as a surrogate measure for their productivity, and this along with the precise nature and generality of the PRR (Adler *et al.,* 2011) has been subject of intense debate. However, for the purposes of this study, the PRR is introduced merely as a conceptual departure point.

As a general rule, the PRR is unimodal (Fraser et al., 2015), with maximal species richness occurring at sub maximal biomass (figure 5.1). This causes the relationship between biomass and species richness to be hump shaped, with species richness increasing with biomass when biomass is low (positive phase), and species richness decreasing with biomass when biomass is very high (negative phase). In terms of understanding interactions between species, these two phases (positive and negative) of the PRR correspond to the identity and number of species within a community having different effects upon biomass: The positive phase of the PRR is that in which species richness increases with biomass. This is indicative of species having facilitative or complementary interactions, with the addition of new species increasing the overall biomass of the community. This may be because the presence of one species facilitates the growth of another (facilitation), or because two species utilise two different, but simultaneously available resources (complementation) (Fraser *et al.,* 2015).

The negative phase of the PRR, where species richness decreases with increasing biomass is indicative of species with greater biomass having a negative effect upon species richness. This occurs when species competitively exclude others and therefore increase in dominance.

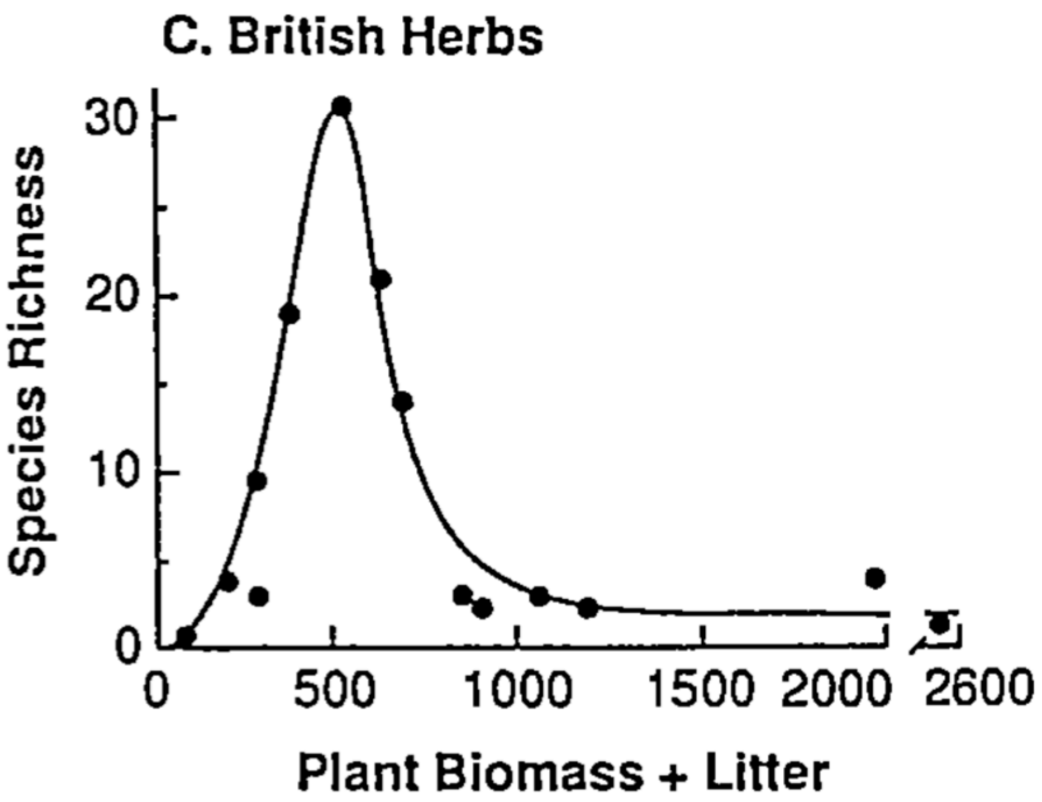


Figure 5.1 Relationship between community biomass and species richness for British herb communities (Tilman & Pacala, 1994). In communities of British herbs, species richness at first increases, then decreases with biomass, indicating a unimodal "humped" productivity richness relationship.

Variation exists in the precise characteristics of reported PRRs with some being linear, some near linear, some positive, some negative and some unimodal. Whilst this variation has fuelled debate surrounding the general effects that biodiversity has upon ecosystem functioning (Mouquet & Loreau, 2004), it does not detract from the PRR as a conceptual tool: Whatever the precise shape of the PRR, it describes the relationship between biomass and species richness, and explains that pattern as the consequence of species identity.

5.1.1.2 THE DEPENDENCE OF THE PRR UPON SPATIAL SCALE

The observations that comprise the PRR are arbitrary units of area (quadrats) replicated throughout a community. This means that the relationship between biomass and species richness is described at the community scale by the relative biomass and species richness of arbitrary quadrats observed within the community. Because of this, the relative distribution of species and biomass both within arbitrary quadrats and between those arbitrary quadrats within the arbitrary community governs the shape of the PRR (Chalcraft *et al.,* 2004, Simova *et al.,* 2012). These effects of spatial scale upon the PRR have been empirically demonstrated by Chase & Leibold (2002) for both the primary producer and consumer communities (figure 5.2). They sampled the productivity and species richness of thirty ponds and found that for both communities, the PRR described by all of these ponds was hump shaped. However, the thirty ponds were nested within ten watersheds (three per watershed) and when ponds were aggregated according to watershed, the PRR for all watersheds proved linear. The unimodal PRR described by all ponds indicates that amongst some ponds the PRR is positive (and therefore those ponds are dominated by relatively unproductive species) and amongst other ponds the PRR is negative (and therefore dominated by relatively productive species). However, the positive linear PRR described by the watersheds indicates that overall, watersheds are dominated by relatively unproductive species. This demonstrates that whilst all watersheds are dominated (to a varying degree) by relatively unproductive species, within all watersheds some ponds are dominated by relatively productive species, whilst others are dominated by relatively unproductive species. As a consequence, the PRR is different for species interactions depending upon spatial scale of observation: In this instance species interactions within ponds and between watersheds have a different PRR to species interactions between ponds within watersheds. In general the PRR can take any form depending upon the scale of observation.

