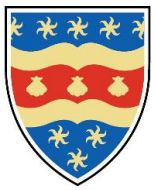
2018

Trophic and ecological implications of the gelatinous body form in zooplankton

McConville, Kristian



UNIVERSITY OF PLYMOUTH

TROPHIC AND ECOLOGICAL IMPLICATIONS OF THE GELATINOUS BODY FORM IN ZOOPLANKTON

By

KRISTIAN M. McCONVILLE

A thesis submitted to the University of Plymouth

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological & Marine Sciences

[In collaboration with Plymouth Marine Laboratory]

June 2018

Trophic and ecological implications of the gelatinous body form in zooplankton

Kristian Michael McConville

Gelatinous zooplankton are characterised as different from other planktonic taxa due to the high relative water content of their tissues. This thesis investigates whether elevated somatic water content (expressed here as carbon percentage) has effects on the biology of zooplankton. My approach was to examine this at a range of scales with a variety of approaches, ranging from experiments on individual ephyra larvae of *Aurelia aurita*, through analysis of a zooplankton time series at the Plymouth L4 station, up to a large scale meta-analysis of zooplankton growth and body composition data. In this meta-analysis, carbon percentage varied continuously across the range of the zooplankton, ranging from 0.01% to 19.02% of wet mass, a difference of over three orders of magnitude. Specific growth rate (g, d^{-1}) was negatively related to carbon percentage, both across the full range of zooplankton species, and within the subset of taxa traditionally classified as gelatinous. The addition of carbon percentage to models of zooplankton growth rate based on carbon mass alone doubled explanatory power. I present an empirical equation of maximum (food saturated) zooplankton growth that incorporates carbon mass and carbon as a percentage of wet mass. Applying this equation to a natural assemblage near Plymouth yielded sometimes double the secondary production, as compared to a simpler model based on crustacean growth. Both interspecifically and intraspecifically, carbon percentage was negatively related to carbon mass; more gelatinous taxa tended to have higher carbon masses. During the early development of *Aurelia aurita* ephyrae, carbon percentage was found to decrease from 2.36% (an intermediate value between crustaceans and classical gelatinous zooplankton) down to 0.1%, the adult value for *Aurelia aurita*. Juvenile forms of gelatinous taxa are often poorly sampled and their intermediate carbon percentages may help to form a continuum between those of crustaceans and adult cnidarians and ctenophores. As ingestion in the ephyrae was related to their diameter, models suggest that this dilution resulted in an increase in carbon-specific ingestion rate by an estimated 28% relative to an ephyra that did not dilute through development. At the species level, carbon percentage was negatively related to indices of temporal variation in numerical density but not related to rate of population increase. A wide variety of zooplanktonic taxa of different carbon percentages were found to increase in population at a rate that could be considered as forming a bloom. Likewise many gelatinous taxa at L4 did not form blooms. Thus the frequent reference to “jellyfish blooms” reflects, in part, the fact that unlike the other zooplankters that regularly reach even higher carbon concentrations, gelatinous taxa are simply more noticeable to the eye when at these concentrations. Calculating the carbon percentage of whole assemblages could be useful for investigating the influence of environmental parameters on zooplankton. Taken together, these results demonstrate the benefits of explicitly recognising the decoupling of metabolic and ecological body size seen in the gelatinous zooplankton.

Contents

Figure Contents

Table Contents

Acknowledgements

Firstly, I would like to thank my supervisors, Angus Atkinson, Elaine Fileman and John Spicer. Each of them have brought their own strengths to the process of helping me complete this work, and I am extremely grateful for all of the effort they have given so willingly.

Secondly, I want to thank all of the other researchers whose data have been used in this thesis. The kinds of questions addressed in this volume require detailed measurements from a wide range of species and independent measurement of each would have been far beyond the scope of this work. For this reason I am very grateful to all of the people who have worked hard to gather this data. I hope that they are pleased that the data presented in their publications is being used again to ask new and interesting questions. One dataset in particular has been used extensively, the L4 zooplankton time series. I wish to thank all of the individuals involved in the gathering of this dataset including the boat crew, plankton analysts and all the others behind the scenes that make this invaluable resource available.

I also wish to thank all those that have supported me during this time. My best friends and brothers (Dan, Jon, Bro and Lex) have been a constant source of help and understanding (as befits pirates of the stars), and I am tremendously grateful for all of their help. All of my friends have been consistently supportive, but I want to especially thank Emilie for really understanding and helping like only a fellow researcher can. I'd like to thank my mother and father for their constant encouragement and sincere belief in my ability to succeed in whatever I undertake.

Finally, the biggest thank you goes to my wife, Jessica. At every single stage of this experience you have had limitless patience and understanding, and have instinctively understood how best to help. This has been a difficult journey but the role you've played in it has showed me how well prepared we are for all that lies before us.

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

This study was financed with the aid of a studentship from the Natural Environment Research Council and carried out in collaboration with Plymouth Marine Laboratory.

A programme of advanced study was undertaken, which included Post Graduate Research Skills and Training, and Laboratory Based Teaching.

The following external institutions were visited for consultation purposes: Queen Mary University of London.

Publications:

McConville, K., Atkinson, A., Fileman, E.S., Spicer, J.I. and Hirst, A.G., 2016. Disentangling the counteracting effects of water content and carbon mass on zooplankton growth. *Journal of Plankton Research.* **39** 246-256.

Atkinson, A., Harmer, R.A., Widdicombe, C.E., McEvoy, A.J., Smyth, T.J., Cummings, D.G., Somerfield, P.J., Maud, J.L. and McConville, K. (2015) Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. *Progress in Oceanography* **137** 498-512.

Presentations and Conferences Attended:

Using carbon percentage as a continuous trait to better understand gelatinous zooplankton growth and feeding. *JellyBlooms 2016, Barcelona, Spain,* 30/05/16 – 03/06/16

Does relative water content of tissues explain growth rates in zooplankton? *ICES Annual Science Meeting, A Coruña, Spain,* 15/09/2014 – 19/09/2014

External Collaborations:

Dr Andrew Hirst, Queen Mary University of London

Word count of main body of thesis: 28302

Signed ……

Date ……

CHAPTER 1 - Introduction

1.1 - Importance of gelatinous zooplankton

Gelatinous zooplankton are a phylogenetically and functionally diverse group of aquatic organisms, including medusae, ctenophores and tunicates. This range of taxa varies in wet mass by over 10 orders of magnitude (Kiørboe, 2013; Uye, 2014), and demonstrates a wide range of remarkable biological properties. Some of the fastest growing metazoans are gelatinous zooplankton (Hopcroft et al., 1995), with among the shortest known metazoan life cycles (completed in 6 days 15^{o}C, Troedsson et al., 2009). Species within the group feed on organisms ranging from bacteria (Sutherland et al., 2010) through to adult fish (Purcell, 1984). Gelatinous zooplankton are also capable of surviving in a variety of environments ranging from oligotrophic subtropical gyres (Acuña, 2010) to eutrophic coasts (Richardson et al., 2009), and are extremely tolerant to hypoxia (Purcell et al., 2001; Thuesen et al., 2005).

Gelatinous zooplankton have a long evolutionary history as they appear in Vendian rocks 600 mya, well before the Cambrian explosion (Sappenfield et al., 2016) and are of interest to evolutionary biologists in several ways. There is evidence to suggest that Phylum Ctenophora, one of the most gelatinous groups, may be the sister taxon to all other metazoans (Dunn et al., 2015). Another subgroup, Order Siphonophora, exhibit the greatest degree of colonial specialisation of any animal (Dunn et al., 2005). Also, the smallest known metazoan genome is found within the group (Seo et al., 2001). Finally, the adoption of a gelatinous body form has occurred multiple times in evolutionary history as the trait is displayed across six phyla (Cnidaria, Ctenophora, Chordata, Mollusca, Annelida, Chaetognatha).

Several gelatinous species have the potential to form characteristic blooms (Uye, 2008; Canepa et al., 2014). Blooms are rapid localised increases in species biomass that have the potential to heavily impact zooplankton communities (Lynam et al., 2005) and compete with fish (Purcell and Arai, 2001; Haraldsson et al., 2012). Some blooms are natural and are a persistent feature over the timescale of millions of years (Condon et al., 2012), others are the result of

biological invasions (Finenko et al., 2006, Fuentes et al., 2010) and it has been suggested, anthropogenically-induced ecosystem change (Purcell et al., 2007).

Gelatinous zooplankton are widely referred to as having negative impacts on marine ecosystems, seen as a danger or nuisance, or a trophic dead end (Richardson et al., 2009). It is true that gelatinous zooplankton can have effects on humans, particularly when blooming. Predation by these taxa on larval fish can decrease fishery viability (Quinones et al., 2013), potentially leading to complete fishery collapse (Oguz et al., 2008). There have also been negative effects on aquaculture, directly by damage from water-borne nematocysts (Marcos-Lopez et al., 2016) and indirectly by, for example, the introduction of pathogens (Delannoy et al., 2008). Some species are hazardous to humans, with contact resulting in injury and even death (Fenner and Hadok, 2002). Consequently, gelatinous zooplankton can have severe socioeconomic impacts, particularly in areas that are reliant on seasonal recreational use of the coast such as the Mediterranean and Australia (Purcell et al., 2007). Blooms of gelatinous zooplankton also result in unexpected secondary effects such as the clogging of power plant water intakes (Lynam et al., 2006).

Given the myriad effects of jellyfish (and in particular, blooms) on human activity, and our increasing interaction with the marine environment, it is not surprising that research into jellyfish blooms has increased rapidly over the last 20 years (Gibbons and Richardson, 2013). This trend continued until recently (Figure 1.1), at a far greater rate than the mean increase in peer reviewed zooplankton articles published each year (STM Report, 2015).

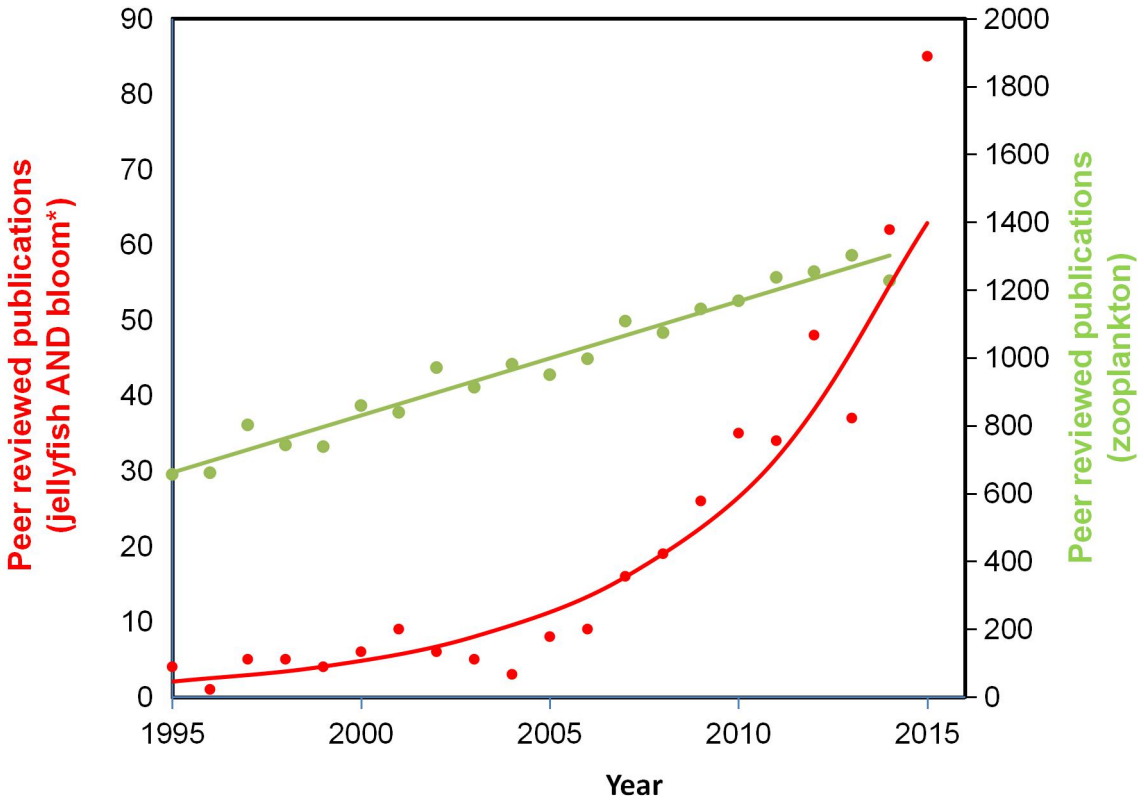


Figure 1.1 – *Number of peer reviewed articles per year returned from a Web of Science search (accessed 26/01/17) with the following criteria: ("jellyfish" OR "gelatinous") AND "bloom*" on the primary y axis (shown in red) and "zooplankton" on the secondary y axis (shown in green).*

While the pace of this research may be now be slowing, it has highlighted that gelatinous zooplankton have a wide range of positive effects, both on marine ecosystems and humans. In some systems, jellyfish are considered keystone species including Chesapeake Bay and the Central North Pacific (Libralato et al. 2006). Blooms can influence nutrient cycling through sinking as "jelly falls" (Sweetman et al., 2011), exporting organic matter to deeper water via their faecal pellets (Madin, 1982) and by releasing carbon as dissolved organic matter (Hansson and Norrman, 1995). In some locations this carbon release can be significant, up to four times the annual carbon input to the benthos (Lebrato et al., 2012).

Gelatinous taxa are also important members of marine food webs and are fed on by a wide range of species (reviewed in Arai, 2005) including numerous fish and crustaceans (Milisenda et

al., 2014; D'Ambra et al., 2015), and charismatic megafauna such as marine birds (Harrison, 1984) and the leatherback turtle, *Dermochelyes coriacea* (Houghton et al. 2006). Some gelatinous species (including *Cyanea capillata*) provide shelter for larval fish in open water, potentially decreasing mortality of the larvae of commercially important gadoid fish (Lynam and Brierley, 2007).

Humans also use gelatinous zooplankton directly in range of ways. Rhizostomid jellyfish are fished commercially, with approximately 425,000 tonnes harvested globally (FAO, 1999) with some jellyfish fisheries actively enriched via stock supplementation (Dong et al. 2010). In folk medicine, consumption of jellyfish is considered by some to be a cure for a range of conditions including hypertension and back pain (You et al. 2007) and experimental medical procedures using jellyfish collagen for treating arthritis and rebuilding damaged tissues have been trialled (Addad et al., 2011).

A more balanced view of the position and function of gelatinous zooplankton in marine ecosystems is thus developing. However, the definition of exactly what should be included within the group remains contentious (Condon et al., 2012). The core groups of the gelatinous zooplankton include the cnidarian medusae and ctenophores, often referred to collectively as "jellyfish" (Pitt et al., 2013), on the basis of their comparatively similar structure and relative phylogenetic proximity. Some authors include salps (Molina-Ramirez et al., 2015), but others exclude them because of their herbivorous trophic mode (Larson, 1987). Other studies include chaetognaths (Raskoff et al., 2005), heteropod and pteropod molluscs, appendicularians (Hamner et al., 1975) and radiolarians (Harbison et al., 1977) as members of the gelatinous zooplankton. Given the ambiguity of the term gelatinous zooplankton, the word "gelata" has been posed as an alternative to encompass the full range of plankton with dilute bodies (Haddock, 2004).

1.2 - Biological implications of a gelatinous body form

The one trait that unites the various gelatinous taxa is the high percentage of water in their bodies, expressed as having carbon mass that is approximately 1% (or less) of wet mass (Kiørboe, 2013; Molina Ramirez et al., 2015). Targeted studies on the effects of having a dilute, gelatinous body form are few, but several authors have suggested that there may be a range of potential implications on the physiology and ecology of these animals (Hamner et al., 1975, Alldredge, 1984). Clarke and Peck (1991) highlighted how the energetics of gelatinous zooplankton are more similar to benthic animals than to other zooplankton, owing to low locomotory and metabolic costs (Gemell et al., 2013), and lack of lipid stores. Alldredge and Madin (1982) suggested that pelagic tunicates had higher clearance rates than other zooplankton potentially as a result of their dilute bodies. Following these studies, other authors began to quantify these differences by modelling the feeding rate increase associated with an inflated body. Acuña (2001) used filter feeding theory to show that the salp, *Pegea confoederata,* would be incapable of meeting its metabolic demand in its nutrient poor environment if its body were not dilute. Kiørboe (2011) modelled the differences in encounter areas between a gelatinous organism (0.01 g C cm^{-3}) and a non-gelatinous organism (0.1 g C cm^{-3}). The increase in carbon mass-specific feeding rate afforded by diluting the body was similar in magnitude to the increase associated with an organism changing from passive ambush feeding to an active foraging mode.

This central idea of increasing feeding potential from having a dilute body was later expanded in a meta-analysis by Acuña et al. (2011). Their study compared the carbon mass-specific and wet mass-specific respiration and clearance rates of three groups; gelatinous zooplankton, crustacean zooplankton and fish. Gelatinous zooplankton had similar carbon mass-specific respiration rates to fish and crustacean zooplankton. This suggested that respiration was a function of carbon mass, and was unaffected by increasing wet mass. The wet mass-specific feeding rates of gelatinous zooplankton were similar to those of crustaceans, suggesting that their feeding methods were equally efficient at the same body volume. In contrast, fish use more efficient visual foraging, resulting in higher feeding rates at the same wet mass. However, as a

result of the low carbon percentage of gelatinous taxa, carbon mass-specific feeding rates were similar to those of visual foraging fish. In concert, this suggests that gelatinous zooplankton have higher scope for growth than other zooplankton, with values more similar to those of fish.

The most recent and comprehensive study of the differences between jellyfish (in their study defined as medusae and ctenophores) and other planktonic animals was carried out by Pitt et al. (2013). They included comparisons of growth rate, excretion rate, longevity and swimming velocity with a similar approach to that of Acuña et al. (2011). Pitt et al. (2013) approached the question by testing whether the carbon and wet mass-specific rates of the gelatinous taxa differed from the non-gelatinous taxa. Pitt et al. (2011) found that carbon-specific growth rates of gelatinous zooplankton were 2.2 times those of other zooplankton, and carbon specific ammonium excretion rates were one tenth of those of other zooplankton.