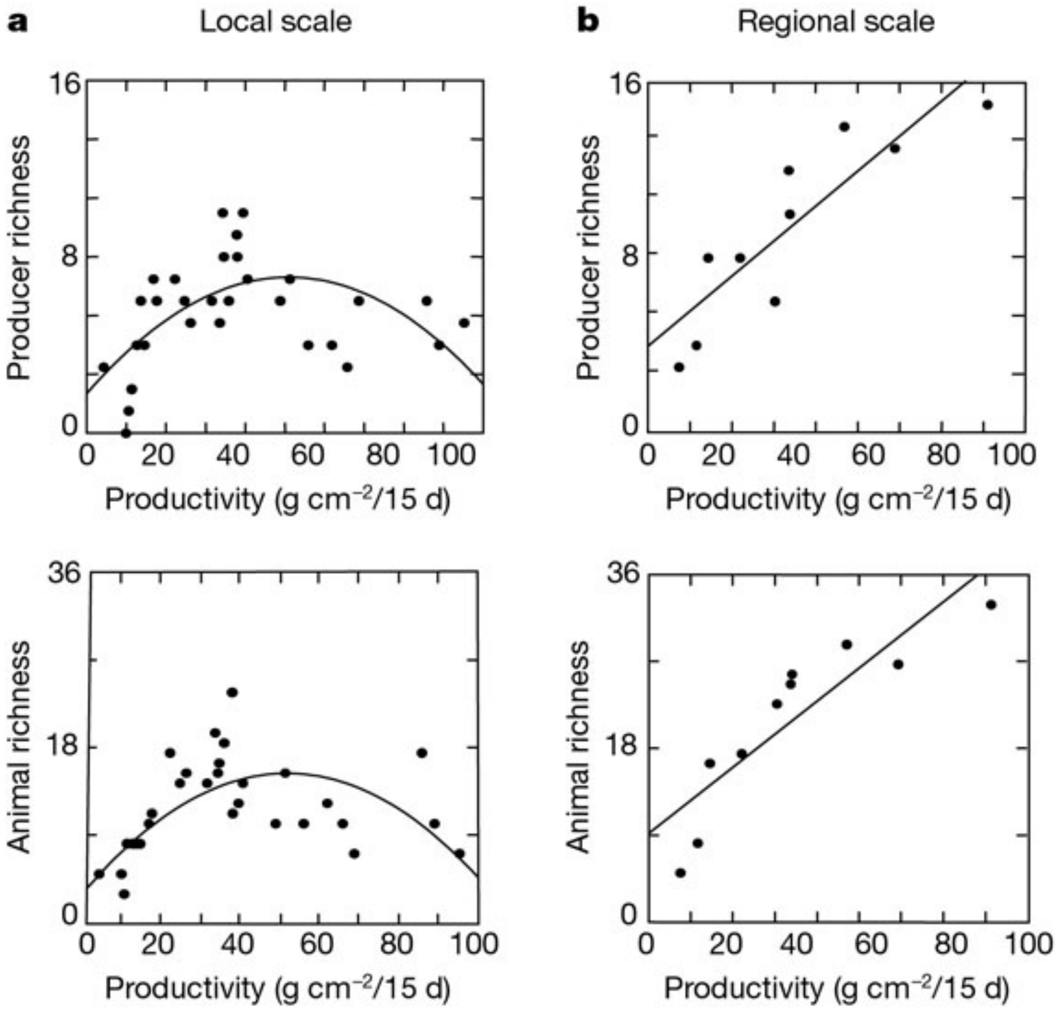


Figure 5.2 Effects of spatial scale upon the PRR (Chase & Leibold, 2002). The spatial scale of observation has equal effects upon the PRR of both producers (top) and consumers (bottom). On the left, dots represent ponds within a landscape. On the right, dots represent the same ponds aggregated by watershed within the landscape. By altering the scale of observation, the shape of the PRR is altered. This shows that whilst negative relationships between productivity and species richness exist in some ponds, only positive relationships between productivity and species richness exist in watersheds.

5.1.2 USING VARIATION IN THE PRR WITH SCALE AS A CONCEPTUAL TOOL

The variable effects of spatial scale upon the PRR (Chase & Leibold, 2002) offers a framework for understanding the relative roles of producer species richness and producer biomass upon consumers. This is because analysis of the relationship between producer biomass and species richness across different spatial scales informs us of whether interactions between producer biomass and producer species richness are dependent upon the local context. With specific reference to the example of Chase and Leibold (2002), they observed a single relationship between productivity and species richness for all ponds within a landscape, and as a consequence the relationship between productivity and species richness within individual ponds is not dependent upon the context of the pond. Equally, they observed a single relationship between productivity and species richness for all watersheds within a landscape and therefore the relationship between productivity and species richness for any watershed is not dependent upon the context of that watershed. In short, observed relationships between productivity and species richness are consistently explained by variation in species identity and scale of observation. The overarching implication of this result for consumers is that producer species richness has consistent effects upon both the availability of resources and habitat suitability across the landscape.

The converse of this result may arise however if the relationship between productivity and species richness of ponds were different for each watershed. This scenario would be indicative of the relationship between productivity and species richness within watersheds being dependent upon the context of the watershed, and would thereby eliminate a universal relationship between productivity and species richness across the landscape. In short: the relationship between productivity and species richness would be dependent upon variation in species identity relative to environmental conditions across the landscape. Under this scenario, because the effects of species identity upon the relationship between species richness and productivity are dependent upon context, the effects of producer species identity upon the availability of resources to consumers should also be dependent upon context. Thus so too should the effects of producer species identity upon consumer habitat be dependent upon context. This demonstrates how an analysis of the PRR at various spatial scales can explain the contextual effects of species richness upon consumers.

5.1.3 AIMS AND HYPOTHESES

The overall aim of this study is to identify the relative roles of producer biomass and species richness upon the consumer community. In order to achieve this aim, I test the hypotheses that producer species richness determines the richness of consumer groups, and that producer biomass determines consumer abundance. In order to fully understand the relative roles of producer biomass and species richness in determining the attributes of the consumer community, it is necessary to understand the relationship between producer biomass and species richness and the dependence of this relationship upon the scale of observation. Therefore I test two further hypotheses: That producer biomass determines producer species richness, and that the relationship between producer biomass and producer species richness changes with scale of observation, and the context of local conditions.

5.2 METHODS

In order to test the hypotheses, I conducted a programme of fieldwork where macroalgae biomass and consumer abundance were sampled on ten shores around Anglesey during February 2013 and August 2013. Sampling occurred two days either side of Spring tides as weather permitted, and specimens were returned to the laboratory in Menai Bridge for analysis.

5.2.1. STUDY SITES

Ten shores were chosen on Anglesey, North Wales to cover a range of conditions found in this region. These shores varied primarily in wave exposure (As determined by the Ballantine scale (Ballantine, 1961), with the sheltered extreme being Ynys Faelog (Ballantine scale: 8) in the Menai Straits and the exposed extreme being Holyhead (Ballantine scale: 3.75). The shore at Holyhead was in the Breakwater country park, with a South-Westerly aspect. The eight remaining shores (Penmon, Moelfre, Bull Bay, Cemlyn, Rhoscolyn, Rhosneigr, Aberffraw and Brynsiencyn) were dotted around the Island of Anglesey and therefore each had a slightly different aspect and exposure. On each shore a 10m x 10m area of rocky shore in the upper area of the lower shore (*Fucus serratus* – *Fucus vesiculosis* transition zone) was established and this same 100m^2 plot studied during each season.

5.2.2 SAMPLING

5.2.2.1 FIELDWORK

During February 2013 and August 2013, each site was visited on a date as close to low spring tide as weather conditions and daylight hours permitted. At each site, ten replicate samples were collected each month. Replicates were sampled by throwing a 0.1m^2 quadrat at random within the 100m^2 plot. From each replicate quadrat, the biomass of canopy algae was sampled by cutting the basal stipe of any macroalgae over 15cm tall within that quadrat using a sharp knife. Cut algae was removed and sealed in labelled plastic bags. This method meant that some quadrats, which at first appeared to have a dense algal cover, actually yielded little canopy biomass because basal stipes occurred outside of the area of the replicate quadrat. However, this method was chosen because it was assumed that observed canopy cover during emersion was not representative of canopy cover during immersion, because during periods of immersion algae are structured vertically throughout the water column. Following removal of the canopy, all other algae was removed to measure understory biomass and samples were sealed in labelled plastic bags.

5.2.2.2 LABORATORY ANALYSIS

5.2.2.2.1 SEPARATING EPIFAUNA FROM ALGAE

Samples of canopy and understory biomass were returned to the laboratory in Menai Bridge for analysis. For canopy samples, this was achieved by cutting fronds from the basal stipe so as to ensure all surfaces from within the complex architecture of individual algae were sampled. Consumers were removed by hosing algae under pressure with fresh tap water. Pressure was applied by attaching a length of 8mm diameter silicon tubing to a tap and squeezing to create a sufficient jet of water. Algae was simultaneously shaken by hand and the resulting run-off from this process was passed through a 0.5mm mesh, to collect epifaunal individuals. This process was repeated for each piece of algae until no further epifauna were sampled.

Understorey samples were analysed differently because of the delicate and intricate nature of the algae sampled. Here, replicates were emptied into a 38 x

24cm clear pyrex roasting dish placed atop a sheet of white paper. This enabled the samples to be easily visualised. Tap water was then added to a depth of approx. 4cm which enabled individual fragments of algae and consumers to be easily separated. Using tweezers and a 3ml plastic pipette, Consumer individuals were then separated from the algae.

5.2.2.2.2 MEASURING ALGAE BIOMASS

For each replicate, fragments of algae were separated and identified to the species level. For each species, fragments were then blotted with tissue paper and the total biomass per species weighed to the nearest 0.001g.

5.2.2.2.3 MEASURING CONSUMER ABUNDANCE AND GROUP RICHNESS

For each replicate, consumers were separated from algae then classed according to taxonomic groups. These groups were Littorinids, Topshells, Crabs, Amphipods, Isopods *(Idotea spp.)* and Sea slaters (*Sphaeroma* spp.). The number of individuals of each group per replicate was then counted.

5.2.3 DATA ANALYSIS

5.2.3.1 EFFECTS OF SCALE UPON MACROALGAE AND CONSUMER INTERACTIONS

The effects of macroalgae species richness and macroalgae biomass upon consumer abundance and consumer group richness were investigated using ANCOVA and selecting the most parsimonious model according to the protocol of (Crawley 2013). In each case, two analyses were performed in order to investigate the effects of scale upon the relationships. At the quadrat scale, data for quadrats were used as replicates and location and season were treated as factors. This tested whether the macroalgae community had effects upon the consumer community at the quadrat scale that were common in both seasons and to all shores in the region of Anglesey. At the shore scale, quadrat data was clustered into shores and season was treated as a factor. This tested whether the macroalgae community had effects upon the consumer community at the shore scales that were common in both seasons across the region of Anglesey.