In the above mentioned comparisons, and indeed in all studies to date investigating the gelatinous body form, comparisons have been made between those phylogenetic groups that are classified as gelatinous and those that are not. However, this dichotomy quickly breaks down as intermediate gelatinous species also exist, such as chaetognaths and pelagic polychaetes (Kiørboe, 2013). When attempting to analyse the zooplankton as a whole it could be, as I will argue below, more appropriate to treat degree of dilution as a continuous trait, expressed as carbon mass as a percentage of wet mass.

1.3 - Aims and layout of this thesis

The relatively few studies comparing highly gelatinous taxa with other zooplankton demonstrate how tissue dilution can have significant effects on physiological rates such as feeding and growth. This thesis will investigate whether adopting a continuous approach using carbon percentage can further our understanding of how dilution affects the biology of zooplankton. A

change in thinking from dividing plankton on the basis of gelatinous vs non-gelatinous, to a trait-based approach which focusses on the continuous variable carbon percentage may seem trivial but could be a major step forward in a number of ways. First, gelatinous taxa and other zooplankton currently need to be modelled separately to incorporate the differences in vital rates described above. This has lead to gelatinous taxa being frequently excluded from ecosystem models, or being poorly parameterised within them (Pauly et al., 2009). If the differences between gelatinous and other zooplankton could be related to carbon percentage as a continuous variable, then variability in vital rates could be included intrinsically without the increase in complexity associated with dividing the zooplankton into different groups.

Secondly, taxa with different carbon percentages are favoured under different environmental conditions. For instance, highly gelatinous non visual predators may be more successful in turbid (Haraldsson et al., 2012) and hypoxic conditions (Thuesen et al., 2005). A greater understanding of how carbon percentage drives these differences will help us to predict how planktonic systems will respond to changing environmental conditions, such as increasing temperature and coastal eutrophication.

Furthermore, understanding carbon percentage as a trait could help us to understand the evolution of different morphological strategies in the plankton. Seven phyla contain planktonic taxa that could be considered gelatinous, and understanding the effects of carbon percentage could help us to better understand why the gelatinous body form is seen in such a wide range of zooplanktonic organisms.

1.3.1 - Aim

The primary aim of this thesis was to address the question: how does tissue dilution affect the biology of zooplankton?

1.3.2 - Objectives

To achieve this aim I have investigated whether the differences in growth and ingestion rate between gelatinous and other zooplankton are a consequence of differences in carbon percentage. A range of different approaches were used including meta-analysis, experiments and analysis of time series data. The aim was completed through a series of sequential objectives, namely:

(I) – HOW DO WE EXPECT CARBON PERCENTAGE TO INFLUENCE ENERGY BUDGETS?

In **Chapter 2**, by applying established scaling theory I have explored how carbon percentage is expected to influence the respiration, feeding and growth rates of zooplankton. These predictions are used as support for the hypotheses advanced in the subsequent chapters. Also within **Chapter 2**, the sampling protocol at the L4 sampling station is detailed to provide background for the use of the zooplankton abundance time series in **Chapters 3, 5, 6** and **7**.

(I) – IS CARBON PERCENTAGE CONTINUOUS?

In **Chapter 3**, synchronous measurements of carbon and wet masses of a wide range of zooplanktonic taxa were compiled from the literature. A meta-analysis of these collected data was used to investigate the distribution of species along the axis of carbon percentage. By assessing to what extent the carbon percentages of zooplankton form a natural division between discrete gelatinous and non-gelatinous groups, I determined whether it was appropriate to treat carbon percentage as a continuous trait. This meta-analysis provided information on the potential variation in traits but the range of species analysed was not representative of the species that inhabit any single ecosystem. For this reason, zooplankton abundance time series data from the Plymouth L4 sampling station (detailed in **Chapter 2**) was used to determine how biomass was distributed along the axis of carbon percentage in a real assemblage.

(II) – IS CARBON PERCENTAGE RELATED TO GROWTH RATE?

Chapter 3 continued by combining the carbon percentage values with a meta-analysis of published zooplankton growth rates to determine whether carbon percentage was related to growth rate. Carbon percentage was combined with carbon mass (alongside standardisations for food and temperature) to provide a unified model of zooplankton growth. The data were also tested for a relationship between carbon percentage and carbon mass, both in the meta-analysis and the real assemblage at L4.

(III) – IS CARBON PERCENTAGE FIXED WITHIN A SPECIES?

Chapter 3 explored whether interspecific variability in carbon percentage affected the biology of zooplankton. **Chapter 4** extends the investigation to intraspecific variability using a series of experiments on ephyra larvae of the moon jellyfish, *Aurelia aurita*. The carbon and wet masses of the growing ephyrae were measured to determine whether carbon percentage varies through early development.

(IV) – HOW DOES INTRASPECIFIC VARIATION IN CARBON PERCENTAGE AFFECT FEEDING AND GROWTH RATES?

Following on from objective iii, **Chapter 4** determined whether variability in carbon percentage through ontogeny influences the feeding and growth rates of ephyrae. The ephyrae were incubated in saturating food conditions, and ingestion and growth rates were measured and related to carbon percentage and carbon mass. A simple mechanistic model was constructed to further explore how variation in carbon percentage affects the energy budget of the ephyrae.

(V) – DOES CARBON PERCENTAGE AFFECT THE FORMATION OF JELLYFISH BLOOMS?

Previous studies have suggested that gelatinous taxa have higher carbon specific feeding and growth rates than other zooplankton. **Chapter 5** investigated whether these organismal differences manifest at the population level by asking whether carbon percentage is related to the formation of rapid population increases i.e. blooms. Using zooplankton abundance from the L4 time series, **Chapter 5** also determined whether carbon percentage affects variability in abundance and population increase rate among the zooplankton.

(VI) WHAT IS THE RELATIONSHIP BETWEEN CARBON PERCENTAGE AND CARBON MASS?

A relationship between carbon mass and carbon percentage was established in **Chapter 3**, and was explored in greater detail in **Chapter 6**. By investigating the variability in this relationship, **Chapter 6** suggested how carbon mass and carbon percentage interact to set constraints on zooplankton body size.

(VII) WHAT DOES THIS MEAN FOR HOW WE THINK ABOUT ZOOPLANKTON AND CARBON PERCENTAGE?

Chapter 7 summarised how the results found in the other chapters could change the way we think about zooplankton. Additionally, **Chapter 7** explored how carbon percentage might be used in different way in future studies, for instance as a response variable for summarising planktonic assemblages.

CHAPTER 2 – Theoretical model of the effects of carbon percentage and L4 sampling details

2.1 - Introduction

Throughout this thesis I have used a theoretical model to make predictions about the effects of carbon percentage on various aspects of zooplankton biology. In this chapter I develop the form and explain the assumptions of this model. To test some of the predictions posed by the model and investigate population level phenomena, the L4 time series of zooplankton abundance has been used. The background information and sampling regime for this time series are detailed below.

2.2 - Dilution as a continuous trait: modelling the potential effects of carbon percentage

Using the differences between gelatinous and non-gelatinous zooplankton presented in Chapter 1 and scaling theory, it is possible to predict how carbon percentage (C% = carbon mass as a percentage of wet mass*)* might affect vital rates using a simple geometric model.

The most immediate effect of variation in carbon percentage is on effective body size (i.e. body volume). Two organisms of the same carbon mass but different carbon percentages will have different wet masses, and therefore different effective body sizes. As body size is integral to the biology of all organisms, hypotheses for the effects of carbon percentage will be formulated by applying existing knowledge of how changing body size alters vital rates. The model below will compare two organisms of the same carbon mass, C, but different wet masses, WM. For the sake of comparison, these organisms will be referred to as gelatinous and non-gelatinous, and represent opposite ends of the range of carbon percentage.

The non-gelatinous organism has a “normal” carbon percentage (C = 10% WM);

$$\text{(eq. 1.1)}\quad WM = C / 0.1$$

The gelatinous organism has a lower carbon percentage (C = 0.1% WM);

$$\text{(eq. 1.2)}\quad WM = C / 0.001$$

As “body size” is described as the primary biological trait determining energy budgets (Andersen et al., 2016), we can use different metrics of body size to estimate a range of energy budget parameters for these two organisms. In the following paragraphs I have applied established scaling theory to our current understanding of how gelatinous zooplankton differ from other planktonic taxa (Acuña et al., 2011; Pitt et al, 2013). By combining this with a logical exploration of whether energy budget parameters are likely to be controlled by carbon or wet mass, I have developed a range of predictions of how carbon percentage might influence the energy budget of zooplankton. These predictions are tested using a range of methods in subsequent chapters.

2.2.1 - Respiration

Water does not have respiratory demand (or capability) so therefore respiration can only be a function of the organic content of the body (Acuña et al., 2011). The organic content or metabolically active mass is represented here as carbon mass, therefore in both cases;

$$\text{(eq. 1.3) Respiration rate} = aC^{b}$$

Respiration rate is a function of carbon mass, C, a constant, *a*, and the body mass scaling exponent, *b*. The value of the body mass scaling exponent of metabolism, *b*, has been a topic of much debate for nearly a century (Kleiber, 1932). However, as we are comparing organisms of identical carbon mass, the values of the exponent and the coefficient do not affect the model. As respiration is a function of carbon mass (and is not affected by wet mass, Acuña et al., 2011), the respiration of the gelatinous and non-gelatinous organisms in the model will be equal.

2.2.2 - Ingestion rate

Ingestion rate is a complex variable that can vary widely depending on feeding mode, food concentration, prey type and a wide range of other factors. For the sake of simplicity, it is assumed that both organisms are neutrally buoyant, ambush feeders that do not actively forage. Following

these assumptions, ingestion rate is a function of encounter rate, which is in turn a function of surface area, and therefore the following equation will apply;

$$\text{(eq. 1.4) Ingestion rate} = x(C/C\%)^{2/3}$$

The constant, x, will be dependent on feeding mode and the other factors mentioned above, and is not critical for this investigation. The scaling exponent of $b = 2/3$ is a consequence of surface area scaling as length^2 and volume scaling as length^3.

From this point the gelatinous and non-gelatinous organisms diverge;

$$\text{(eq. 1.5) Non-gelatinous feeding rate} = (C/0.1)^{2/3} = (10C)^{2/3}$$

$$\text{(eq. 1.6) Gelatinous feeding rate} = (C/0.001)^{2/3} = (1000C)^{2/3}$$

Both surface area and volume are functions of wet mass, and therefore feeding rate differs between the gelatinous and non-gelatinous organisms. It could be argued that given the wide variety of feeding modes that exist, modelling ingestion rate using surface area is too great an assumption. However, the purpose of this model is not to produce quantitative estimates of the effect of carbon percentage, but to suggest the form of this relationship for testing in subsequent chapters. In the case of feeding rate, scaling exponents of $b < 0$ are very rare both interspecifically (Kiørboe and Hirst, 2014) and intraspecifically (Hirst and Forster, 2013), and b values typically vary between 0.66 and 1. With this in mind, it is predicted that decreasing carbon percentage will typically increase carbon-specific ingestion rate. In this model, the gelatinous organism will have higher carbon specific ingestion rates than the non-gelatinous, with the difference between the two depending on carbon mass and the difference in carbon percentage.

2.2.3 - Scope for growth

Scope for growth is an estimate of the energy available for growth, it is a function of feeding rate minus respiratory cost;

(eq. 1.7) Scope for growth = food intake – respiration loss = $(C/C\%)^{2/3} – C^b$

Therefore;

(eq. 1.8) Non-gelatinous growth = $(10C)^{2/3} – C^b$

(eq. 1.9) Gelatinous growth = $(1000C)^{2/3} – C^b$

As shown above, while the carbon specific respiration rate of the gelatinous and non-gelatinous organisms is the same, carbon specific feeding rate differs and therefore scope for growth differs also. The scope for growth of the gelatinous organism is higher than that of the non-gelatinous organism, with the magnitude of the difference dependent on carbon mass. Scope for growth does not equal growth rate, but as an estimate of the resources available for growth can be used to estimate relative growth rate.

2.3 - Introduction to the Western Channel Observatory

The Western Channel Observatory is the collective name given to a series of atmospheric, planktonic and benthic monitoring and process stations in the shelf waters south of Plymouth (Figure 2.1). The centrepiece stations are known as L4 (13 km SSW of Plymouth) and E1 (40 km SSW of Plymouth) which are in water depths respectively of ~54 and 75 m. These stations have been sampled periodically for over a century (Southward et al., 2005), but zooplankton sampling at L4 was resumed on a weekly basis by Plymouth Marine Laboratory in March 1988. It thus provides a particularly valuable time series and the zooplankton data set used in my study.

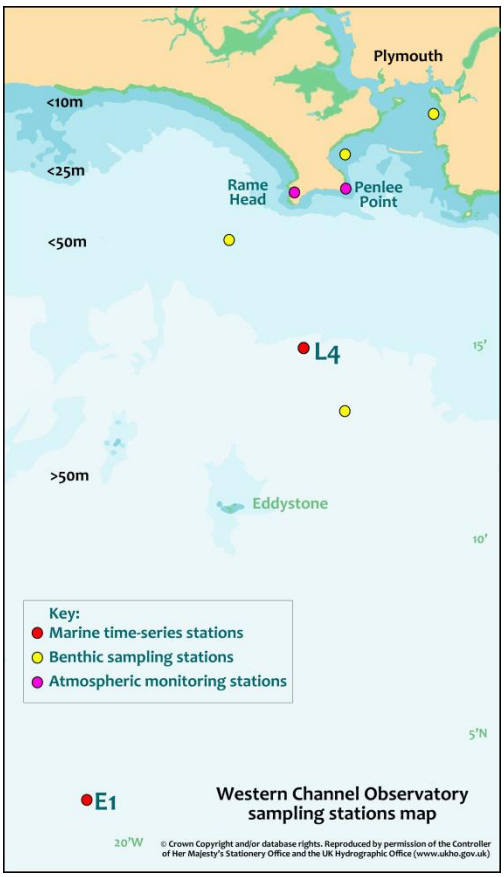


Figure 2.1 – *Location of the sampling stations within the Western Channel Observatory off Plymouth, UK (http://www.westernchannelobservatory.org.uk).*

Detailed study of this area of the Western English Channel began in 1888 with the formation of the Marine Biological Association (Southward et al., 2005). Various investigations into the area, especially with reference to herring and mackerel fisheries continued until the establishment of profiles of chlorophyll a, salinity and temperature in 1970. In 1988, PML established the first measurements at station L4 as a result of several concurrent research projects. Since this time, the time series has expanded and now includes benthic survey, flow cytometry, data buoys and a wide range of biogeochemical parameters alongside measurements of zooplankton and phytoplankton (Smyth et al., 2015).

The work that has been made possible as a result of the observatory has been varied and impactful (summarised in Smyth et al., 2015). Studies from the observatory have enhanced our knowledge of plankton ecology over the full range of biological scales, from viral interactions (Nizzimov et al., 2015) to the effects of microplastics (Cole et al., 2015). One of the key sampling efforts that takes place at the observatory is the L4 zooplankton time series. This provides a rich dataset that began in 1988, and since then has expanded to weekly recordings of the abundance of 199 taxa. As a result of this time series, there is a good understanding of zooplankton dynamics at L4 (Eloire et al., 2010). Zooplankton abundance peaks in April and September, driven by abundant phytoplankton and temperature. The assemblage is dominated by copepods, with seven of the ten species with the highest average abundance at L4 belonging to this group. Diversity varies throughout the year. In winter, most of the zooplankton sampled come from a fairly narrow group of primarily crustacean taxa. In the summer the assemblage is much more diverse, with abundance distributed more evenly through a wide range of taxa. Meroplanktonic larvae contribute significantly to the assemblage at L4 at specific times of year, with cirripedes, echinoderm larvae and bivalve larvae occurring in high numbers in spring, summer and autumn respectively. Also, several gelatinous taxa, particularly siphonophores and ctenophores, can form the majority of the sampled assemblage for short periods during summer.

A key strength of the L4 zooplankton time series is the weekly resolution, which has allowed researchers to investigate the formation and timing of seasonal events (Atkinson et al., 2015). In this thesis I have used the L4 time series in a similar manner to investigate population level traits of zooplankton in chapters 3, 5, 6 and 7. As these data have been used in multiple chapters, I have detailed the sampling protocol and method below to avoid repetition.

2.3.1 - L4 zooplankton time series sampling

Sampling at the L4 site consists of a pair of vertical hauls with a 200 μm WP2 zooplankton net from 50 m to the surface (maximum depth 54m). The nets are retrieved at 20 cm s^{-1} and are

immediately fixed in 4% formaldehyde solution in 0.2 µm filtered seawater (Maud et al., 2015). Mesozooplankton from the formalin-preserved vertical net hauls are enumerated and identified by microscopy. Two sub-samples of different size are analysed per sample. The smaller one is taken with a Stempel pipette for the abundant taxa. Typical subsamples ranged from 1-10ml from 300 ml. A second, larger aliquot is analysed for rarer and large taxa, typically 12.5%, 25% or 50% (Eloire et al., 2010). Abundances across the two hauls were averaged and numbers expressed as individuals per m^3 allowing for a 95% net filtration efficiency (UNESCO, 1968). Some species are enumerated further according to maturity stage, e.g. *Calanus helgolandicus* copepodites CI-CV and *Calanus helgolandicus* adults. For the purposes of my analyses, these groups were combined to yield a single value for each taxon at each time point. To estimate biomass of each zooplankton taxon (mg C m^{-3}) from numerical density (no. m^{-3}), a total of 3780 individuals of the dominant taxa from the formalin-preserved catches at L4 taken throughout 2014 and 2015 were measured. From standard length measurements (e.g. cnidarian bell height or diameter, copepod prosome length), length-carbon mass relationships from the literature were used to estimate carbon masses per individual. The derived values were then averaged into seasons, namely spring (March-May), summer (June-August), autumn (September-November) and winter (December to February) to account for the high intraspecific variability in length observed at L4 (Atkinson et al., 2015). From this, season-specific mean carbon masses per individual were derived, which were multiplied by numerical densities to estimate biomass density (mg C m^{-3}). Previously measured L4-specific seasonal values of individual carbon biomass were used when available (e.g. *Calanus helgolandicus;* Pond et al., 1996).

CHAPTER 3 – Disentangling the counteracting effects of water content and carbon mass on zooplankton growth

This chapter was published as the following reference and is appended at the end of this volume;
McConville, K., Atkinson, A., Fileman, E.S., Spicer, J.I. and Hirst, A.G., 2016. Disentangling the counteracting effects of water content and carbon mass on zooplankton growth. *Journal of Plankton Research* **39** *246-256.*

3.1 - Introduction

Gelatinous zooplankton have been attracting increasing attention from scientists and the popular press alike, and the current literature tends to emphasise the differences between gelatinous taxa and other zooplankton (e.g. Richardson et al., 2009; Kiørboe et al., 2011; Gibbons and Richardson, 2013). This chapter takes a different approach by investigating whether carbon percentage can be treated as a continuous variable, and whether a relationship exists between carbon percentage and growth rate. Based on a compilation of body composition data, Kiørboe (2013) found that most zooplankton species are either gelatinous (carbon mass ~0.5% of wet mass) or not gelatinous (5-10%), with comparatively few intermediates. Much recent research has been directed toward comparing and contrasting gelatinous versus non-gelatinous zooplankton. For example, compared to other planktonic animals, gelatinous zooplankton have higher carbon mass-specific feeding rates (Hamner et al., 1975; Acuña, 2001; Acuña et al., 2011), lower locomotion costs and higher specific growth rates (Hirst et al., 2003; Pitt et al., 2013). Indeed, gelatinous taxa such as salps are amongst the fastest growing metazoans (Bone, 1998).

The use of a categorical approach to zooplankton body composition (i.e. gelatinous versus non-gelatinous) contrasts with the treatment of carbon mass (Peters, 1983), which is used as a continuous variable in many models of growth (Hansen et al., 1997; Gillooly et al., 2002; Hirst et al. 2003). However, the carbon percentage of zooplankton species also varies widely, even among gelatinous taxa (Molina-Ramirez et al., 2015). A recent review suggested that water content was second only to body size in determining key aspects of the biology of zooplankton (Andersen et al., 2015b). So far, empirical models of zooplankton growth use equations that are specific to various taxonomic groups (e.g. Hirst et al., 2003; Kiørboe and Hirst, 2014) and these equations have not yet been unified. As carbon mass and carbon percentage are capable of varying independently, it is important to consider them together in empirical models of zooplankton growth. Furthermore, quantifying the relationship between growth rate and carbon percentage may help to explain how carbon percentage functions as an evolutionary trait, and, for example, why there are gelatinous representatives from six phyla found in the plankton.

In this chapter, I have used both a meta-analyses approach and an *in situ* time series of zooplankton abundance data from weekly sampling at the Plymouth L4 time series (detailed in Chapter 2). The first step was to quantify the degree of variability in carbon percentage both in "trait space" from the meta-analysis dataset and in a natural plankton assemblage, to gauge whether it was appropriate to treat water content as a continuous variable. The second aim was to investigate the degree of collinearity between carbon mass and carbon percentage, again both in a meta-assemblage and in the L4 assemblage. Dependent on the outcome of these two objectives, the third was to construct a model of zooplankton growth that combines carbon mass and carbon percentage to provide a simplified prediction of growth for modellers and empiricists.

3.2 - Methods

3.2.1 - Carbon percentage data

Ratios of carbon mass to wet mass were combined from a series of recent compilations (Kiørboe, 2013; Pitt et al., 2013; Molina-Ramirez et al., 2015). The amalgamated dataset with sources is presented in Appendix I. Only concurrent measurements of carbon and wet mass of the same individual were used to calculate carbon percentage.

The degree of tissue dilution of zooplankton taxa has been expressed previously as body carbon content (Molina-Ramirez et al., 2015). However, to avoid confusion with carbon mass, throughout my thesis it is referred to as "carbon percentage" (carbon mass as a percentage of wet mass). The levels of taxonomic organisation used for comparison were selected based on functional diversity and body form (e.g. phylum for Chaetognatha, but orders Cydippida and Lobata).

3.2.2 – Analysis of the zooplankton assemblage from the L4 site

The sampling, subsampling protocol and environment of the L4 time series are detailed in section 2.3. Of the approximately 189 taxa recorded at L4, only 22 contributed more than 0.5% to the total estimated biomass for all species. To examine how biomass was distributed across the spectrum of carbon percentage, these taxa were assigned to $\log_2$ classes (0.1 - 0.2%, 0.2 – 0.4%, 0.4 – 0.8%, 0.8 – 1.6%, 1.6 – 3.2%, 3.2 – 6.4%, 6.4 – 12.8%, > 12.8%) using the carbon percentage data in Appendix I. The distribution of carbon biomass in each carbon percentage category across the seasons was then calculated.

3.2.3 - Growth rate data

Using the references from the appendices of Kiørboe and Hirst (2014) as a starting point, zooplankton growth rate data were extracted from the original sources and augmented by searching the literature (Appendix II). To improve comparability of source data I restricted the meta-analysis to data from laboratory incubations with food available in high (assumed non-limiting) concentrations. By using only data collected under these conditions I suggest that the measurements are more directly comparable, with the observed patterns more likely to reflect the intrinsic biology of the species than external factors.

Published growth rates are normally expressed either as increase in length or body mass over time. When organism size was expressed as length, published length-mass regressions were used to convert to body carbon mass (Hirst, 2012; Kiørboe and Hirst, 2014). To express growth rates in the terms commonly used for zooplankton (as an exponential rate; see Hirst and Forster, 2013), the mass-specific growth rate, g (d^{-1}) was determined as:

$$\text{(eq. 2.1)}\quad g = (\ln M_t - \ln M_0)/d$$

M_t is mass at time t, M_0 is mass at the previous time point, and d is the time period between the two measurements of mass (in days).

Growth data were temperature-corrected to 15^{o}C using a Q_{10} of 2.8 (following Hansen et al., 1997; Kiørboe and Hirst, 2014). General Linear Models (GLMs) were constructed in R (R Core Team, 2014) to test for relationships between growth rate, carbon percentage and carbon mass. To determine whether there was collinearity between the predictor variables I examined the condition indices for the variables in the model using the *colldiag* function in the *perturb* package in R (Hendrickx, 2012). A condition index of greater than 30 is considered large (Belsley et al., 1980) and suggests that the variable should be removed from the model.

When growth data were available for a species but carbon percentage values were not, the latter was estimated using the mean value for the highest level of taxonomic relatedness available. For instance, if composition values for a species were not available, then the composition values for all other species within the genus were averaged and used as an estimate. The estimates were typically at the genus level but no lower relatedness than family (38% estimated at family level, primarily for copepods).

3.2.4 - Growth rate analysis

Four analyses were performed; the first two were based on mean and maximum growth rates for all zooplankton taxa in the meta-analysis dataset, the second two as above but for the classical gelatinous taxa only (Cnidaria, Ctenophora and Thaliacea). Maximum growth values were defined as the highest temperature-adjusted growth rate value available for each species. Issues of non-independence between data were avoided by using single growth rate values per species per study. For illustrative purposes only (i.e. the plots in Figure 3.4), I adjusted all growth rates to a fixed body carbon mass of 1mg C after correcting to 15^{o}C. This mass correction was performed by assuming that $\log_{10}$ mass-specific growth (g) scales against $\log_{10}$ mass with a slope of -0.25 (Brown et al., 2004).

3.2.5 – Secondary production

The unified growth equations described in section 3.2.3 were used to simplify and improve estimates of secondary production. Two growth models were compared to investigate the effect of inclusion of carbon percentage on estimates of secondary production. The model of growth rate including both carbon mass and carbon percentage developed in this chapter was compared with a model of planktonic crustacean growth rates from Kiørboe and Hirst (2014).

3.3 - Results

3.3.1 - Variability in carbon percentage across the zooplankton

The range in body volume for two animals of equal carbon mass but at either end of the carbon percentage spectrum is demonstrated in Figure 3.1. For the compiled dataset, the range in carbon percentage extended over four orders of magnitude in zooplankton, from 0.01% in the lobate ctenophore, *Bathycyroe fosteri*, to 19.02% in the copepod, *Calanus hyperboreus* (Figure 3.1, 3.2a, Appendix I).

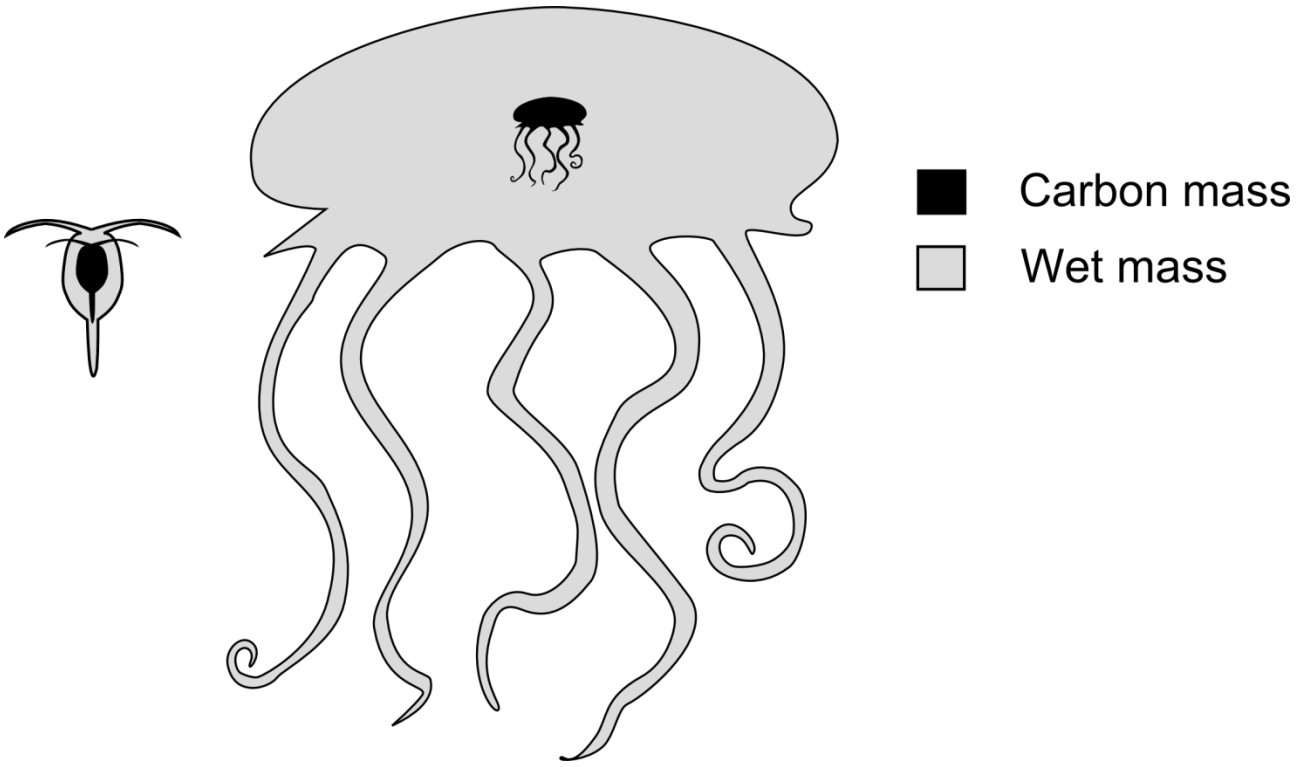
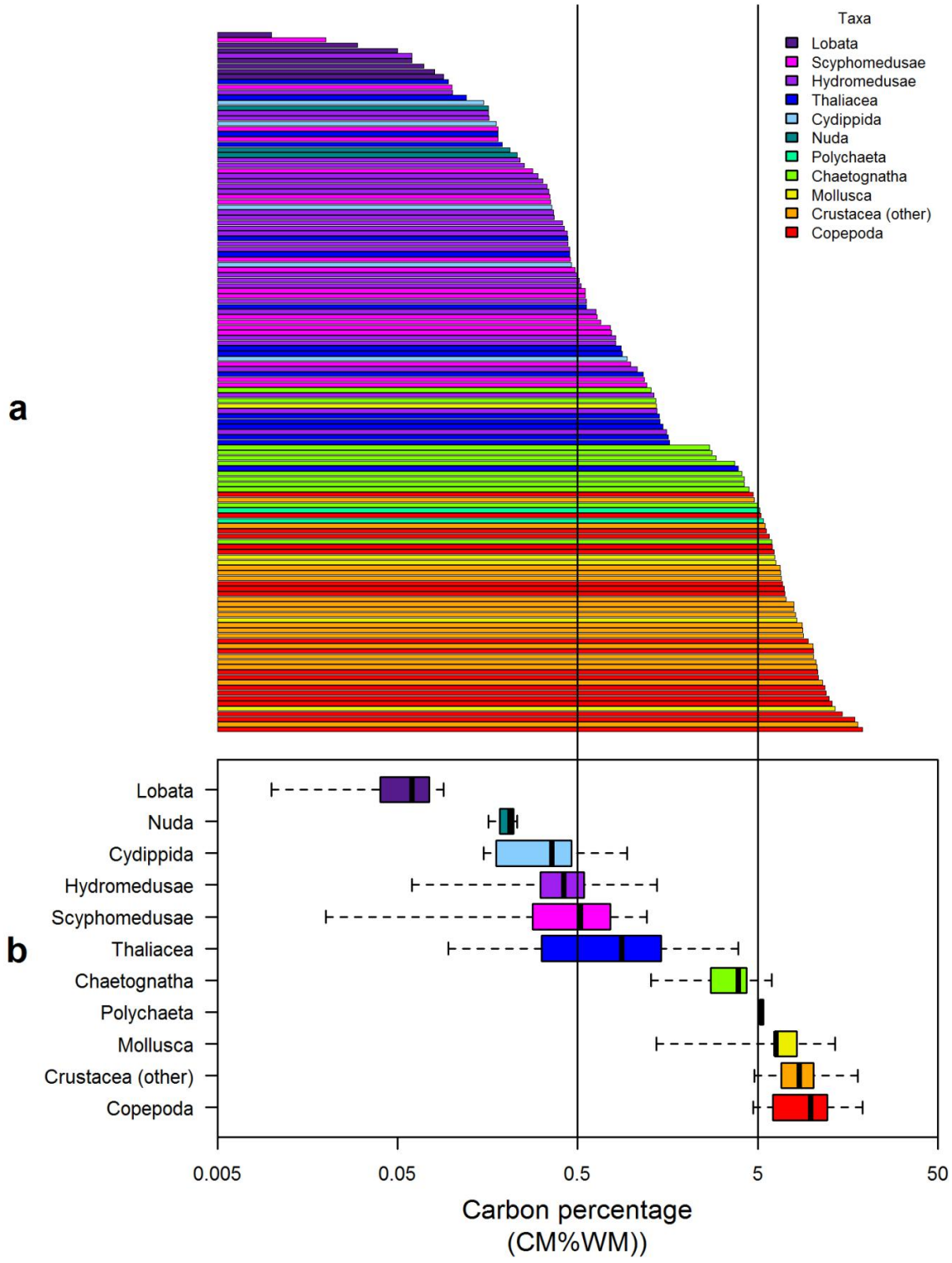


Figure 3.1 - *Comparison of the relative carbon (black) and wet masses (grey) of* Calanus hyperboreus *(left, carbon percentage = 19.02%) and* Bathycyroe fosteri *(right, carbon percentage = 0.01%). The relative area of each shade is scaled as volume so the silhouettes are representative of true size.*

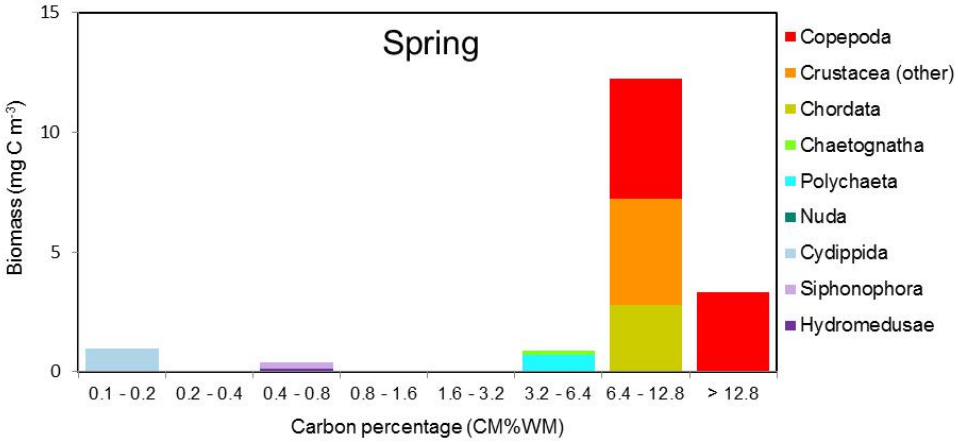
The intervals between adjacent ranked species were small relative to the range covered (Figure 3.2a), suggesting that water content could be considered as a continuous variable.