5.2.3.2 RELATIONSHIPS BETWEEN PRODUCTIVITY AND RICHNESS

The relationship between macroalgae biomass and species richness was analysed using ANCOVA. In total, two analyses were performed, one at the quadrat scale and one at the shore scale. At the quadrat scale, ANCOVA was performed upon all quadrats in the region of Anglesey. Here, season and location were treated as factors, and biomass treated as a covariate in order to establish whether a common relationship between productivity and richness existed for all quadrats, during both seasons and on all shores around Anglesey. At the shore scale, ANCOVA was performed upon the total number of species recorded throughout the ten quadrats on each shore in each season. Here, season was treated as a factor and total biomass of the ten quadrats for each shore (biomass per m^2) treated as a covariate in order to establish whether a common relationship between productivity and richness exists for all shores during both seasons around Anglesey. Throughout, the most parsimonious models were selected according to the manual protocol described by Crawley (2013).

5.3 RESULTS

5.3.1 EFFECTS OF THE MACROALGAE COMMUNITY UPON CONSUMERS

5.3.1.1 EFFECTS OF MACROALGAE BIOMASS UPON THE CONSUMER COMMUNITY

5.3.1.1.1 EFFECTS OF MACROALGAE BIOMASS UPON CONSUMER ABUNDANCE

Consumer abundance generally increased with macroalgae biomass. However, the relationship between macroalgae biomass and consumer abundance was significantly affected by both season ($F_{1,197}=134.65$, $p<0.001$) and site ($F_{9,197}=3.71$, $p<0.05$) (figure 5.3). These different relationships between macroalgae biomass and consumer abundance existed between shores, and for each shore, a different relationship occurred according to season. During the summer (figure 5.3 (top)), no significant correlation was observed between macroalgae biomass and consumer abundance ($F_{1,197}=3.54$, $p=0.0063$) and instead variation in consumer abundance was explained by the significant effects of location ($F_{1,197}=2.47$, $p=0.014$). This is in contrast to during the winter (figure 5.3 (bottom)), when consumer abundance was determined by significant effects of macroalgae biomass, ($F_{1,197}=106.71$, $p<0.001$), location ($F_{9,197}=12.604$, $p<0.001$), and the interaction between macroalgae biomass and location ($F_{9,197}=3.848$, $p=0.0004$). This caused the relationship between macroalgae biomass and consumer abundance to be described by a significant slope parameter which was common to all shores except Rhoscolyn and Ynys Faelog, and a significant intercept parameter that was common to six of the ten shores (all except Bull Bay, Holyhead, Rhoscolyn and Ynys Faelog). Thus consumer abundance significantly and consistently increased with macroalgae biomass during winter but not summer, and location affected this relationship on some shores.

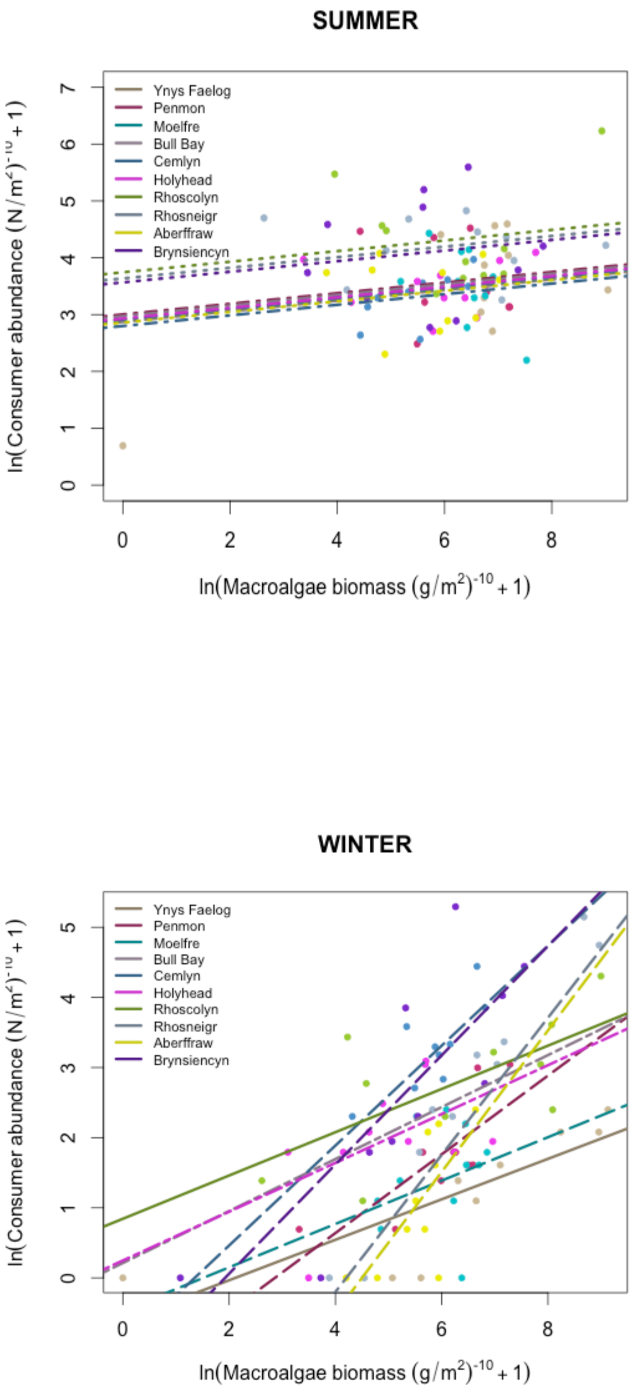


Figure 5.3 Effects of season upon the relationship between macroalgae biomass and consumer abundance at the quadrat scale. (top) The relationship between macroalgae biomass and consumer abundance for quadrats across Anglesey during summer. None of the relationships have significant slope parameters. Those shown with dotted lines have significant intercept parameters. Those shown with dotted-dash-dot lines have intercept parameters that do not differ significantly from the

cohort. **(bottom)** The relationship between macroalgae biomass and consumer abundance for quadrats across Anglesey during winter. All relationships are described by significant slope and intercept parameters. Relationships shown in solid lines have both slope and intercept parameters significantly different to all others. Relationships shown in long dash – short dash lines have only intercept parameters significantly different to all others. Relationships shown in long dash lines are not significantly different from each other.

At the regional scale, season significantly affects consumer abundance (F1,17=20.47, p=0.0003) (figure 5.4). However, despite consumer abundance increasing significantly with macroalgae biomass within shores during winter, no significant relationship (F1,17=0, p=0.99) exists between shores during either summer or winter (figure 5.4). These results indicate that macroalgae biomass determines consumer abundance at the quadrat scale during winter and because this relationship is affected by local conditions, no regional relationship between macroalgae biomass and consumer abundance exists.

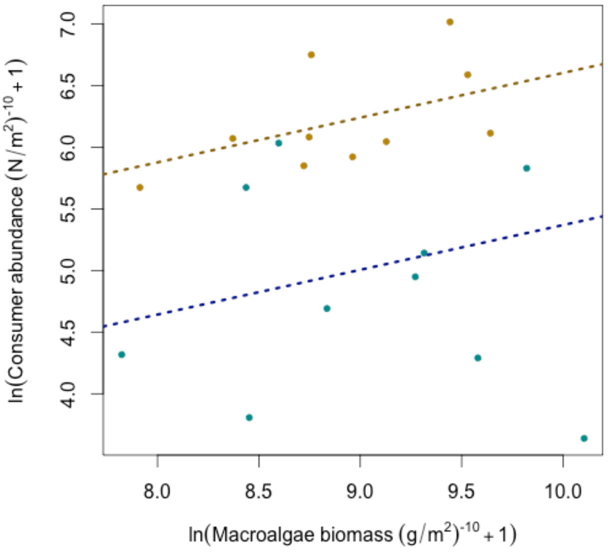


Figure 5.4 Effects of season upon the relationship between macroalgae biomass and consumer abundance at the shore scale. The relationship between macroalgae biomass and consumer abundance for shores across Anglesey is non significant during both summer (yellow dots and trend line) and winter (blue dots and trend line). The slopes of both relationships are non significantly different but the intercept differs significantly between season.