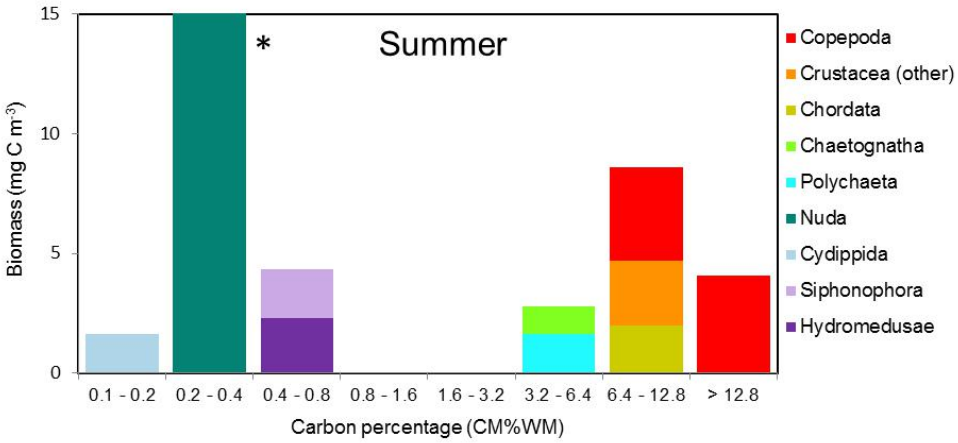
Figure 3.2 - *(a) Zooplankton species ranked according to their carbon percentage (CM%WM; log_{10} scale), each horizontal bar represents a single species. Colours indicate taxonomic groups as detailed in the legend. (b) Zooplankton taxonomic groups ranked according to their carbon mass (as % of wet mass; log_{10} scale). Boxes indicate median, lower and upper quartiles with whiskers showing the range. (Vertical lines at 0.5 and 5 CM%WM represent the composition of the gelatinous and non-gelatinous taxa defined by Kiørboe, 2013).*

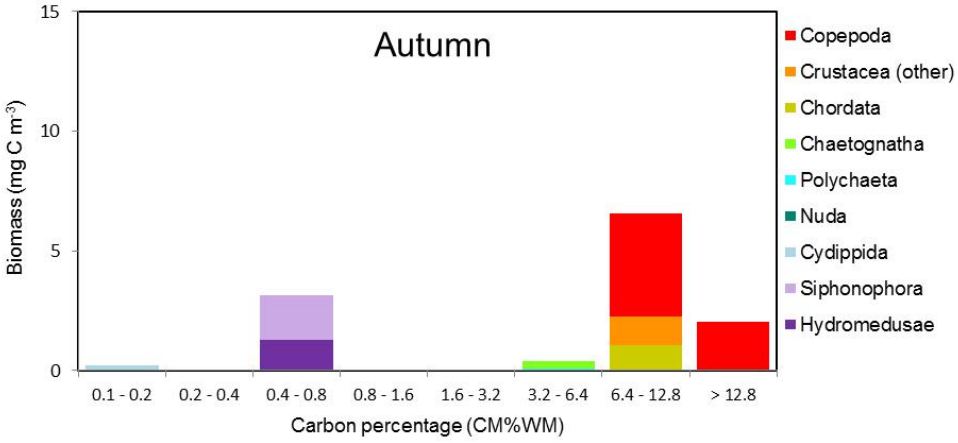

a
b
Taxa
Lobata
Scyphomedusae
Hydromedusae
Thaliacea
Cydippida
Nuda
Polychaeta
Chaetognatha
Mollusca
Crustacea (other)
Copepoda
0.005
0.05
0.5
5
50
Carbon percentage
(CM%WM))

The largest carbon percentage interval between species coincided with the shift from the classic gelatinous taxa to other zooplankton (i.e. from Thaliacea to Chaetognatha). However, this difference between species constituted a relatively small fraction of the total range (6.8%). In addition, there was an overlap of classic gelatinous and non-gelatinous groups. For example, some chaetognaths were within the traditional gelatinous range (1.27% and 1.35% for *Pseudosagitta lyra (as P. scrippsae)* and *Pseudosagitta* (as *Sagitta) gazellae* respectively), whereas one tunicate had a carbon percentage which lay within the non-gelatinous range (3.87% for *Doliolum denticulatum*). This overlap of taxonomic groups was extensive across the spectrum of water content, as can be seen by the mixing of colour across Figure 3.2a. This was particularly the case among the Ctenophora and Thaliacea, with the range of both taxa approaching two orders of magnitude in carbon percentage, corresponding to a 100-fold difference in body volume at the same carbon mass.

The wide variation in body carbon percentage observed at a species level in Figure 3.2a is also summarised at the broader taxon level in Figure 3.2b. Median values for groups loosely cluster into gelatinous and non-gelatinous taxa following the bimodal distribution of species suggested by Kiørboe (Kiørboe, 2013). The ranges of all adjacent taxa (excluding lobate ctenophores) overlapped, with Thaliacea and Chaetognatha bridging the gap between the classical gelatinous and non-gelatinous taxa. The variability within groups was greater for gelatinous taxa, with the greatest range in the scyphomedusae, closely followed by the thaliaceans. The gelatinous taxa sort into their respective phyla when ranked (i.e. Lobata, Nuda, Cydippida for the Ctenophora, then Hydromedusae and Scyphomedusae for Cnidaria) suggesting that taxa within phyla are on average more similar to each other than with other phyla. In the natural assemblage sampled at the Plymouth L4 site (Figure 3.3) there is an alternative picture with biomass distributed bimodally along the spectrum of carbon percentage.


Spring
Biomass (mg C m-3)
15
10
5
0
0.1 - 0.2
0.2 - 0.4
0.4 - 0.8
0.8 - 1.6
1.6 - 3.2
3.2 - 6.4
6.4 - 12.8
> 12.8
Carbon percentage (CM%WM)
Copepoda
Crustacea (other)
Chordata
Chaetognatha
Polychaeta
Nuda
Cydippida
Siphonophora
Hydromedusae


*
Summer
Biomass (mg C m-3)
15
10
5
0
0.1 - 0.2
0.2 - 0.4
0.4 - 0.8
0.8 - 1.6
1.6 - 3.2
3.2 - 6.4
6.4 - 12.8
> 12.8
Carbon percentage (CM%WM)
Copepoda
Crustacea (other)
Chordata
Chaetognatha
Polychaeta
Nuda
Cydippida
Siphonophora
Hydromedusae


Autumn
Biomass (mg C m-3)
15
10
5
0
0.1 - 0.2
0.2 - 0.4
0.4 - 0.8
0.8 - 1.6
1.6 - 3.2
3.2 - 6.4
6.4 - 12.8
> 12.8
Carbon percentage (CM%WM)
Copepoda
Crustacea (other)
Chordata
Chaetognatha
Polychaeta
Nuda
Cydippida
Siphonophora
Hydromedusae

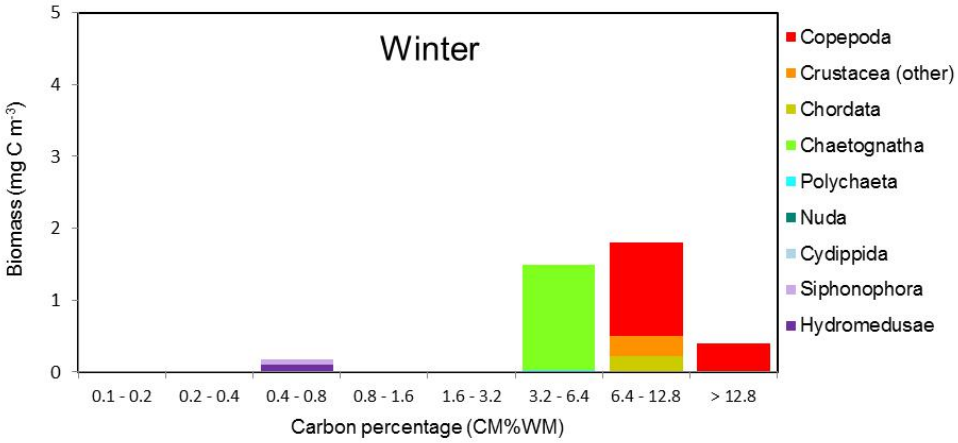

Winter
Biomass (mg C m-3)
5
4
3
2
1
0
0.1 - 0.2
0.2 - 0.4
0.4 - 0.8
0.8 - 1.6
1.6 - 3.2
3.2 - 6.4
6.4 - 12.8
> 12.8
Carbon percentage (CM%WM)
Copepoda
Crustacea (other)
Chordata
Chaetognatha
Polychaeta
Nuda
Cydippida
Siphonophora
Hydromedusae

Figure 3.3 - *Distribution of carbon biomass (mg C m^{-3}) between log_2 carbon percentage categories through spring, summer, autumn and winter (2009-2015) at the L4 sampling site, Western Channel Observatory, Plymouth. The same colour coding of taxa is used as in Figure 3.1 – see legend. * - Biomass value for the category 0.4 – 0.8 exceeds the scale in summer (crudely estimated at 34 mg C m^{-3}) as a result of 7 high abundance observations of* Beroe *spp. (of total 318 time-points). Upper limit of biomass scale in winter is 5 mg C m^{-3}.*

The biomass was primarily concentrated in the categories that are either highly gelatinous (carbon mass 0.1 – 0. 8% of wet mass) or non-gelatinous (6.4 - > 12.8%). However, there is considerable variability within the carbon percentage categories, as some gelatinous taxa are as much as 8 times larger in wet mass for the same carbon mass as others. The biomass in the intermediate categories (0.8 – 1.6% and 1.6 – 3.2%) was very low and below our threshold for inclusion. This area of the spectrum is populated by thaliaceans and large rhizostomid scyphomedusae, which are not commonly recorded at L4 and may be poorly sampled by the 0.57m mouth diameter (200µm mesh) nets used. Gelatinous taxa comprised a greater proportion of biomass in summer than the other seasons. In winter, chaetognaths (carbon mass 3.56% of wet mass) have similar total biomass to the dominant copepods. There is also a broad trend of increasing carbon percentage through the year within the gelatinous taxa. In spring, the cydippids (the most gelatinous group frequently encountered at L4) are dominant, followed by Nuda (Beroe) in summer and finally hydromedusae and siphonophores in autumn.

3.3.2 - Relationship between carbon mass and carbon percentage

Based on the meta-analysis datasets there was a negative relationship between carbon mass and carbon percentage (Figure 3.4).

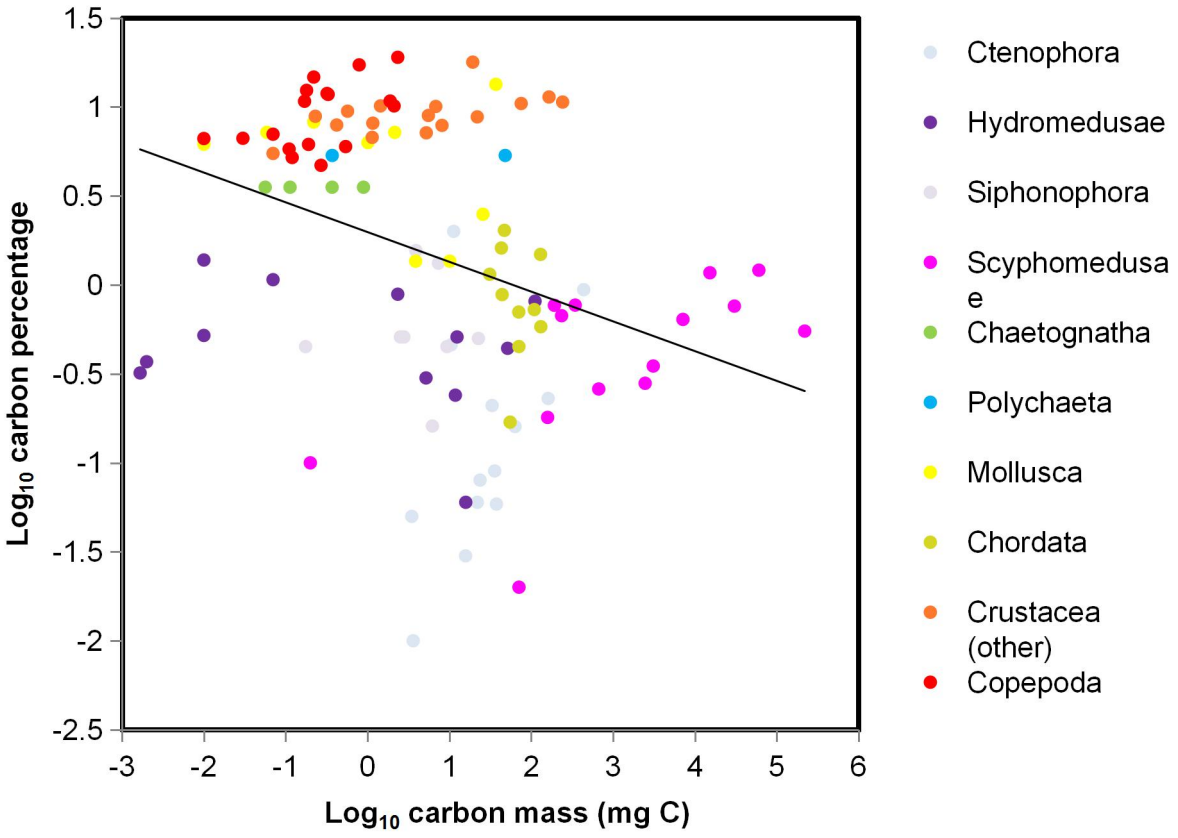


Figure 3.4 – *Log_{10} carbon percentage (CM%WM) as a function of log_{10} carbon mass (mg) for the meta-analysis dataset (log_{10} carbon percentage = - 0.17 * log_{10} carbon mass – 0.3, p = 0.0003, R^2 = 0.12, df = 108). Taxonomic groups are coloured as indicated in the legends.*

While the more gelatinous taxa tended to have higher carbon mass there was considerable variability, with some organisms of similar carbon mass differing 100-fold in carbon percentage (Figure 3.4). To ensure that collinearity was not influencing the growth model the condition indices for the variables were inspected. The highest condition index observed was 3.05, lower than the threshold of 30 suggested by Belsley et al. (1980) confirming that carbon mass and carbon percentage can be used in combination in models of zooplankton growth.

3.3.3 - Relationship between carbon percentage and growth rate

I first conducted GLMs on the subset of data comprising the classical gelatinous taxa alone (Table 3.1). These showed that mean growth rate declined significantly with increasing mass and

increasing body carbon percentage. The GLMs on the whole dataset established that $\log_{10}$ mass-specific mean and maximum growth rate were significantly related with both $\log_{10}$ carbon mass and $\log_{10}$ body carbon percentage (Figure 3.5, Table 3.1). As expected, there was a negative relationship between $\log_{10}$ mass-specific growth rate (g), and $\log_{10}$ carbon mass, in line with the results of Kiørboe and Hirst (2014). In the analyses of all zooplankton taxa, mean and maximum growth rate decreased with increasing carbon mass and carbon percentage.

In all analyses, the addition of body carbon percentage to models of growth based on carbon mass alone increased the explanatory power (Table 3.2). The second order Akaike criterion, AICc, (Burnham and Anderson, 2002) was lower in the model including water content in all analyses, supporting the inclusion of this factor in analyses of zooplankton growth. In the maximum analysis including all taxa, Akaike weights (ω_i) were approximately 10 times higher in the models including body carbon percentage (mass $\omega_i = 0.08$, mass + carbon percentage $\omega_i = 0.92$). This suggests that these models performed significantly better than models based on mass alone (Royall, 1997). A similar pattern was observed in the analysis of maximum growth rates of the gelatinous taxa however it was not observed for mean growth rates (mass $\omega_i = 0.02$, mass + GI $\omega_i = 0.98$).

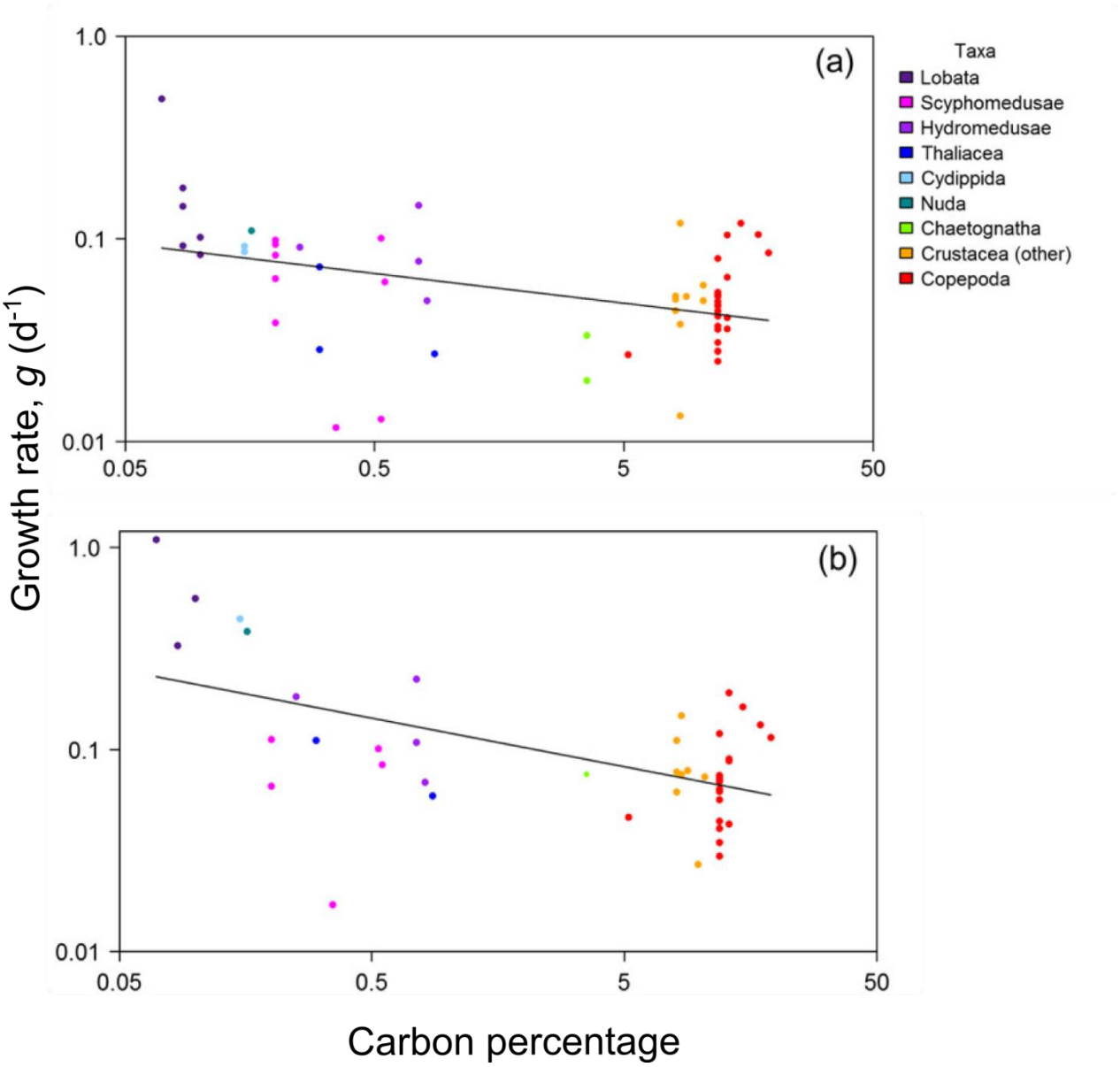


Figure 3.5 – *Log_{10} specific growth rate, g (d^{-1}) as a function of log_{10} carbon percentage (CM%WM). Growth values were temperature-adjusted to 15°C then mass adjusted to 1 mg C. (a) mean mass-specific growth rate values for each species in each study and (b) maximum specific growth rate values for each species.*