5.3.1.1.1.2 EFFECTS OF MACROALGAE BIOMASS UPON CONSUMER GROUP RICHNESS

At the quadrat scale, a significant positive relationship was observed between macroalgae biomass and consumer group richness ($F_{1,197}$=71.814, p<0.001) and this relationship was significantly affected by both season ($F_{1,197}$=148.09, p<0.001), location ($F_{1,197}$=8.622, p<0.001), the interaction between season and location ($F_{1,197}$=2.202, p=0.0245) (figure 5.5). This meant that a different relationship between macroalgae biomass and consumer group richness was observed for every shore in each season (figure 5.5). During both summer and winter, significant relationships occurred between macroalgae biomass and consumer group richness (Summer: $F_{1,197}$=4.46, p=0.038; Winter: $F_{1,197}$=56.8, p<0.001) and during both seasons, these relationships interacted significantly with location (Summer: $F_{9,197}$=2.76, p=0.007; Winter: $F_{9,197}$=2.109, p=0.038). However, despite these interactive effects being significant during both seasons, individual relationships between macroalgae biomass and consumer group richness were only significant during winter (figure 5.5). During winter, the relationship between macroalge biomass and consumer group richness was described by a significantly different slope parameter for all shores within the cohort except three shores (Aberffraw, Rhosneigr and Cemlyn), and a significantly different intercept parameter for all except two shores (Aberffraw and Rhosneigr). These results indicate that the macroalgae community biomass of quadrats determines consumer group richness during winter and that relationship is dependent upon local conditions.

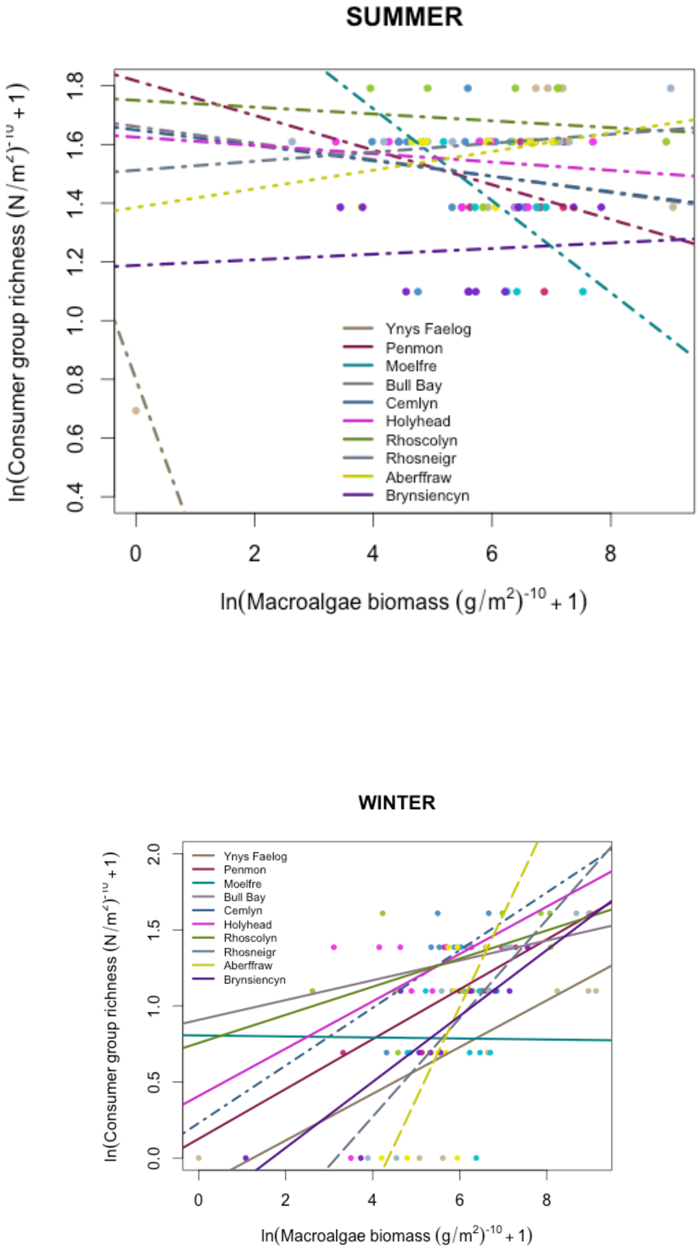


Figure 5.5 Effects of season upon the relationship between macroalgae biomass and consumer group richness at the quadrat scale. (top) The relationship between macroalgae biomass and consumer group richness for quadrats across Anglesey during summer. None of the relationships have significant slope parameters. Those shown with dotted lines have significant intercept parameters. Those shown with dotted-dash-dot lines have non significant intercept parameters. **(bottom)** The relationship between macroalgae biomass and consumer group richness for quadrats across Anglesey during winter. All relationships are described by significant slope and intercept parameters. Relationships shown in solid lines have both slope and intercept parameters significantly different to all others. Relationships shown in

long dash – short dash lines have only intercept parameters significantly different to all others. Relationships shown in long dash lines are not significantly different from each other.

At the regional scale, no significant relationship was observed between macroalgae biomass and consumer group richness ($F_{1,17}$=0.537, p=0.59) and season had no significant effect upon this relationship ($F_{1,17}$=-1.842, p=0.08) (figure 5.6). These results indicate that macroalgae biomass determines consumer group richness only at the quadrat scale during winter and because this relationship is affected by both local conditions and season, no regional relationship is observed.

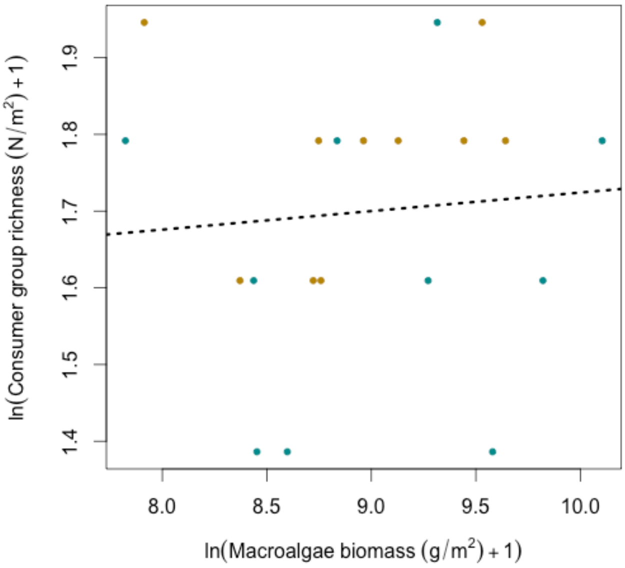
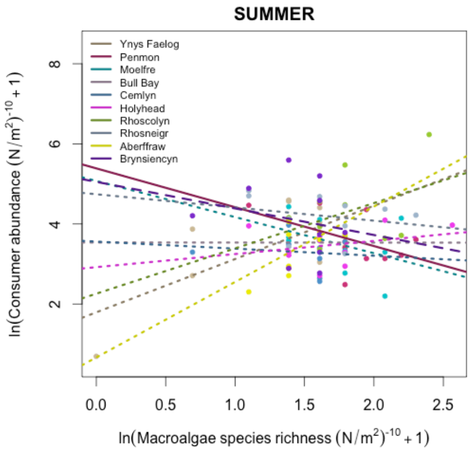


Figure 5.6 Effects of season upon the relationship between macroalgae biomass and consumer group richness at the shore scale. The relationship between macroalgae biomass and consumer group richness for shores across Anglesey is non significant during both summer (yellow dots) and winter (blue dots). Season has no significant effect upon the non significant relationship (black dashed line).

5.3.1.2 EFFECTS OF MACROALGAE SPECIES RICHNESS UPON THE CONSUMER COMMUNITY

5.3.1.2.1 EFFECTS OF MACROALGAE SPECIES RICHNESS UPON CONSUMER ABUNDANCE

At the quadrat scale, the relationship between macroalgae species richness and consumer abundance was significantly affected by both season ($F_{1,197}$=174.01, p<0.001), location ($F_{9,197}$=6.152, p<0.001) and the interaction between season and location ($F_{9,197}$=2.05, p=0.037). This meant that a different relationship between macroalgae biomass and consumer group richness was observed for every shore in each season (figure 5.7). During both summer and winter, significant relationships occurred between macroalgae species richness and consumer abundance (Summer: $F_{1,197}$=4.15, p=0.045; Winter: $F_{1,197}$=17.21, p= p<0.001) although only during summer was this relationship significantly interactive with location (Summer: $F_{9,197}$=2.57, p=0.012; Winter: $F_{9,197}$=1.546, p=0.146). As a consequence, different patterns in relationships between macroalgae species richness and consumer abundance were observed during summer and winter (figure 5.7). During summer, the relationship between macroalge biomass and consumer group richness was described by non significant slope parameters for all except one shore (Penmon), and non significant intercept parameters for all except two shores (Penmon and Brynsiencyn). These results indicate that for nine of the ten shores, the relationship between macroalgae species richness and consumer abundance is non significant during summer. During winter however, a significant (t=4.212, p p<0.001) and common slope parameter described the relationship between macroalgae species richness and consumer abundance for all of the ten shores, with variation between the shores described by five shores (Brynsiencyn, Bull Bay, Cemlyn, Rhoscolyn and Rhosneigr) having intercept parameters significantly different from all others. These results indicate that whilst no significant relationship between macroalgae species richness and consumer abundance is observed on any shore during summer, a significant relationship is observed that is common to half of the shores during winter. In addition to this, during winter consumer abundance increases at the same rate for all shores when a macroalgae species is added to a quadrat. This implies that at the quadrat scale, consumer abundance is more dependent upon macroalgae species richness, and less dependent upon the local environment, during winter than in summer.



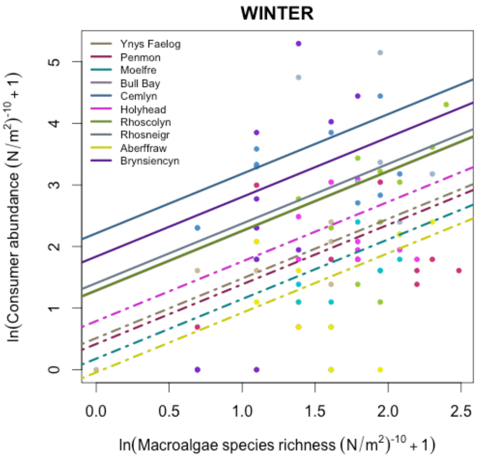


Figure 5.7 Effects of season upon the relationship between macroalgae species richness and consumer abundance at the quadrat scale. (top) The relationship between macroalgae species richness and consumer abundance for quadrats across Anglesey during summer. Only Penmon (solid line) has a significant slope parameter. Those shown with dotted lines have significant intercept parameters. Those shown with dotted-dash-dot lines have non significant intercept parameters. **(bottom)** The relationship between macroalgae species richness and consumer abundance for quadrats across Anglesey during winter. All relationships are described by significant slope parameters. Relationships shown in solid lines have intercept parameters significantly different to all others. Relationships shown in long dash – short dash lines are not significantly different.

At the regional scale, no significant relationship was observed between macroalgae species richness and consumer abundance ($F_{1,17}$=1.142, p=0.3) although season had a significant non-interactive effect upon this relationship ($F_{1,17}$=-4.518, p=0.0003) (figure 5.8). These results indicate that macroalgae species richness determines consumer abundance only at the quadrat scale during winter and because this relationship is affected by both local conditions and season, no regional relationship is observed.

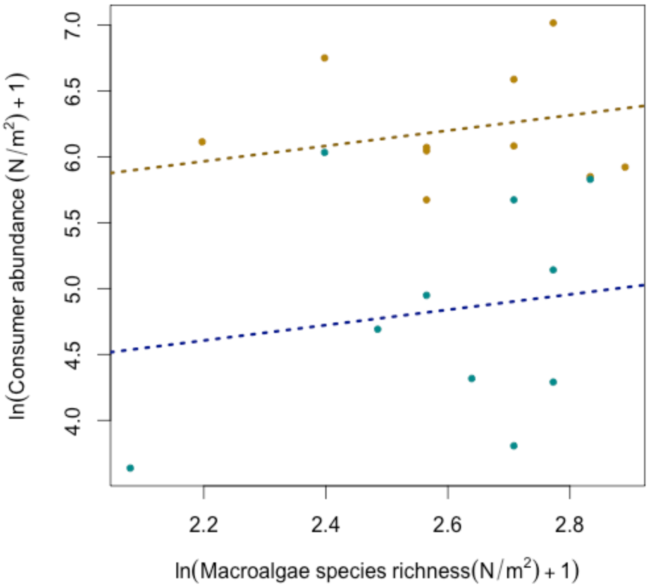


Figure 5.8 Effects of season upon the relationship between macroalgae species richness and consumer abundance at the shore scale. The relationship between macroalgae species richness and consumer abundance for shores across Anglesey is non significant during both summer (yellow dots, yellow trendline) and winter (blue dots, blue trendline). The slopes of both relationships are non significant but the intercept differs significantly between season.

5.3.1.2.2 THE EFFECTS OF MACROALGAE SPECIES RICHNESS UPON CONSUMER GROUP RICHNESS

At the quadrat scale, the relationship between macroalgae species richness and consumer group richness was significantly affected by both season ($F_{1,197}$=113.01, p<0.001), location ($F_{1,197}$=4.95, p<0.001) and the interaction between season and location ($F_{9,197}$=2.53, p=0.009) (figure 5.9). This meant that a different relationship between macroalgae species richness and consumer group richness was observed for every shore in each season (figure 5.9). During both summer and winter, significant relationships occurred between macroalgae species richness and consumer group richness (Summer: $F_{1,197}$=12.025, p=0.0008; Winter: $F_{1,197}$=29.576, p<0.001) although only during summer was this relationship significantly interactive with location (Summer: $F_{9,197}$=4.294, p=0.0001; Winter: $F_{9,197}$=0.94, p=0.496). As a consequence, different patterns in relationships between macroalgae species richness and consumer group richness were observed during summer and winter (figure 5.9). During summer, the relationship between macroalge species richness and consumer group richness was described by non significant slope parameters for all shores, and non significant intercept parameters for all except one shore (Aberffraw). Thus the relationship between macroalgae species richness and consumer group richness is non significant for all locations during summer. However, during winter, a significant (t=4.597, p<0.001) and common slope parameter described the relationship between macroalgae species richness and consumer group richness for all of the ten shores, with variation between the shores described by four shores (Bull Bay, Cemlyn, Rhoscolyn and Holyhead) having intercept parameters significantly different from all others. These results indicate that whilst no significant relationship between macroalgae species richness and consumer group richness is observed on any shore during summer, a significant relationship is observed that is common to 60% of the shores during winter. In addition to this, during winter consumer group richness increases at the same rate for all shores when a macroalgae species is added to a quadrat. This implies that at the quadrat scale, consumer group richness is more dependent upon macroalgae species richness, and less dependent upon the local environment, during winter than in summer.

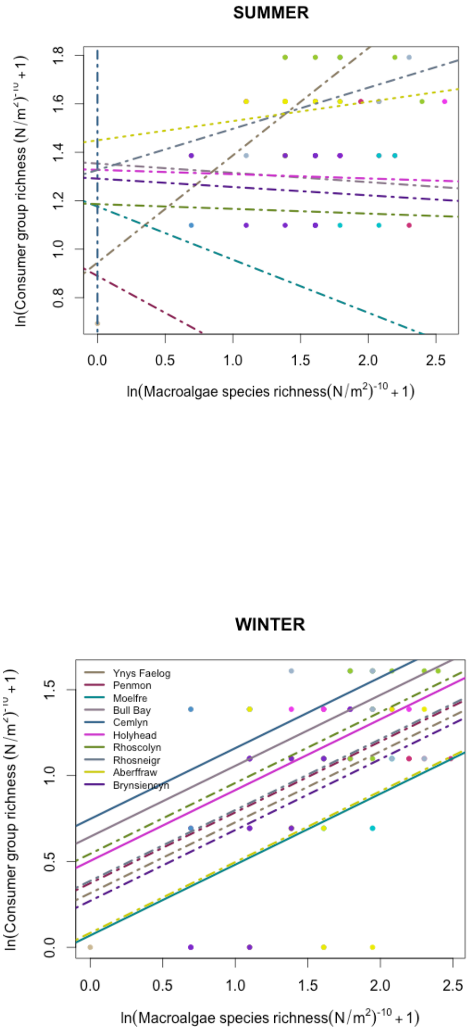


Figure 5.9 Effects of season upon the relationship between macroalgae species richness and consumer group richness at the quadrat scale. (top) The relationship between macroalgae species richness and consumer group richness for quadrats across Anglesey during summer. No relationships have a significant slope parameter. That shown with a dotted line (Aberffraw) has a significant intercept parameter. Those shown with dotted-dash-dot lines have non significant intercept parameters. **(bottom)** The relationship between macroalgae species richness and consumer group richness for quadrats across Anglesey during winter. Anglesey during winter. All relationships are described by significant slope parameters. Relationships shown in solid lines have intercept parameters significantly different to all others. Relationships shown in long dash – short dash lines are not significantly different.