Group		Factor	df	*p*	Slope	Intercept	Adj R^2
All zooplankton	Mean growth rate,*g*	log_{10} carbon mass	58	<0.0001	-0.17	-1.12	0.43
		log_{10} carbon percentage		0.036	-0.18		
	max growth rate,*g*	log_{10} carbon mass	42	<0.0001	-0.16	-0.81	0.31
		log_{10} carbon percentage		0.013	-0.16		
Gelatinous taxa only	mean growth rate,*g*	log_{10} carbon mass	22	0.027	-0.19	-1.18	0.33
		log_{10} carbon percentage		0.038	-0.17		
	max growth rate,*g*	log_{10} carbon mass	13	0.011	-0.16	-1.15	0.42
		log_{10} carbon percentage		0.018	-0.72		

Table 3.1 - *General linear models predicting log_{10} mean specific and log_{10} maximum specific growth rate, g (d^{-1}), as a function of both log_{10} carbon mass (mg) and log_{10} body carbon percentage (100*(CM/WM)). All models pertain to growth rate data that were first Q_{10}-adjusted to 15°C.*

Group	*g*	R^2		AICc		Δ_i	ω_i	
		Mass	Mass + C%	Mass	Mass + C%		Mass	Mass + C%
All zooplankton	Mean	0.39	0.43	18.63	16.67	2.47	0.19	0.81
	max	0.22	0.31	21.99	17.57	4.42	0.076	0.92
Gelatinous taxa only	mean	0.33	0.33	18.51	19.96	1.44	0.54	0.46
	max	0.09	0.42	21.55	16.26	5.29	0.019	0.98

Table 3.2 - *Changes to measures of explanatory power of models of growth based solely on carbon mass when body carbon percentage (C%) was added as a factor. AICc is the corrected Akaike information criterion, Δ_i is the AIC difference, and ω_i is the Akaike weight. Models with Akaike weight values 10 times greater than that of the other models being compared are considered statistically significant as optimal models (mass + GI for mean and max all zooplankton and max gelatinous taxa only). All models pertain to growth data that were first Q_{10}-adjusted to T = 15°C.*

3.3.4 – Secondary production

The comparison between secondary production estimates based on carbon mass and carbon percentage and carbon mass alone are shown in Figure 3.6.

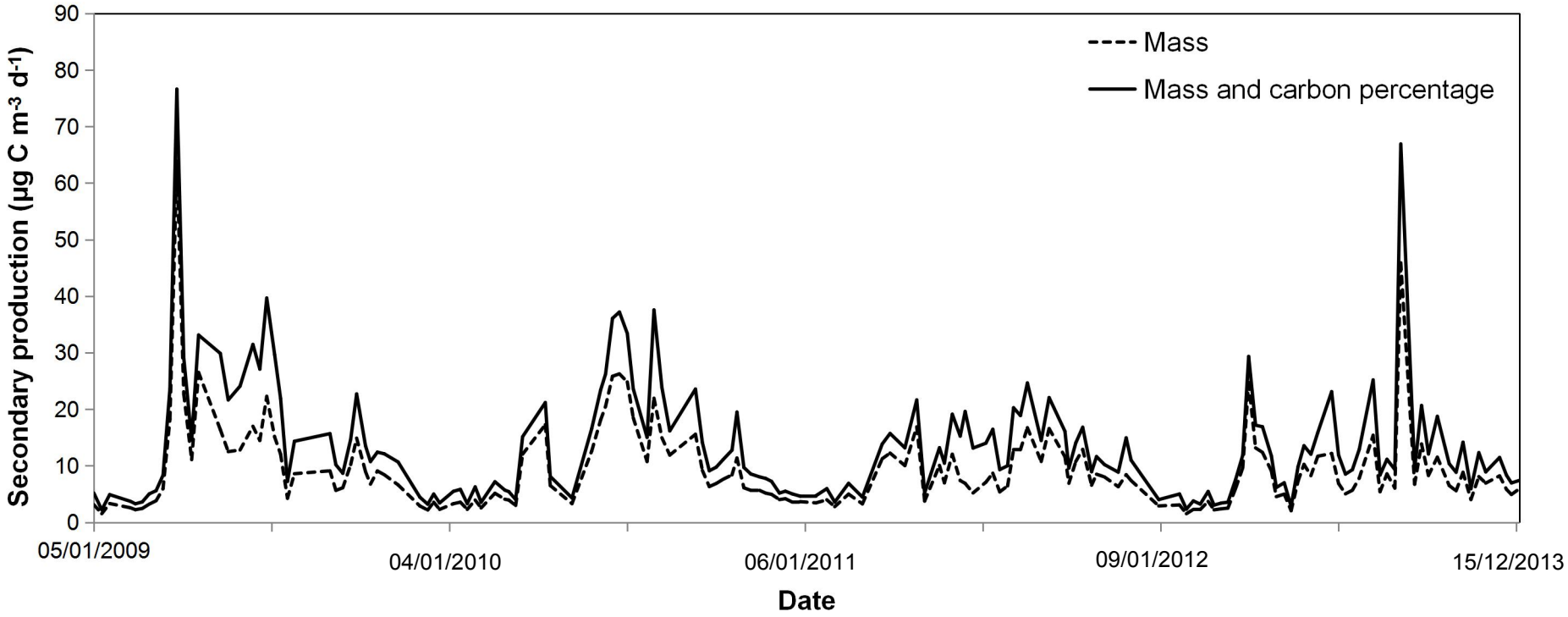


Figure 3.6 – *Illustrative estimates of maximum secondary production at the L4 sampling site at weekly resolution between 05/01/2009 and 15/12/2012. Growth rates were estimated on the basis of carbon mass alone (log_{10} carbon specific growth rate (mg C mg C^{-1} h^{-1}) = - 2.82 - 0.31 log10 carbon mass(mg)) using the equation for crustaceans from Kiørboe and Hirst (2014) and carbon mass alongside carbon percentage (log_{10} specific growth rate, g, ((d^{-1}) - 0.81 - 0.16 log_{10} carbon mass (mg) - 0.16 log_{10} carbon percentage ((CM/WM)*100) using the maximum growth rate equation for all zooplankton shown in Table 3.1. Growth rates were temperature adjusted using a Q_{10} of 2.8 (Hansen et al., 1997). Secondary production for each species was estimated as the growth in carbon mass per individual, multiplied by abundance. Species secondary production was summed across species at each time point to estimate total secondary production.*

3.5 - Discussion

This study provides support for: body carbon percentage being a continuous trait, for a negative relationship between body carbon percentage and growth rate, and for considerable increases in model predictive power as a result of inclusion of this trait. Below I discuss the implications of each of these findings in turn.

Kiørboe (2013) demonstrated that if zooplankton are arranged in a frequency distribution based on body composition, most taxa are either gelatinous (carbon mass is ~0.5% of wet mass) or non-gelatinous (~5-10%), with little overlap. At first glance the results would appear to contradict this, since I found a fairly continuous distribution of carbon percentage. However, this does not conflict with the findings of Kiørboe (2013) as while most species fall into one of these two groups, there is considerable variability in carbon percentage within each group and there are representatives across much of this spectrum (Figure 3.2). The distribution of zooplankton biomass at L4 supports both of these views (Figure 3.3). Biomass is clustered at either end of the spectrum as described previously, and this could suggest that the fitness landscape for this trait favours extremes. However, at either end of the spectrum there is considerable variability (as noted for medusae, ctenophores and tunicates in Molina Ramirez et al., 2015). The traditional gelatinous group alone spans an 8-fold range in carbon percentage, with implications for growth rate. For example, there is a trend of increasing carbon percentage among the gelatinous zooplankton through the year, with cydippids being replaced by beroids in summer and finally by hydromedusae and siphonophores in autumn (Hosia and Bamstedt, 2007)

In the meta-analysis compilation, the largest interval was between taxa typically considered as gelatinous and intermediate, between the pelagic tunicate, *Thalia* (as *Salpa) democratica* (1.6 % body carbon percentage) and a chaetognath, *Eukrohnia hamata* (2.7 % body carbon percentage. Molina-Ramirez et al. (2015) highlighted that considerable variation in carbon percentage existed even within the classic gelatinous taxa (Cnidaria, Ctenophora and Tunicata). My results are in

agreement, albeit with even higher degree of variability (350-fold). Taken together, the relatively small interval between values for gelatinous and non-gelatinous species and the high variability observed within the gelatinous taxa suggest that growth models can indeed incorporate carbon percentage as a continuous trait.

When $\log_{10}$ mass-specific growth rate was regressed against $\log_{10}$ body carbon percentage as a continuous variable, a negative relationship was observed in all analyses, though the variance was variable. The relationship had the highest adjusted R^2 when calculated using mean growth rate of all zooplankton taxa and the adjusted R^2 value increased in all analyses when carbon percentage was added. Crucially, the pattern persisted when considering the gelatinous taxa alone (Table 3.2). The existence of the relationship among the gelatinous taxa alone is important as this demonstrates that the relationship is not due to a categorical difference between gelatinous organisms and non-gelatinous organisms.

One potential mechanism that could explain the relationship between body carbon percentage and growth rate is enhanced feeding rate (Acuña et al., 2011). These authors suggested that the large dilute bodies of gelatinous zooplankton facilitate higher carbon-specific feeding rates than other zooplankton taxa of the same carbon mass. If this increased feeding rate drives faster growth, then this might explain the relationship of increasing growth rate with decreasing carbon percentage. As many gelatinous taxa are filter or ambush feeders that rely on capture surfaces to feed, assuming that feeding rate scales with surface area, then we may expect the scaling exponent between surface area and body carbon percentage to match the exponent for growth rate and body carbon percentage. To investigate this, I used a simple geometric calculation. Assuming isomorphic growth, surface area (SA) scales with body volume with a power of 0.67. By altering carbon percentage for a fixed amount of body carbon, SA then scales with carbon percentage with a power of -0.67. Hence, with an assumption that growth rate is a fixed proportion of feeding rate, this would give the same slope of -0.67 for $\log_{10}$ mass-specific growth versus $\log_{10}$

carbon percentage (Table 3.1). The exponents that I determined empirically across the various zooplankton taxa are less steeply negative than -0.67 (at -0.18 and -0.16 for mean and maximum respectively), i.e. with decreasing carbon percentage, organisms increase their growth rate less rapidly than these surface considerations would predict. This could indicate a potential feeding inefficiency associated with decreasing carbon percentage, or that factors additional to surface area may also be important.

In common with Ikeda (2014), I found that species with larger total carbon masses also tended to be more watery. Since high carbon masses and water content are both associated with high growth rates, the effects of carbon mass and carbon percentage tend to counteract, underscoring the need to include these variables together in order to better predict growth. Molina-Ramirez et al. (2015) found a similar result for tunicates but found that body carbon percentage was invariant with increasing mass for cnidarians and ctenophores. The authors suggested that this might be due to differences between internal filter feeding in tunicates and external ambush or cruise feeding in the other groups. It has been suggested that feeding modes decrease in efficiency with increasing volume (Kiørboe et al., 2011), so high water content may help to mitigate this decrease in efficiency and maintain relatively higher carbon specific feeding rate at large carbon masses. This assertion is supported by the findings of Acuña et al. (2011), suggesting that gelatinous plankton had higher carbon-specific feeding rates than other zooplankton of a similar carbon mass.

While the increase in capture surface area and associated feeding and growth rates is one potential advantage of the gelatinous body form, there are other implications. There are potential negative implications such as limited swimming speed and escape responses. While medusae have potential defences in the form of nematocysts, many gelatinous taxa such as ctenophores and thaliaceans do not, and may have limited ability to escape from potential predators as a result of their large dilute bodies (Acuña, et al., 2011). Understanding why some taxa are gelatinous is

not always straightforward. The most gelatinous mollusc in this analysis is *Clione limacina*, a gymnosome predator that feeds almost exclusively on *Limacina helicina*. *Clione* does not rely on large capture surfaces or on generating a feeding current as it ambushes individual, relatively large prey items (Lalli and Gilmer, 1989). In this case, low carbon percentage does not appear to be a derived trait to increase body volume relative to carbon for feeding, suggesting that this may not be the only driver of low carbon percentage in zooplankton. It has been suggested that potential other causes include physical or ecological factors such as transparency to impair visual predation (Hamner et al., 1975) or the efficiency of neutral buoyancy (Kiørboe, 2013). Together these factors may help to explain why semi-gelatinous bodies are observed in at least six major planktonic phyla (Cnidaria, Ctenophora, Chordata, Annelida, Chaetognatha, Mollusca, see Appendix I).

The newly established relationship between carbon percentage and growth rate was applied to improve estimates of secondary production in Figure 3.6. The addition of carbon percentage to models of secondary production had a significant effect on the outputs. Inclusion of carbon percentage increased estimates of secondary production at all time points. This was particularly evident in summer when a range of gelatinous and semi-gelatinous taxa co-occurred with the crustaceans. The difference between the two estimates was negatively related to carbon percentage ($df = 158$, $p < 0.0001$). This is logical as when the average carbon percentage is lower, the carbon percentage term will have a greater effect on the estimate and the estimates will differ further.

To make production estimates including the effects of carbon percentage would normally require dividing into different groups. For instance, other studies have presented 11 different growth equations for specific zooplankton groups (Kiørboe and Hirst, 2014). This can be useful for modelling the growth rate of a specific taxon; however, when attempting to represent the growth of a full zooplankton assemblage dividing into these constituent groups increases model complexity and increases uncertainty for important groups poorly served with data, such as siphonophores, chaetognaths and meroplanktonic larvae. Conversely, if a unified model is used that estimates

growth for all zooplankton on the basis of mass alone, the considerable effects of carbon percentage will be overlooked (Figure 3.6). Adding carbon percentage to the growth model thus represents a solution; the additional trait information is now relatively easily derivable, and can be incorporated into a single equation that substantially increases the explanatopry power of growth rate.

3.6 - Conclusions

Body size is often described as a master-trait, and is frequently used as the sole intrinsic variable in empirical and simulation models involving zooplankton growth (Moloney and Field, 1991; Kiørboe and Hirst, 2014; Anderson et al., 2015a). But what do we mean by "body size"? Carbon mass is often used as the unit for size, but both my meta-analysis and the real assemblage data show that carbon percentage also varies greatly. It may even vary negatively with carbon mass, levering an opposing effect on growth. I argue that as carbon mass and carbon percentage are both intrinsic factors that influence energy budgets, then we should disentangle their separate effects in a unified growth model. By adding carbon percentage to models of growth based on carbon mass alone, we substantially increased their explanatory power, with smaller body masses and lower body carbon percentages leading to higher specific growth rates. Building on the work of previous publications (Kiørboe, 2013; Pitt et al., 2013; Molina-Ramirez et al., 2015), I provide a carbon percentage dataset in Appendix I. By using these source data alongside carbon masses, the maximum growth rate equation in Table 3.1 may then be used as a starting point to estimate growth rates attainable by zooplankton.

Alongside the "size" based simplifications used for modelling, there has also been an increase in "trait-based" modelling in which categorical variables or functional groups are allowed to vary continuously. A purpose of this chapter is to allow carbon percentage also to be used as a continuous trait; to facilitate its inclusion alongside carbon mass and other traits such as feeding mode (Litchman, 2013; Andersen et al. 2015a; Hébert et al., 2017). Since I found that growth rate

depended on carbon percentage even among the gelatinous taxa alone, I suggest that considering and modelling carbon percentage as a continuous trait will reveal the ecological and evolutionary factors that influence the water content of zooplankton.

CHAPTER 4 – Intraspecific effects of variable carbon percentage through ontogenetic development: morphometrics, feeding and growth of *Aurelia aurita* ephyrae

4.1 - Introduction

Carbon percentage (carbon mass as a percentage of wet mass) can affect the biology of zooplankton, even within the gelatinous taxa alone (Chapter 3). In Chapter 3, a negative relationship was found between carbon percentage and growth rate of zooplankton, suggesting that more gelatinous taxa have higher growth rates (as predicted in Chapter 2). The ecological implications of this relationship are numerous, as variability in this trait occurs across different phylogenetic scales. Carbon percentage varies over four orders of magnitude across the zooplankton as a whole, and congeneric species can differ by as much as an order of magnitude (Kiørboe, 2013).

Despite this interspecific variability, studies have suggested that there is limited intraspecific variability in carbon percentage, such that species-specific values are reasonable approximations (Kiørboe, 2013; Molina-Ramirez et al., 2015). However, these studies focussed almost exclusively on adult zooplankton, not investigating early ontogeny. Adults of many species of zooplankton are more ecologically and structurally different from their own larvae than from adults of other species. For instance, scyphomedusae have a metagenetic life cycle, with separate planktonic sexual (medusae) and benthic asexual phases (polyp) (Arai, 2012). Polyps are structurally and ecologically distinct from medusa of the same species, and therefore might also differ in carbon percentage. During the life cycle of most scyphozoan jellyfish, the polyps strobilate and form larval jellyfish called ephyrae. As the ephyrae develop they gradually take on the characteristics of the planktonic medusae stage (Arai, 2012), and therefore are might be expected to change from the carbon percentage of the polyp to that of the medusa.