At the regional scale, no significant relationship was observed between macroalgae species richness and consumer group richness ($F_{1,17}$=0.046, p=0.833) and season had no significant effects upon this relationship ($F_{1,17}$=-3.273, p=0.09) (figure 5.10). These results indicate that macroalgae species richness determines consumer group richness only at the quadrat scale during winter, and because this relationship is affected by both local conditions and season, no regional relationship is observed.

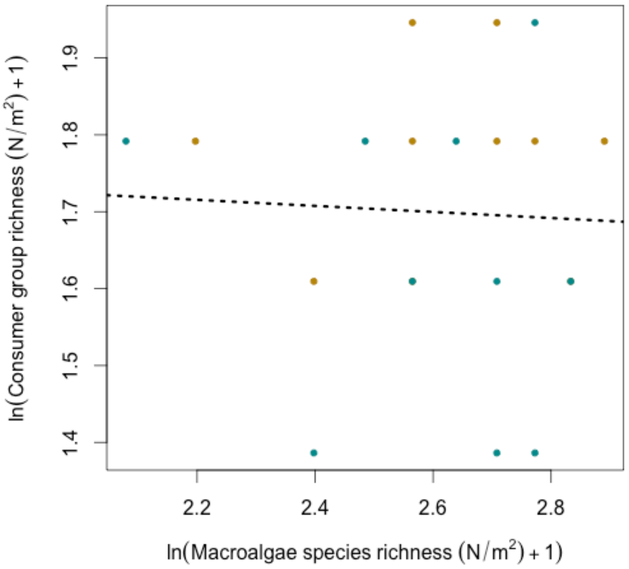


Figure 5.10 Effects of season upon the relationship between macroalgae species richness and consumer group richness at the shore scale. The relationship between macroalgae species richness and consumer group richness for shores across Anglesey is non significant during both summer (yellow dots) and winter (blue dots). Season has no significant effect upon the non significant relationship (black dashed line).

5.3.2 RELATIONSHIPS BETWEEN PRODUCTIVITY AND SPECIES RICHNESS IN THE MACROALGAE COMMUNITY

5.3.2.1 RELATIONSHIP BETWEEN ALGAE PRODUCTIVITY AND SPECIES RICHNESS WITHIN SHORES

Across the region of Anglesey, the species richness of quadrats significantly increased with productivity (t=6.78, p<0.001) ($F_{1,196}$=48.78, p<0.001) and this relationship was not affected by season ($F_{1,196}$=0.051, p=0.822) (figure 5.11). However, this positive relationship was significantly affected by location ($F_{9,196}$=6.48, p<0.001), with four of the ten shores having significantly different intercept parameters (figure 5.11). This means that the addition of species to quadrats causes productivity to increase at the same rate for all quadrats in the region of Anglesey. However, the actual productivity of quadrats with equal species richness is dependent upon location. This means that the relationship between productivity and species richness is determined by species identity within the context of local conditions and that these conditions are not consistent for all quadrats across Anglesey.

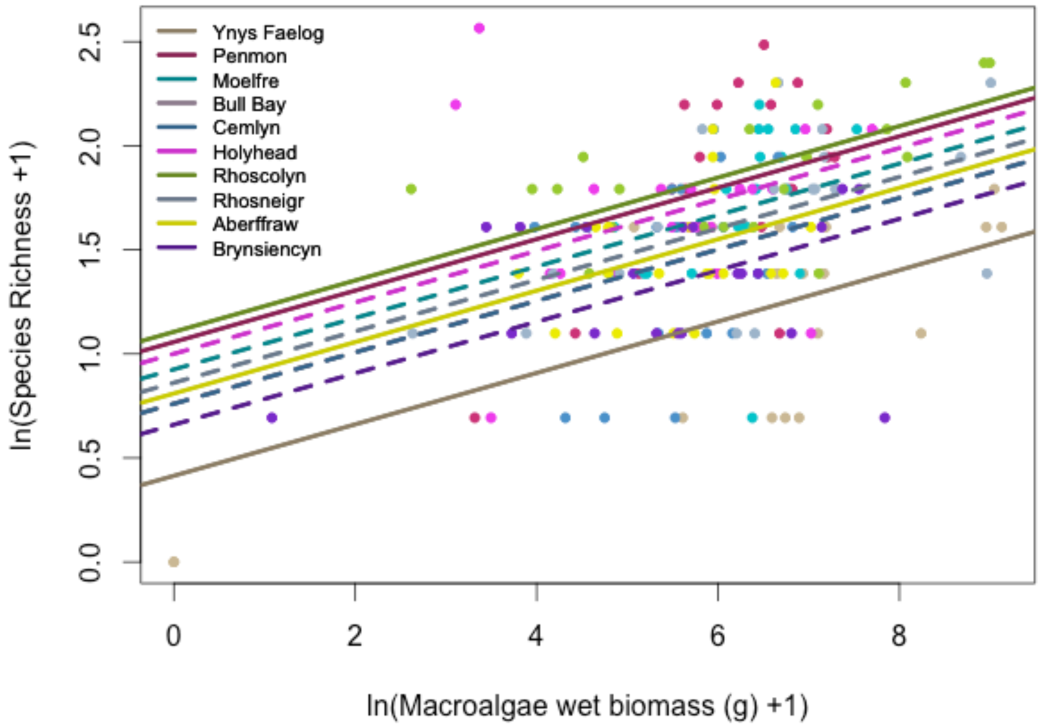


Figure 5.11 Relationship between macroalgae community biomass and macroalgae species richness at the quadrat scale. Season had no significant effects upon the relationship and all slopes are significant. Solid trendlines have significant intercept parameters whilst dashed trendlines have non significant intercept parameters.

5.3.2.2 RELATIONSHIP BETWEEN ALGAE PRODUCTIVITY AND SPECIES RICHNESS BETWEEN SHORES

In accordance with the observation that the relationship between the productivity and species richness of quadrats is dependent upon local factors (figure 5.6), no significant relationship ($F_{1,17}$=0.22, p=0.646) was observed between the productivity and species richness of shores (figure 5.12). This non significant negative relationship was unaffected by season ($F_{1,16}$=0.16, p=0.697). This result indicates that the species richness of shores does not determine the productivity of shores, implying that instead, shore productivity is determined by local conditions.

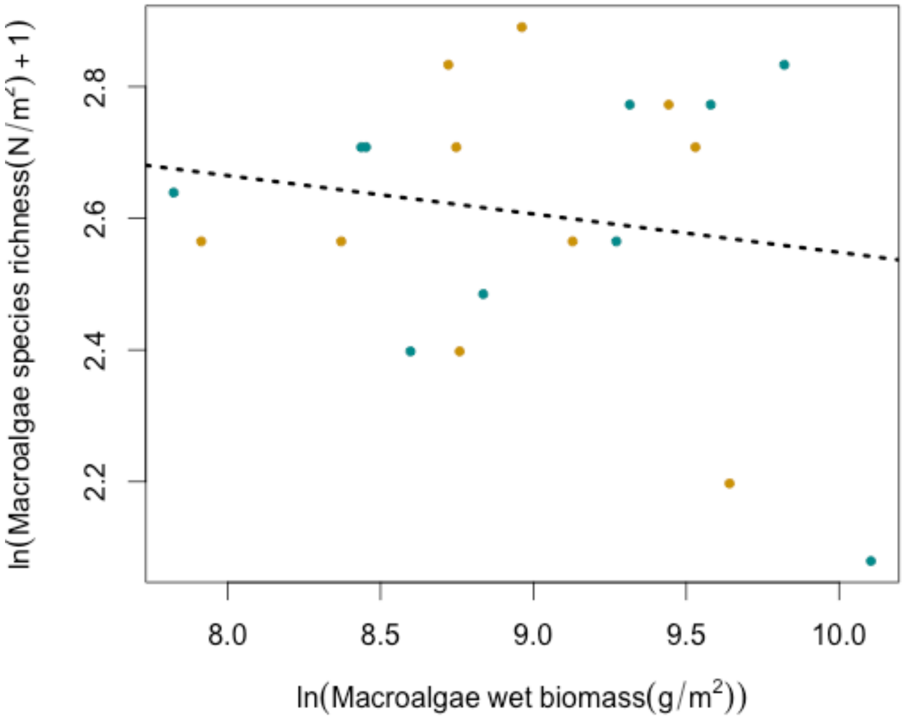


Figure 5.12 Relationship between macroalgae community biomass and macroalgae species richness at the shore scale. No significant difference was observed in this relationship between summer (yellow dots) and winter (blue dots). The general relationship (black dotted line), has a significant intercept parameter yet non significant slope.