This chapter investigated whether ephyrae changed in carbon percentage through development, and how this change influenced growth and ingestion rates. The interspecific results in Chapter 3 suggested that taxa with larger bodies tended to be more gelatinous, so it was predicted that carbon percentage will decrease with increasing diameter as the ephyrae develop. If

the range of carbon percentage observed is of a similar magnitude to that of the interspecific study (0.07 to 0.87%, Chapter 3) then growth rate may be affected.

If a relationship exists between carbon mass and carbon percentage, then demarking between the effects of these two variables could be difficult. One way to investigate the effects is to compare the values and exponents with studies on other zooplankton species through development. Hirst and Forster (2013) found that the intraspecific growth rate (mg C d^{-1}) of many invertebrates can be described as an exponential relationship with a body mass scaling exponent of $b = 1$. If the general growth exponent is approximately 1, then the exponent of the ephyrae is expected to be greater than this as decreasing carbon percentage is expected to increase growth rate.

In addition to investigating how variability in carbon percentage through development affected growth rate, this chapter also aimed to understand how ingestion rate is affected. Ingestion rate is a key metabolic factor that is expected to be influenced by carbon percentage (Acuña et al., 2011). This study by Acuña demonstrated that the carbon specific ingestion rate of gelatinous zooplankton is higher than that of other zooplankton as increased wet mass leads to higher effective body volumes and therefore higher ingestion rates. However, specific feeding modes decrease in efficiency with increasing body volume (Kiørboe, 2011). Therefore, I hypothesised that carbon specific ingestion rates would be similar to comparable zooplankton at low carbon masses, but would be higher at higher carbon masses. This effect could manifest as the ephyrae in this chapter having a higher exponent for carbon mass specific ingestion than other comparable zooplankton.

Taking these points together, carbon percentage was predicted to decrease through ontogeny in *Aurelia aurita* ephyrae. This was predicted to increase the scaling exponents of carbon

specific growth and ingestion rates of the ephyrae relative to other zooplankton. These hypotheses were tested by incubating *Aurelia aurita* ephyrae and measuring diameter, carbon mass, wet mass, growth rate and ingestion rate. These values were then compared to expected exponents from meta-analyses and measured exponents from other experimental studies.

4.2 - Methods

This investigation comprised of 55 incubations of between three and five ephyrae (total ephyrae = 228) between 14/10/15 and 16/12/15. The number of ephyrae incubated in each bottle varied depending on their diameter and the availability of different size classes. The incubations had a duration of 24h as this period was long enough to generate a significant growth signal, but not to fully deplete the available food. These short term incubations minimised the potential for deleterious container effects, as the organisms were kept in the bottles for 24h only, rather than culturing them under these conditions for several weeks.

Performing the experiment in full on separate batches of relatively few ephyrae had a range of benefits. Firstly, this design avoided the statistical and practical issues of repeatedly sampling from a population, as all organisms were measured only before and immediately following incubation. Any problem associated with the incubation vessel, such as contamination or loss of sample, was more likely to be limited to a single incubation. This design also facilitated representative sampling across the size spectrum investigated, as the ephyrae that went into each incubation were individually selected on the basis of diameter.

4.2.1 - Experiment and measurement

Aurelia aurita polyps provided by the Marine Biology and Ecology Research Centre (Plymouth University) were kept at 15^{o}C in a 12 hr light/dark cycle in 0.22μm filtered sea water

(collected from the L4 sampling site, Chapter 2). Strobilation took place naturally over several months, with the ephyrae developing in aerated plastic buckets (vol. = 15 l) with full water changes every two days.

For each experiment, between 22 and 25 ephyrae were selected and photographed under low magnification (Olympus SZX16, Martin Company MDSLR, Canon EOS 550D, 13x magnification). The inter-rhophalial diameter (IRD, distance between rhopalia (cnidarian sensory organs found between the lappet tips) on opposite sides of the animal (Figure 4.1), was obtained from each image using appropriate computer software (Image J). As all ephyrae were the same distance from the lens, the number of pixels corresponded to length. A reference picture of a ruler was taken to convert the values from pixels in mm (IRD varied between 1.2 and 9.1 mm). It was not possible to match up the identities of the ephyrae before and after the incubation. Therefore, to get the best possible estimates of individual growth, the ephyrae were ranked based on IRD and organised into groups of between three and five individuals (depending on diameter). Ephyrae of a similar diameter were pooled to decrease the standard deviation in diameter of each bottle when measured after incubation.

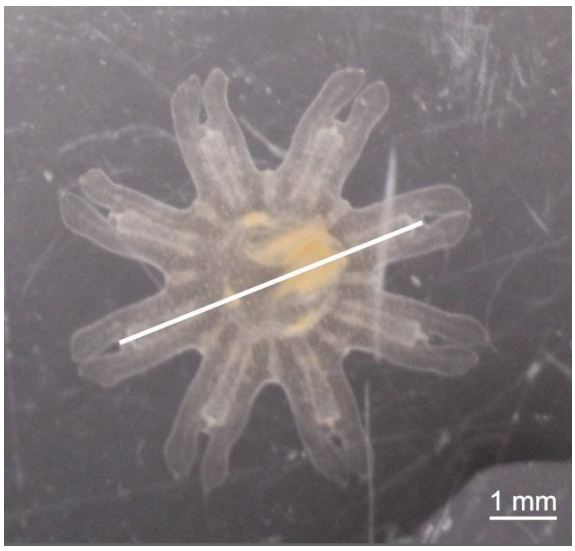


Figure 4.1 – *Photomicrograph of an* Aurelia aurita *ephyra; the inter-rhopalial diameter is indicated by the white line superimposed on the image (IRD = 4.8mm).*

Glass bottles of either 250 or 500ml capacity (depending on the diameter of the ephyrae) were filled with 0.22µm filtered seawater (35 psu). The volume of the incubation bottles was kept greater than 10,000 times the volume of the ephyrae to help reduce container effects. Newly hatched *Artemia salina* nauplii (Zebrafish Management Ltd, UK) were added to a concentration of 400 individuals per litre. The ephyrae were added to the bottles (with the minimum possible airspace) then incubated on a plankton wheel rotating at 4 rpm, at 15^{o}C in dark conditions for 24 h. I ran controls to estimate nauplii mortality in incubations without predators and found that mortality was minimal (98% of nauplii recovered from three incubations of 24 h).

Following the incubation, the ephyrae and remaining *Artemia* nauplii were collected on a 50 µm sieve. The *Artemia* nauplii were fixed in acid Lugol's solution (2% w/v, to facilitate enumeration) and counted under a dissecting microscope (Wild Heerbrugg, 2x magnification). The ephyrae were photographed and the IRD was measured again as before. The ephyrae were transferred to aluminium foil pieces and surface water was removed by blotting. The wet mass was determined immediately using a microbalance (Sartorius Digital Microbalance). This immediate measurement

of wet mass was chosen because on removal from the incubation and blotting, water was continually lost from the ephyrae at different rates according to their volume, preventing proper standardisation. After weighing, the samples on the foil pieces were transferred to a drying oven (Binder Drying Oven) set at 60°C (a sufficient temperature to remove body water, Lucas et al., 2011) and dried to constant weight (minimum 2 days). Carbon and nitrogen mass was measured using an Eager 200 Flash Elemental Analyser 1112 Series (CHN). The CHN was calibrated using acetanilide and all calibrations were robust (minimum $R^2 = 0.993$). The measured values approached but never exceeded the thresholds for accurate measurement for the CHN (minimum 50 µg C).

4.2.2 - Numerical methods

As measuring carbon and wet masses required sacrificing the samples, it was not possible to measure mass before the growth incubations. Therefore, initial carbon and wet masses (mg) were estimated from diameter (mm) using the following conversions derived from the data:

(eq. 4.1) $\log_{10}$ carbon mass = 1.37 * $\log_{10}$ diameter - 2.09 ($p<0.0001$, $R^2 = 0.81$, df = 190)

(eq. 4.2) $\log_{10}$ wet mass = 2.3 * $\log_{10}$ diameter - 0.35 ($p<0.0001$, $R^2 = 0.94$, df = 190)

Growth rate (mg h^{-1}) was defined as ($mass_t$ – $mass_{t0}$) /t, and mass specific growth rate (mg mg $^{-1}$ h^{-1}) as ($mass_t$ – $mass_{t0}$)/$mass_{mean}$ /t. Specific growth rate *g* (d^{-1}) was also calculated for comparison to other studies as (ln $mass_t$ – ln $mass_{t0}$)/t. The number of *Artemia* ingested was converted into carbon mass terms (1 *Artemia* nauplius = 4.64 µg C; Weltzein et al., 2000). Mass specific ingestion rates (µg C $µg^{-1}$ body C d^{-1}) were calculated as the difference in total mass of *Artemia* between the start and end of the experiment, divided by the mean estimated total mass of ephyae between the start and end of incubation. Gross growth efficiency was calculated as the change in mass of the ephyrae divided by the total mass of *Artemia* that were eaten.

4.3 – Results

4.3.1 - Morphometrics

Carbon mass of the ephyrae ranged between 0.01 mg and 0.19 mg and wet mass between 0.6 mg and 81.9 mg. Ephyrae increased in wet mass exponentially with increasing carbon mass (Figure 4.2), decreasing in carbon percentage from 2.36% to 0.1%. Diameter and carbon percentage were negatively related (Figure 4.3) and there was a significant positive relationship between carbon mass and nitrogen mass (Figure 4.4). The mean C:N mass ratio was 4.34, and this ratio remained constant as the ephyrae grew and became more dilute.

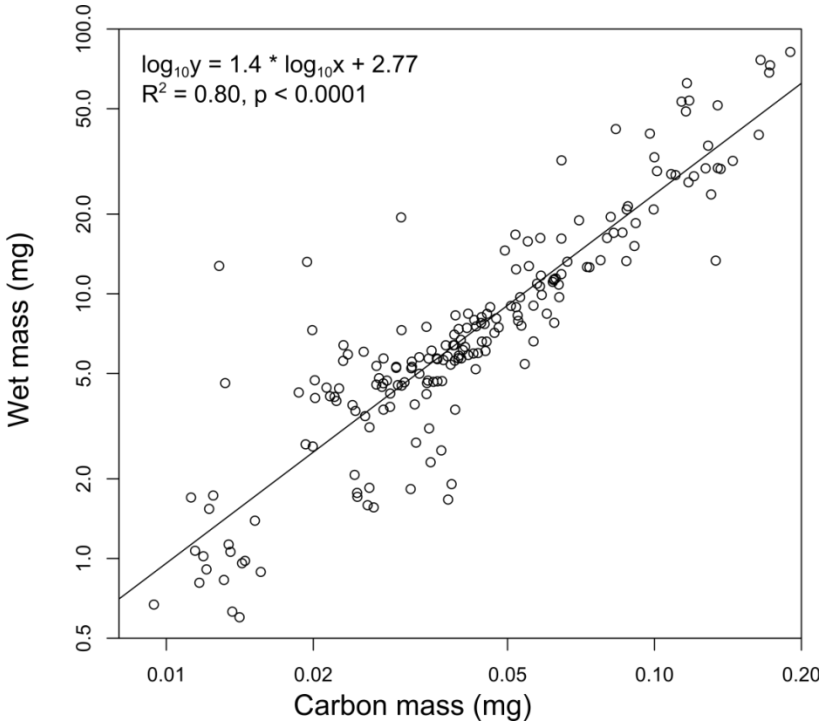


Figure 4.2 – *Wet mass (mg) as a function of carbon mass (mg) in Aurelia aurita ephyrae. Axes are on a logarithmic scale (base 10), each point represents an individual ephyra (df = 190).*

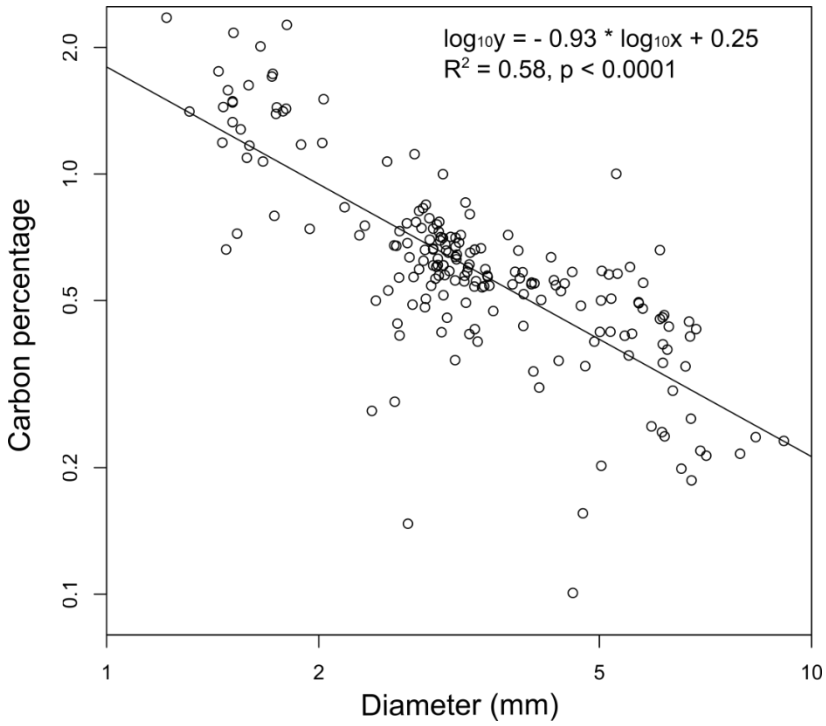


Figure 4.3 – *Carbon mass as a percentage of wet mass, as a function of diameter (mm) in Aurelia aurita ephyrae. Axes are on a logarithmic scale (base 10), each point represents an individual ephyra (df = 190).*

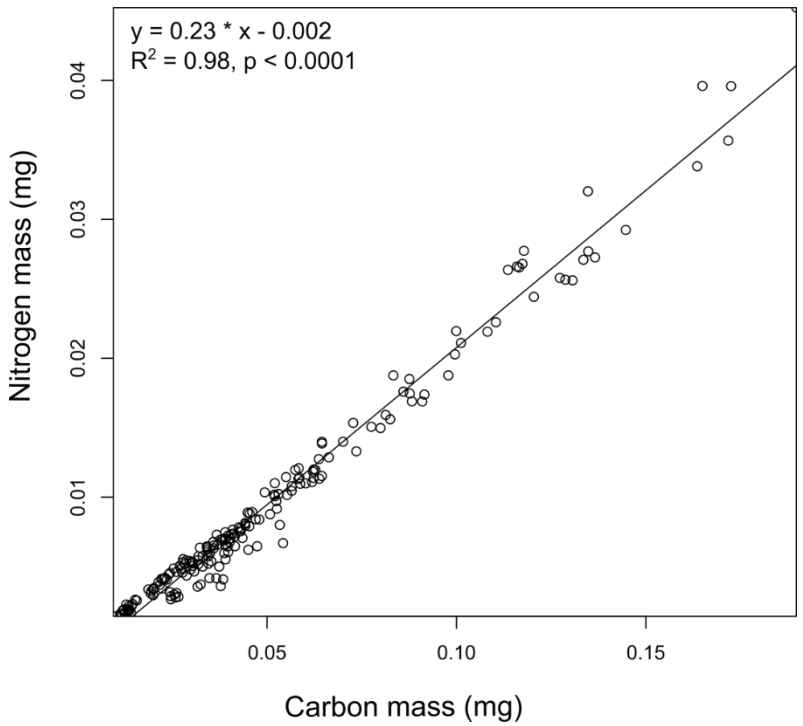


Figure 4.4 – *Nitrogen mass (mg) as a function of carbon mass (mg) in Aurelia aurita ephyrae. Each point represents an individual ephyra (df = 190).*

4.3.2 – Ingestion rate

Ingestion rate varied between 4.6 and 91.5 µg C d^{-1} (Figure 4.5) and was positively related to diameter (Figure 4.6). The scaling exponent for ingestion rate with increasing carbon mass was 0.6 (Figure 4.5) and with increasing wet mass was 0.33. Ingestion rate decreased with increasing carbon percentage.