5.4 DISCUSSION

The effects of the macroalgae community upon the consumer community were heavily dependent upon season, with a general pattern emerging: Relationships between the macroalgae community and the consumer community were generally more positive, and more significant, during winter than summer. During winter and at the quadrat scale, macroalgae biomass and macroalgae species richness had generally divergent effects upon the consumer community: Macroalgae biomass had effects upon consumer abundance and consumer group richness that were interactive with location and as a consequence, the addition of macroalgae biomass to any quadrat is likely to have divergent effects upon the abundance and group richness of consumers within that quadrat depending upon local conditions. Regarding macroalgae species richness however, this had effects upon consumer abundance and consumer group richness which were non interactive with location. Therefore the addition of a macroalgae species to any quadrat is likely to have the same effect upon consumer abundance and consumer group richness within that quadrat irrespective of which shore it is part of. Thus the overall implication is that variation in macroalgae species richness has consistent effects upon consumers whilst variation in macroalgae biomass has effects upon consumers that are dependent upon context. This result is explained by relationships between macroalgae community biomass and species richness. This is because the species richness of quadrats increases with biomass within shores (figure 5.11), whilst species richness of shores marginally and non significantly decreases with macroalgae biomass (figure 5.12). Thus variation in the species richness of quadrats within shores is explained by variation in macroalgae biomass whereas variation in the species richness of shores is not. This means that within shore heterogeneity in macroalgae biomass is the key driver of macroalgae species richness within shores. However, because the intercept describing these relationships is different for each shore, then two quadrats occurring on different shores but with identical biomass may have different levels of species richness. This result indicates that whilst the effects of within shore heterogeneity in macroalgae producer biomass upon macroalgae species richness are constant across shores, the interactions between species that determine the relationship between macroalgae community biomass and species richness are not. The observation that interactions between macroalgae community biomass and macroalgae species richness are different between shores explains why macroalgae community biomass and macroalgae species richness have inconsistent effects upon consumers: The interactions between macroalgae species which determine the relationship between macroalgae biomass and species richness are dependent upon local conditions.

The overarching implication of this work is that the principle determinant of community structure is heterogeneity in species interactions. This is in accordance with observations that heterogeneity in species interactions determines community structure and stability (O'Gormon & Emmerson, 2009, Menge, 2000) and that the strength and relative roles of interactions can vary according to context (Wootton, 1993, Menge, 1995). However, heterogeneity in the strength of interactions is an artifact, manifested from variation that exists in species identity, body size, physiology, behavior etc. and therefore this does not mechanistically explain why heterogeneity, as a more general concept is so important in determining community structure. Instead, MacArthur's paradox (Schoener, 1983) illuminates the issue: According to MacArthur & Wilson, (1969), communities are structured according to the random immigration by species and the non-random selection of those species by competition (Loreau & Mouquet, 1999). The paradox thus arises: How is diversity maintained? This paradox is overcome by the regional similarity hypothesis (Mouquet & Loreau, 2002), which describes immigration not as a random regional scale process, but as a local process determined by emigration from other communities. As a consequence, the community is described as a meta-community, comprised of a series of subunits that are sufficiently similar for them to exchange species, yet sufficiently diverse for the same species not to go extinct from all subunits at one time. Thus heterogeneity is both promoted and constrained. In the context of this study, the regional similarity hypothesis means that quadrats within a shore must be sufficiently similar in species composition to provide immigrants to each other, yet diverse enough to provide refuge for species that have gone extinct from other quadrats. In shores where the interaction between wave exposure, geography, topography and geology creates a mosaic of habitats, this means that in order for similarity to exist between quadrats, the species of each shore must be capable of adapting to several of these different habitats. Such adaptation is observed in response to wave exposure in the body size of fucoid (Blanchette, 1997) and lamineria algae (Pederson *et al.,* 2012), the consumption and growth rates of Patellid limpets (Jenkins & Hartnoll, 2001) and the feeding preferences of *Idotea baltica* (Engkvist et al., 2004). In each case, the response of individuals to their environment enables them to persist with modified density in various habitats and thereby enable the colonization of further habitats. However, in order to do so, organisms interact differently with their surroundings in each habitat. Similarity between quadrats may be further enhanced by the dominance of canopy forming fucoid algae. This is because fucoids engineer the environment (Coleman *et al.,* 2006), mediating the extremes of wave exposure, desiccation risk etc. (Lobban & Harrison, 1994). Thus whilst this dominance increases similarity between habitats across the shore, it also means that fucoids interact slightly differently with their surroundings in each habitat, and therefore interactions between fucoids and other organisms may also be different in each environment. Despite dominant species promoting similarity across shores, variation in the way they interact with their environment promotes diversity. For example, in habitats where hydrodynamic forces are low, fucoid algae are infrequently sheared and therefore host epiphytes (Lubchenco & Menge, 1978). This can promote the diversity of algae species and thereby provide habitat for consumers, or alternatively, by supporting more productive, ephemeral species, provide a food source for consumers (Pavia *et al.,* 1999).

Thus as a general concept, heterogeneity may be the principle determinant of community structure because it is the product of regional similarity. Adaptation by species to a variety of habitats enables them to persist on a shore and this adaptation generates diversity in interaction strengths and provides habitat for further species. As a consequence, whilst weak and contextual relationships are observed between specific parameters such as species richness and producer community biomass, those weak relationships follow the strong pattern: Variation has constant effect.

5.5 CONCLUSION

Within-shore variation in macroalgae community biomass is correlated with macroalgae species richness and within shore variation in macroalgae species richness has consistent effects upon the consumer community. This indicates that community structure is dependent upon within shore variation in relationships between macroalgae biomass and species richness. Such variation in biomass-species richness relationships may be a key to maintaining diversity and community stability.

CHAPTER 6: DISCUSSION

The predicted effects of warming upon food web structure are a decrease in the ratio of consumer to producer biomass, explained by warming increasing the mass specific consumption rate (section 1.5.1.1). However, for this theory to hold true requires that warming has effects upon the relationship between individual body size and metabolic rate that are consistent across all organisms. In natural situations, this may not be the case because despite warming having ubiquitous metabolic effects upon individuals, individuals adapt to those effects.

6.1 SYNTHESIS OF RESULTS

In chapter 2 of this thesis, warming was observed to cause the mass specific consumption rate of *Idotea granulosa* to increase and this result is in accordance with the prediction that warming has ubiquitous mechanistic effects upon individuals. However, in both chapters two and three of this thesis, this effect of warming upon individuals was observed to not necessitate an effect upon the ratio of consumer biomass to producer biomass. Furthermore, the results of chapters four and five indicated that community structure was determined by factors other than trophic dynamics:

6.1.1 VARIABLE EFFECTS OF TEMPERATURE UPON INDIVIDUALS

In Chapter 2, warming did not have an effect upon the ratio of consumer to producer biomass. This was because in addition to warming causing an increase in mass specific consumption rates, warming caused an increase in both producer growth rates, and maximum producer body size. This enabled *Ulva lactuca* to respond to increases in consumption with an increase in the rate of individual growth, a response that caused warming to have non-constant effects upon the ratio of consumer to producer biomass. In addition, the duration over which *Ulva lactuca* individuals could effectively compensate for warming, and thereby render the ratio of consumer to producer biomass independent of temperature, was determined by individual consumer growth rate. This is because the rate at which individual consumers grow determines the rate at which their consumption rate increases through time. Because individual consumer growth rate was observed to increase with temperature yet decrease with individual body size, this caused the duration over which *Ulva lactuca* individuals could compensate for consumption to become dependent upon both consumer body size and temperature. This means that despite temperature having predictable mechanistic effects upon individuals, its effects upon the ratio between consumer and producer biomass are dependent upon both the relationship between consumer and producer body size at a single point in time, and variation in the relationship between consumer and producer body size between points in time.