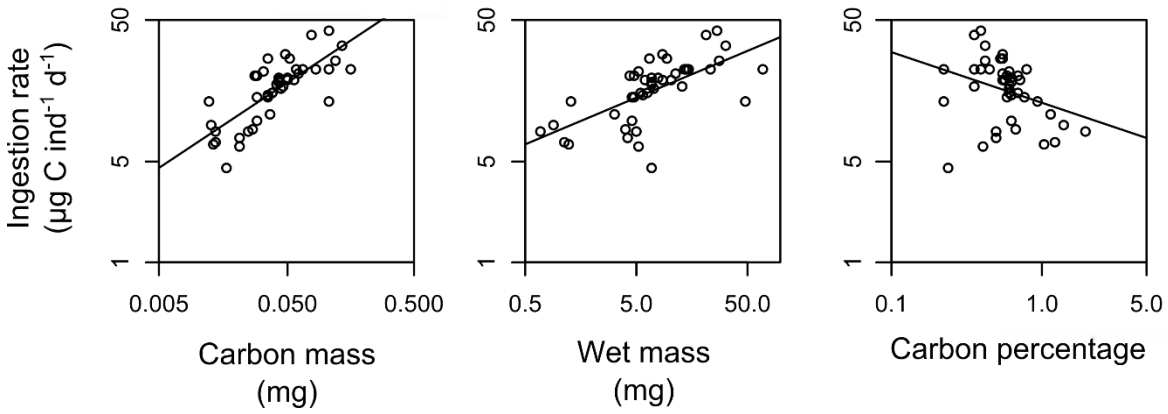


Figure 4.5 – *Ingestion rate (µg C ind^{-1} d^{-1}) of* Aurelia aurita *ephyrae as a function of carbon mass (mg, $log_{10}y = 0.6 * log_{10}x + 2.04$, $R^2 = 0.58$, $p < 0.0001$), wet mass (mg, $log_{10}y = 0.33 * log_{10}x – 2.07$, $R^2 = 0.4$, $p < 0.0001$) and carbon percentage ($log_{10}y = - 0.35 * log_{10}x + 1.12$, $R^2 = 0.07$, $p = 0.047$). Axes are on a logarithmic scale (base 10), each point represents an individual ephyra (df = 41).*

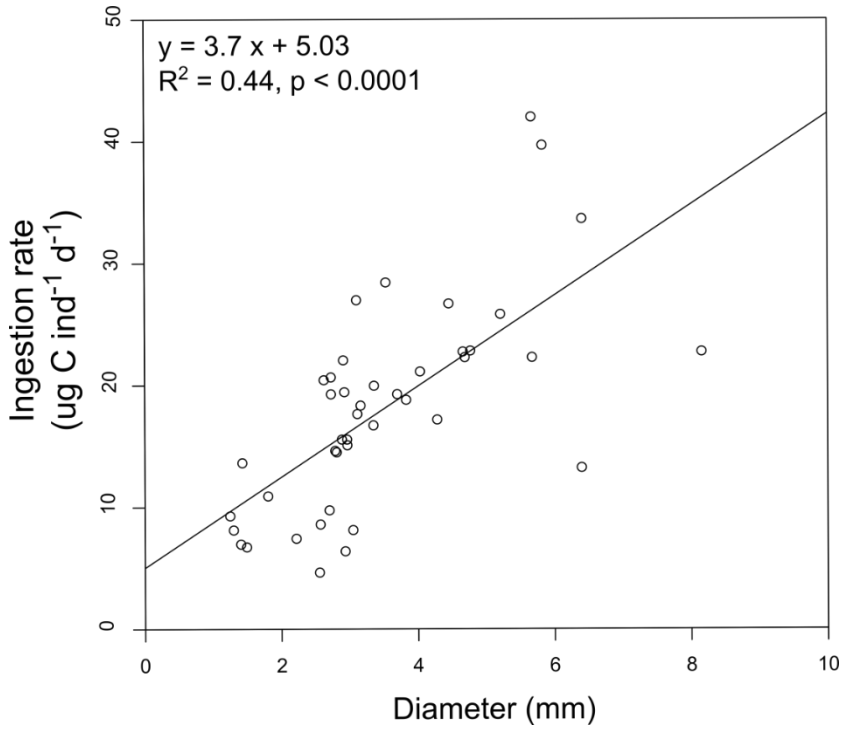


Figure 4.6 – *Ingestion rate (ug C ind^{-1} d^{-1}) as a function of diameter (mm) in Aurelia aurita ephyrae, (df = 55).*

4.3.3 - Growth rate

Growth rate varied between 0.018 mg C and -0.024 mg C d^{-1} (negative growth rate accounted for 12% of the data). The carbon mass scaling exponent for carbon mass growth (mg C h-1) was 0.5 (Figure 4.7A) and the wet mass scaling exponent for wet mass growth was 0.62 (Figure 4.7D). There was no relationship (Figure 4.7G) between carbon percentage and carbon mass growth, however there was a positive relationship between carbon percentage and both carbon specific growth rate (Figure 4.7H) and specific growth rate, *g* (Figure 4.7I). Growth efficiency (for positive growth) varied between 0.03% and 61% with no relationship with carbon mass (mean = 21%, p = 0.76, R^2 = 0.002, df = 40).

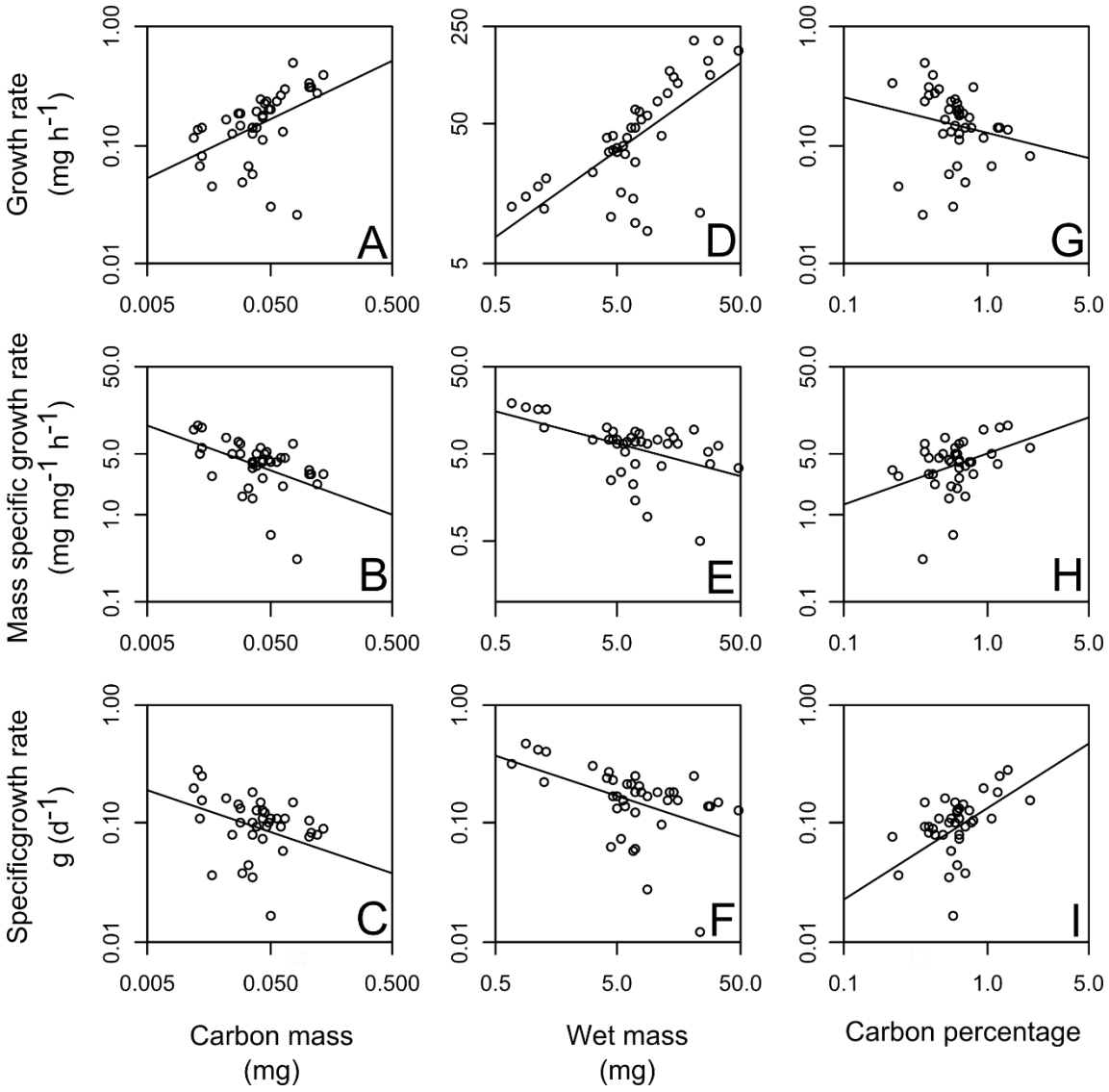


Figure 4.7 – *Growth rate as a function of mass in Aurelia aurita ephyrae. Axes are on a logarithmic scale (base 10), each point represents one replicate bottle (n=55); effect of carbon mass (mg) on carbon mass growth rate (mg C h^{-1}, **A**, $log_{10}y = 0.49 * log_{10}x – 0.14$, $R^2 = 0.2$, $p = 0.0028$), carbon mass specific growth rate (mg C mg C h^{-1}, **B**, $log_{10}y = - 0.51 * log_{10}x – 0.14$, $R^2 = 0.21$, $p = 0.0022$), specific growth rate, g (d^{-1}, **C**, $log_{10}y = - 0.36 * log_{10}x – 1.54$, $R^2 = 0.08$, $p = 0.04$), effect of wet mass (mg) on wet mass growth rate (mg WM h^{-1}, **D**, $log_{10}y = 0.62 * log_{10}x - 1.07$, $R^2 = 0.46$, $p < 0.0001$), wet mass specific growth rate (mg WM mg WM h^{-1}, **E**, $log_{10}y = - 0.3 * log_{10}x + 1.07$, $R^2 = 0.23$, $p = 0.0013$), specific growth rate, g (d^{-1}, **F**, $log_{10}y = - 0.34 * log_{10}x – 0.53$, $R^2 = 0.2$, $p = 0.0028$) and effect of carbon percentage on carbon mass growth rate (mg C h^{-1}, **G**, $log_{10}y = – 0.31* log_{10}x - 0.9$, $R^2 = 0.01$, $p = 0.23$), carbon mass specific growth rate (mg C mg C h^{-1}, **H**, $log_{10}y = 0.59 * log_{10}x + 0.7$, $R^2 = 0.12$, $p = 0.02$) and specific growth rate, g (d^{-1}, **I**, $log_{10}y = 0.77 * log_{10}x - 0.87$, $R^2 = 0.21$, $p = 0.002$).*

4.3.3 - Implications of changing carbon percentage for ingestion and growth rates

An alternative method to investigate the effects of carbon percentage is to determine how the energy budget would differ if the ephyrae tested did not dilute though ontogeny. Using the relationships between diameter, carbon mass and wet mass it was possible to calculate how an average ephyra changes in morphometrics through development. The same relationships were used to model a similar organism that increases in carbon mass over the range investigated, but was fixed at the starting carbon percentage. By comparing these two idealised animals, it was possible to ask how much higher in wet mass the diluting ephyra was, and how ingestion rate was affected. The difference in wet mass between these two treatments is displayed in Figure 4.8;

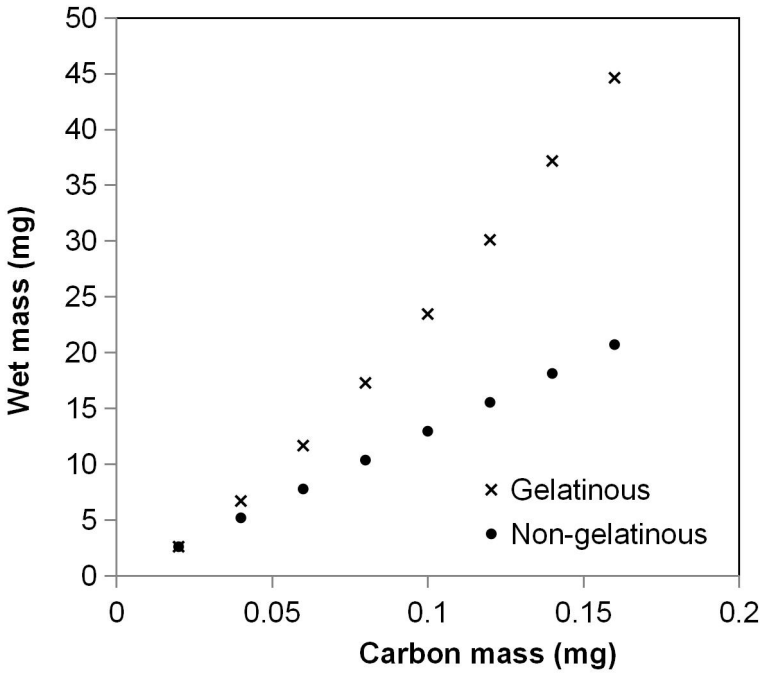


Figure 4.8 – *Effect of carbon mass (mg) on wet mass (mg) of* Aurelia aurita *ephyrae. Values are modelled based on calculated carbon percentage across the range of diameters measured in this study. In the gelatinous treatment, carbon percentage is allowed to vary following the relationship shown in Figure 4.2, in the non-gelatinous treatment the carbon percentage is fixed at the starting value.*

When the theoretical carbon percentage was calculated using morphometric relationships, the diluting ephyra had double the final wet mass at the maximum carbon mass (Figure 4.8).

Acuña (2001) has used a similar approach to investigate how the carbon percentage of *Pegea confoederata* allows this salp to feed sufficiently to survive the oligotrophic conditions they inhabit. Assuming that wet mass was the primary factor driving ingestion, as suggested by Acuña et al. (2011), then the morphometric model can be extended using the relationships above to predict how ingestion rate was be affected. This is a reasonable assumption because in gelatinous zooplankton, wet mass is the most effective proxy for physical body size (volume) i.e. the physical space that is taken up by the animal. In the case of these ephyrae and many other gelatinous zooplankton, feeding is a function of encounter rate, and therefore is highly dependent on body volume. The scaling of ingestion rate in these ephyrae appears to be related to a length dimension (linear scaling with diameter) and therefore wet mass (a direct representation of volume, L^3) seems an appropriate explanatory variable.

An alternative hypothesis for what constrains maximum ingestion rate of an animal is focussed not on food capture, but food digestion (Wirtz, 2013). This hypothesis suggests that digestion rate is a function of digestive surface area, and assuming that both the diluting and non-diluting animals are geometrically similar, this too will scale with wet mass. The second assumption of the model is that changing the carbon percentage of the ephyrae would not influence the scaling of ingestion. It is plausible that the undiluted model ephyrae may swim faster as a result of having higher amounts of muscular tissue relative to their total body volume. However, the results of Acuña et al. (2011) suggested that gelatinous zooplankton have higher carbon specific feeding rates than other more concentrated zooplankton as a direct result of their dilution, despite other zooplankton being capable of faster swimming. Therefore, despite the simplicity, this model could be useful in understanding how variation in carbon percentage potentially affects the ingestion of developing ephyrae. The results of the model are shown below; the difference in wet mass between the gelatinous and non-gelatinous treatments shown in Figure 4.8 corresponded to an increase in ingestion of 28% (Figure 4.9).

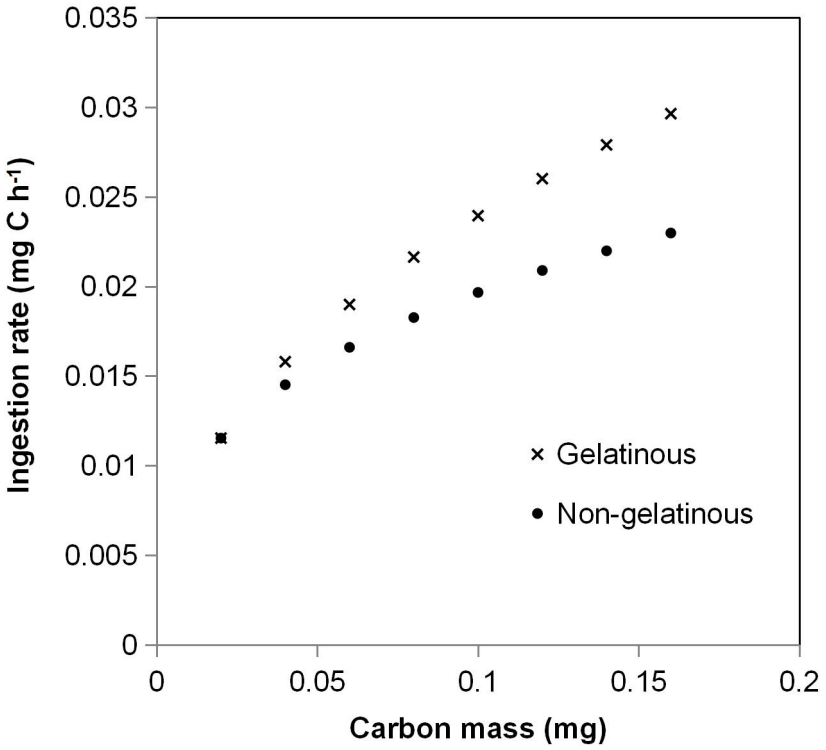


Figure 4.9 – *Effect of carbon mass (mg) on ingestion rate (mg C h^{-1}) of* Aurelia aurita *ephyrae. Values are modelled based on the relationships between wet mass and ingestion rate shown in Figure 4.5. In the gelatinous treatment the carbon percentage is allowed to vary in the relationship shown in Figure 4.2, in non-gelatinous the carbon percentage is fixed at the starting value.*

In addition to ingestion rate, growth rate can be estimated to develop a more comprehensive picture of how carbon percentage is influencing the energy budget. However, while Chapter 3 demonstrates the effect of carbon percentage on growth across species, it is not certain that the effect is the same within species. With ingestion rate, it was assumed that it was a function of physical body volume (and therefore wet mass or diameter) that was driving the observed relationship (Acuña et al., 2011). This meant that carbon mass was relatively unimportant in determining ingestion, and therefore did not have to be incorporated into the model. However, as both the wet mass and the carbon mass are likely to be important in determining growth rate (McConville et al., 2017), an equivalent assumption cannot be made. One way to unite composition, ingestion rate and growth rate into a single model is to calculate growth from ingestion rate using gross growth efficiency (Frandsen and Riisgard, 1997; Straile, 1997). Gross growth efficiency was not related to carbon mass or carbon percentage so a single average value (21%) is a sufficient

approximation. Taking GGE to be a constant value means that growth can be estimated based on ingestion alone, and the model can estimate the carbon or wet mass of the two treatments over time. Figure 4.10 shows that when the change in wet mass over time is estimated, the gelatinous treatment reaches a disproportionately higher wet mass than would be expected based on Figure 4.8 alone. This is a result of the positive feedback interaction between progressive dilution and ingestion rate, the dilution of the gelatinous treatment leads to higher feeding rates, which in turn leads to faster growth rate. As a result of this positive feedback, the model quickly becomes unrealistic beyond the range of the data observed in our experiment. In reality, the relationship seen above could not continue past the range shown as carbon percentage of *Aurelia aurita* does not dilute indefinitely, but to a minimum carbon percentage of 0.1% (Kiørboe, 2013).