6.1.2 VARIABLE EFFECTS OF TEMPERATURE UPON POPULATIONS

In chapter 3, the effects of consumer body size upon individual consumer growth rates were observed to determine the effects of temperature upon the ratio between consumer biomass and producer biomass at the population level. This was because temperature and consumer body size were observed to interact in determining consumption rates whilst warming had non-interactive effects with body size in determining the growth rate of individuals. As a consequence, the gross growth efficiency of consumer individuals (the rate at which consumption of producer biomass caused an increase in consumer body size) decreased with individual body size but at all body sizes, increased with temperature. This had two effects: Firstly it caused change in the ratio of consumer to producer biomass to be explained at all temperatures by the growth efficiency of the population, and secondly it meant that change in the ratio of consumer to producer biomass could be equal for populations existing at different temperatures provided that mean consumer body size was greater in warmer than cooler environments.

6.1.3 VARIABLE EFFECTS OF ABIOTIC CONDITIONS UPON MAINTENANCE COSTS

Chapter 4 of this thesis supports the hypothesis that in natural ecosystems, the catabolic maintenance costs of individuals, and therefore the ratio between consumer and producer biomass, can be determined by abiotic factors other than temperature. Support for this hypothesis comes from the observation that whilst the degree of wave exposure on a shore does not significantly affect the body size of *Idotea granulosa*, it does affect the growth rate of *I. granulosa* populations. In general, this means that consumer population growth may incur higher energetic costs in exposed environments. However, the effects of this upon the relationship between producer and consumer biomass were limited. This is because despite a causal link between producer and consumer biomass being observed on exposed shores, that is likely caused by wave action pruning algae and thereby removing both producer and consumer. In response to wave action, the macroalgae community exhibited a similar, but independent response to *I. granulosa*: On exposed shores when macroalgae community biomass was low, macroalgae community growth rates were higher than on sheltered shores. This indicates that the body size of macroalgae individuals may be lower on exposed than sheltered shores as an adaptive response to wave exposure. These processes indicate that it is unlikely that the ratio of consumer to producer biomass can always be predicted from temperature alone.

6.1.4 EFFECTS OF PRODUCER SPECIES RICHNESS UPON CONSUMER ABUNDANCE

The hypothesis that heterogeneity in producer biomass and species richness determines community structure is supported in chapter 5. Here, significant relationships between the producer community and consumer community were only observed during winter, indicating that overall, seasonal variation in relationships between producers and consumers occurred. However, during winter producer biomass and producer species richness had fundamentally different effects upon consumers. At the quadrat scale within shores during winter, the effects of producer biomass upon the consumer community were interactive with location, whereas the effects of variation in producer species richness upon the consumer community were consistent across all locations. These results indicate that relative to variation in producer biomass, variation in species richness has more consistent effects upon the consumer community and this result is explained by the relationship between producer biomass and producer species richness. This is because no relationship between producer biomass and producer species richness was observed between shores across Anglesey whilst a positive relationship was observed between quadrats within all shores across Anglesey. This indicates that instead of producer species richness increasing with biomass as a fundamental principle, producer species richness increases with producer biomass because of variation in biomass between quadrats within shores. This means that the species interactions that determine relationships between producer biomass and producer species richness are dependent upon context and this drives divergence in their relative effects upon consumers.

6.2 IMPLICATIONS OF THIS WORK

The results of this study can be distilled into two key findings: Firstly, warming was observed in the laboratory studies to promote *Ulva lactuca* biomass and growth rates, and *Idotea granulosa* growth rates, independently of individual body size. This ultimately meant that the effects of warming upon mass specific consumption rates did not necessitate shifts in the ratio of consumer to producer biomass and much of the explanation for this is centred around these experiments being conducted at sub optimal temperatures. Secondly, in the field based studies, the relationship between producer biomass and consumers was observed to be highly dependent on context: Abiotic drivers such as wave exposure affect the maintenance costs of individuals, the growth rates of individuals, and can even affect the trophic link. Furthermore, producer biomass is determined by local environmental conditions and heterogeneity in producer species richness within that environment.

These two key findings can be crystalized into a single over arching implication: That the biomass of both producers and consumers is not determined in any single location or at any point in time, by a single factor. This is because organisms adapt to their environment and each other in many ways, and over various spatial and temporal scales. This causes species interactions to be both determined by the environment and determinant of the effects of that environment upon the ecosystem. As a consequence, it appears that shifts in food web structure cannot be predicted from changes in temperature alone.

6.2.1 FROM EMPIRICAL OBSERVATIONS TO THEORY AND BEYOND…

Due to the spherical geometry of our planet, a latitudinal temperature gradient exists (Burrows *et al.,* 2014). Surface temperatures of the earth generally decrease as distance from the equator increases because the equator is closer to the sun than the poles. The general effect of global warming upon this latitudinal temperature gradient is a phase-shift, whereby environments of any given temperature are moving pole-wards. This causes the coolest environments; found at the poles, to be replaced by environments previously found at lower latitudes, and novel, warmer environments to be generated around the equator. The general pole-ward shift in species range distributions can thus be explained by the dispersal of individuals being sufficient for them to track the latitudinal shift in suitable environments. According to this explanation, adaptation to new environments is unnecessary because species merely keep pace with the shifting geography of the environment to which they are adapted. However, this explanation is unsatisfactory on two counts: Firstly, species at higher latitudes will be more prone to extinction as their suitable environment contracts, and secondly, a species vacuum will occur in equatorial regions where new environments, to which species do not adapt, are generated (Burrows *et al.,* 2014). Whilst it is accepted that species at higher latitudes are experiencing habitat loss, we have yet to observe a species vacuum in the tropics. Thus it is necessary to incorporate within this explanation, the adaptation of species to novel environments.

Decreases in ectotherm body size and age at maturity have been observed as adaptive responses by species to warming (Ohlberger, 2013). These responses cause a fundamental shift in the relationship between temperature and individual performance that causes smaller individuals to perform better in warmer environments. Thus whilst some species appear capable of tracking changes in the geography of their suitable habitat, others are capable of multigenerational adaptation to warmer habitats (Garcia-Molinos *et al.,* 2015). In effect, this means that from the perspective of the observer, the attributes of species with a particular identity, the identity of species within a particular location, and the environment of the particular location are non-constant variables. Thus observations require a frame of reference and that is achieved by making two reasoned assumptions: That all individuals are *adapted* to their environment and all species are *adapting* to their environment. The first of these assumptions explains that everything an individual is describes the adaptive response to everything that has happened until now. The second assumption explains that the first assumption is only true up until now.

Thus predicting the future is as dependent upon observation as it is upon imagination and a theory is required: A theory that makes assumptions based upon the past but does not assume the future. For this, the metabolic theory of ecology (MTE) appears to suffice. This is because MTE, which scales individual metabolic rate with body size and the temperature of the environment, predicts the future without making *a priori* assumptions of what the environment, the species identity of individuals, or the body size of individuals will be (Brown *et al.,* 2004). Instead, metabolic theory predicts that the laws of physics that have operated upon individuals until now will continue to operate in the future. Yet herein lies this theory's downfall: Whilst the laws of physics set a maximum on individual body size, the laws of ecology set a minimum. This is because of the complex relationships between competition (Goldberg & Barton, 1992) and facilitation (Chu *et al.,* 2008) that ultimately determine the size individuals must be in order to be fitter than their neighbours. Thus whilst it may be that some individuals optimise fitness by accumulating biomass according to the physical laws of MTE, others may simply evade those laws and live in an environment where the law does not apply. This therefore is what leads to the downfall of theory, a return to the beginning, and an elegant end: In the living world, these are not laws at all.

6.3 CONCLUSION

The extent to which warming affects the structure of natural food webs is determined by the capacity of individuals to adapt to warming. The capacity for individual adaptation is determined by genotype, and instead of being determined by the immediate environment, genotype is the result of processes that operate across a species' broader geographic range. Because of this, processes operating over broad geographic scales determine the ability of an individual to adapt to its immediate environment. This introduces relativity into all individual responses to warming: It is not a specific temperature that determines the individual response, but instead the specific temperature relative to the range of temperatures that the species is adapted to. In diverse species assemblages, this means that temperature has different relative effects upon each species and that takes beautiful effect: It makes any generalisation of how food webs will respond to warming totally impossible.

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