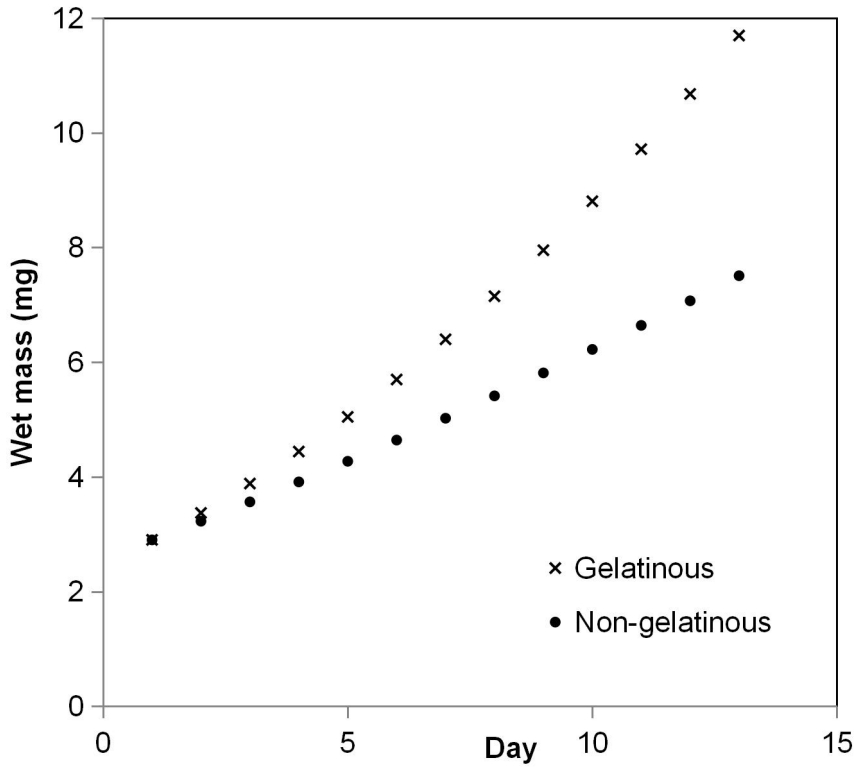


Figure 4.10 – *Growth in terms of daily change in wet mass (mg) of* Aurelia aurita *ephyrae. Values are modelled based on the relationships between wet mass and ingestion rate observed in our data. In the gelatinous treatment, carbon percentage is allowed to vary in the relationship observed in our data, in non-gelatinous the carbon percentage is fixed at the starting value*.

Using the model shown in Figure 4.10, it is possible to calculate what the mass scaling exponent for growth would be if dilution only influenced growth rate through increasing ingestion rate. The exponent for the specific growth rate, *g* (d^{-1}), generated from the model is 0.39, which is similar to the exponent derived from measured growth rates shown above (0.36, Figure 4.7C). This value is the result of the interaction between dilution and ingestion rate alone so it is surprising that it is so similar to the measured exponent. This could suggest that the exponent observed for growth rate in the experimental study is primarily determined by limitations in maximum possible feeding rate. This could be a consequence of sub-optimal food quality, as Moller and Riisgard (2007) found that *Aurelia aurita* ephyrae were capable of growing more quickly when offered the hydromedusae, *Rathkea octopunctata* (even with lower prey carbon mass). The model also implies that as the ephyrae grow and decrease in carbon percentage, feeding rate increases as growth efficiency remains constant, leading to proportionally higher growth. Therefore wet mass would increase exponentially through time until the adult carbon percentage was reached. This is ecologically relevant as predation mortality in zooplankton is often related to length along the major axis, or wet mass. Mortality due to predation is a major factor in determining recruitment of larval zooplankton (Platt, 1985), therefore minimising the time spent at a relatively small body size can lead to increased adult abundance. Through dilution, ephyrae grow through this vulnerable size range faster than other zooplankton, potentially decreasing mortality.

4.4 - Discussion

This chapter is the first study, to my knowledge, to investigate the effects of intraspecific variation in carbon percentage on the energy budget of zooplankton, although other studies have taken growth and ingestion measurements of *Aurelia aurita* ephyrae (Olesen et al., 1994; Hannson, 1997; Bamstedt et al., 2001). The most directly comparable study is that of Møller and Riisgard (2007) on *Aurelia aurita, Sarsia tubulosa* and *Aequorea vitrina*. In common with this chapter, Møller and Riisgard (2007) measured the specific growth rate and ingestion rate of *Aurelia aurita* ephyrae feeding on *Artemia* nauplii. As the food provided and ephyrae size range of Møller and Riisgard

(2007) is similar to those of this chapter, their study provide a valuable comparison with my measurements.

The smallest epyhrae had carbon percentage of 2.3% and diluted through development to the adult value of 0.1%. The newly strobilated ephyrae differed in carbon percentage from both adult *Aurelia aurita* and the mean carbon percentage of gelatinous zooplankton as a whole (~0.5%, Kiørboe, 2011). The smallest ephyrae were closer to the carbon percentage of chaetognaths and other intermediately gelatinous zooplankton than other cnidarians (Kiørboe, 2013). This suggests that the early developmental stages of gelatinous taxa represent a group of intermediately gelatinous zooplankton that may not have been previously appreciated. In the study by Kiørboe (2013) it was suggested that there are relatively few taxa of intermediate carbon percentage. However, if at least some gelatinous taxa dilute through development, then a far greater number of taxa are of intermediate carbon percentage at some point in their ontogeny. Gelatinous zooplankton are routinely under-sampled with nets, due to their delicacy and difficulty of identification (Raskoff et al., 2003) and larval animals are often more numerous than adults of the same species (Cross et al., 2015). Taken together, this could suggest that a substantial fraction of some zooplankton assemblages are of intermediate carbon percentage. In addition, the range of carbon percentage observed also suggests that it is unreliable to use taxon-specific averages for carbon percentage of early life stages of *Aurelia aurita,* and potentially other scyphomedusae.

The C:N mass ratio did not change with ontogeny (mean = 4.34) across all body sizes suggesting that all somatic carbon was metabolically active, not being stored as lipid (Schmidt et al., 2003). This value is similar to other non-lipid storing zooplankton (Ikeda and Takahashi, 2012; Ikeda, 2013) and to other gelatinous zooplankton (Ikeda, 2014). This value is lower than the Redfield ratio (Redfield, 1934), as expected for an obligate carnivore. The C:N ratio for *Artemia* nauplii is approximately 3.65, lower than that of the ephyrae but is likely similar enough for adequate nutrition (based on the fixed C:N of the ephyrae through development).

4.4.1 - Ingestion

For an ephyra of 16.8 µg C feeding on *Artemia nauplii*, this chapter reported an ingestion rate of 9.5 µg C d^{-1}, compared to 20.2 µg C d^{-1} reported in Møller and Riisgard (2007). The values observed were also lower than the ingestion rates reported for *Calanus helgolandicus* over a range of carbon masses (Harris et al., 2007). The ephyrae fed at lower rates than other comparable zooplankton, despite being offered high concentrations of food at the same temperature (400 µg C l^{-1} in this study relative to 280 µg C l^{-1} in Harris et al., 2007). This could suggest that the incubation vessels were deleterious to ephyra condition. There was however, limited support for deleterious tank effects as mortality was low (mortality rate = 1.3%) and behaviour was not significantly different post-incubation. It is unclear why the ephyrae fed at lower rates than other comparable zooplankton, as previous studies have suggested that decreased carbon percentage increases carbon specific feeding rate (Acuña et al., 2011).

With increasing mass, specific feeding modes are expected to become less efficient (Kiørboe, 2011), resulting in intraspecific ingestion rates to scaling at $b < 1$. Ingestion rate increased with increasing carbon mass, with a scaling exponent of 0.6 with increasing carbon mass (Figure 4.5), and 0.33 with increasing wet mass (Figure 4.5). The carbon mass scaling exponent of the ephyrae is very similar to that of *C. helgolandicus* (0.59, Harris et al., 2007). This was unexpected as the dilution of the ephyrae was predicted to increase the ingestion rate exponent with increasing carbon mass. As carbon mass increased, wet mass increased disproportionately (Figure 4.2). As ingestion rate is a function of wet mass (Acuña et al., 2011), it was expected that this dilution would increase the carbon mass scaling exponent of the ephyrae relative to the non-diluting *C. helgolandicus*. As the exponent was similar, either the intraspecific variation in carbon percentage was insufficient to reproduce the interspecific pattern identified by Acuña et al. (2011), or other factors are more important in determining the ingestion rate of ephyrae.

In addition, the wet mass scaling exponent was also lower than predicted. As *C. heloglandicus* does not have a gelatinous body form, it is assumed that carbon percentage remains relatively constant through development, therefore the wet mass scaling exponent for ingestion for *C. helgolandicus* should be equal to the carbon mass scaling exponent (0.59). The exponent of 0.33 observed for the ephyrae is lower than the exponent for *C. helgolandicus* (0.59), which could suggest that tissue dilution has a negative effect on feeding. However, there is an alternative hypothesis as the specific value of the exponent (b = 0.33) suggests that feeding may be a function of a length dimension, and not a function of wet mass (b = 1) or surface area (b = 0.67). In a study on ephyra prey capture mechanics, Sullivan et al. (1997) reported that 61% of captures took place on the lappet tips. If prey capture is much more likely on the lappet tips than other areas of the ephyrae, then it would follow that ingestion rate would increase at a rate similar to the rate at which the lappet tip area increases (potentially due to nematocyst distribution or flow regime). The lappet tips are the outermost areas of each lappet, and therefore are a proportion of the circumference. As the lappet tips constitute a proportion of the circumference of the ephyra, they are a length dimensions, and could be expected to scale at approximately b = 0.33 with wet mass. If this is the case, ingestion rate is expected to increase linearly with increasing diameter, as seen in Figure 4.6.

There was a negative relationship between carbon percentage and ingestion rate. I believe this was driven by low carbon percentage individuals being much larger (in both carbon and wet mass terms) and therefore having higher gross ingestion rates. This is also reflected in the relationship between carbon percentage and specific ingestion rate ($\log_{10}y = 0.56 * \log_{10}x + 2.73$, $R^2 = 0.33$, $p < 0.0001$), as the relatively low carbon mass of high carbon percentage ephyrae led to high specific ingestion rates. In this instance, the strong relationship between carbon mass and carbon percentage (shown by proxy in Figure 4.3) render carbon percentage uninformative.

4.4.2 - Growth

Maximum specific growth rate, *g* (d^{-1}), was 0.28, comparable but higher than the values reported by Møller and Riisgard (2007) of 0.22 and Olesen et al. (1994) of 0.2. This is likely a result of using smaller ephyrae in our experiments than the above authors (1.2 mm compared to 3.5 mm and 4 mm respectively), as the highest *g* value in this chapter was observed for the smallest ephyrae. The growth rates of *Aurelia aurita* ephyrae in this study (*g* = 0.12) are lower than those of *C. helgolandicus* of similar carbon mass *(g* = 0.20, Harris et al., 2007). This suggests that during early development of gelatinous zooplankton, carbon percentage may not be as important as other factors in determining growth rate.

A meta-analysis by Hirst and Forster (2013) on the growth scaling of a wide range of marine invertebrates suggested that growth rate (mg C d^{-1}) scales most commonly at or approaching *b* = 1 within species. Following this, I hypothesised that the growth exponents observed would be greater than other zooplankton species, as in my interspecific study in Chapter 2, decreasing carbon percentage led to an increase in growth rate. As increasing carbon mass led to decreasing carbon percentage, I predicted growth rate would increase with increasing carbon mass, and therefore expected the carbon mass scaling exponent to be greater than 1. The scaling exponent for wet mass growth rate (mg WM d^{-1}) was 0.62 and for carbon mass growth rate (mg CM d^{-1}) was 0.49, both lower than predicted. If the ephyrae were reaching maximum adult body size at the upper range of diameter then this exponent might be expected, however this was not the case. An alternative hypothesis for a low growth body mass scaling exponent is that the ephyrae were becoming food limited. Møller and Riisgard (2007) found that with increasing food concentration, ephyrae grew faster to a maximum rate at 100ug C l^{-1}. Prior to the experiment, the ephyrae were fed regularly and during the incubations I provided a food concentration considerably greater than this (460 µg C l^{-1}) minimising the chance that growth was food limited. The low exponents could suggest that tissue dilution has an associated energetic cost, such that diluting tissues diverts energy away from increasing in carbon mass. The relationship between carbon percentage and growth rates mirrors that of carbon percentage and ingestion rate. Carbon mass is

the cause of these relationships, as at high carbon percentages, growth rate (mg h^{-1}) is low and specific growth rate (both mg mg^{-1} h^{-1} and g d^{-1}) are low. As with ingestion, the relationship between carbon mass and carbon percentage means that, in this experiment, carbon percentage provided limited information about growth.

The mean value for gross growth efficiency (ingestion/growth, GGE = 0.21) observed lies within the range reported by Straile (1997) for a wide range of other zooplankton. This value was also comparable to the net growth efficiencies (NGE) reported for ephyrae by Olesen et al. (1994) 0.35 and Frandsen and Riisgard (1997) of 0.37. As the NGE values from the other authors are based on the proportion of assimilated carbon these values are expected to be higher than the gross growth efficiency reported in this study, which is calculated from ingested carbon. Previous studies on other gelatinous zooplankton have observed that gross growth efficiency (GGE) can decrease or remain constant with increasing length or mass (Kremer and Reeve, 1989; Sullivan and Gifford, 2007). It is unclear whether the lobate ctenophores in their studies were diluting over the course of the above investigations, and whether this influenced their GGE. In my study, gross efficiency was invariant with increasing carbon mass, despite progressive dilution. Above, it was suggested that the low exponents for growth rate could be due to the costs of dilution. However, there was no evidence for a relationship between wet mass and gross growth efficiency. This suggests that the ratio between food ingested and carbon mass increase was constant, despite wet mass increasing proportionately more in larger ephyrae. While not definitive, this could suggest that the costs of tissue dilution are minimal and that the low exponents have some other cause.

4.5 - Conclusion

This chapter has demonstrated that carbon percentage is not fixed during the development of *Aurelia aurita.* While adult *A*. *aurita* have similar carbon percentage values to those of many other gelatinous taxa, larval ephyrae are more similar to that of chaetognaths or some tunicates. Carbon percentage was found to vary continuously across the size range investigated, showing a

gradual decrease from the ephyrae to the adult value. This lends further support to the notion of substituting the current categorical view of gelatinous and non-gelatinous zooplankton with a continuous view based expressed as carbon percentage. Given the absence of data for other species, it is currently unclear whether this represents a general trend, and whether other gelatinous taxa also dilute through development. If so, these larvae could constitute a considerable fraction of the zooplankton that is intermediately gelatinous and not often sampled or considered.

This chapter suggests that biologically relevant variation in carbon percentage does occur across ontogeny. Ingestion and growth rates in both carbon and wet mass were observed to scale at lower exponents than those expected from general theory and observed in other zooplankton. It is difficult to determine whether this is the result of dilution occurring in parallel with growth, and it is possible that the scaling of growth rate may have a different exponent once the adult carbon percentage is reached.

In the simple model presented, dilution of the magnitude observed in this chapter lead to an increase in carbon specific feeding rate of 28% over a similar non-diluting organism. However, this is uncertain as this difference was not found when comparing with other organisms. The interacting effects of dilution and ingestion rate on growth suggest that through dilution ephyrae may escape vulnerable body size classes faster than would be possible through carbon mass growth alone. Taken in concert, these observations suggest that intraspecific variation in carbon percentage could have functional implications and demonstrate potential evolutionary drivers for this rapid dilution in early ontogeny.

CHAPTER 5 – The influence of carbon percentage on bloom formation

5.1 - Introduction

Recent years have seen a resurgence in the study of phenology, the seasonal timing of biological events (Edwards and Richardson, 2004; Yang and Rudolf, 2010; Anderson et al., 2012), partially as a result of concerns over anthropogenic climate change. These changes in timing have the potential to affect ecosystems in a number of ways, including premature spawning relative to the timing of suitable foods (Mackas et al., 2012) and trophic mismatching (Beaugrand et al., 2003; Atkinson et al., 2015). In order to better predict how biological communities will respond to these changes in seasonal timing, it is important to first establish a robust understanding, terminology and definition for seasonally recurring phenomena.

One term that is frequently used when discuss timing and seasonality in plankton communities is “bloom”. Despite its common use, the specific meaning of the word bloom is ambiguous. For instance, the term bloom is applied to the flowering of angiosperms and rapid population increase of different groups within the zooplankton. Furthermore, within different scientific communities, the term bloom is defined differently. Even within the relatively narrow field of gelatinous zooplankton, some ambiguity remains. An important division made by Graham et al. (2001) between true and apparent blooms, was later expanded by Lucas and Dawson (2014) into the definition below;

“*A true bloom is in part a consequence of seasonal life cycles, and consequently all metagenic organisms have the potential to bloom pending suitable environmental conditions; thus normal and/or abnormal seasonal biomass is directly attributable to population increase due to reproduction and growth, sometimes enhanced by anthropogenic activity. An apparent bloom, in contrast, is a local increase in biomass of animals associated with temporary or transient chemical or physical phenomena (such as aggregation at fronts or local advection to a new location) or longer term accumulation of large numbers in enclosed habitats; apparent blooms may, but do not necessarily reflect true blooms that occurred elsewhere” (Lucas and Dawson, 2014)”*

Following this definition, the one of the criterion determining whether a transient population is a bloom is whether the species has a metagenic life cycle (undergoes an alteration of generations between different phases in the life cycle). Such a definition is incomplete as many gelatinous taxa that do not have metagenic lifecycles do form blooms. These include the holoplanktonic medusa, *Pelagia noctiluca* (Hamner and Dawson, 2008) and the lobate ctenophore,

Mnemiopsis leidyi (Fuentes et al., 2010). The opposite is also true. Not all metagenic taxa form blooms, as documented in the Stauromedusae by Miranda et al. (2012). This demonstrates the limitations of a definition of blooming based on the intrinsic qualities of the organisms it comprises.

This loose definition of blooming in gelatinous zooplankton contrasts with that used for phytoplankton blooms, where proxies of abundance (measurements of ocean colour and other remotely sensed data) are used to produce quantitative definitions. A population is considered to be blooming when chlorophyll *a* concentration (as a proxy for biomass) is greater than an established threshold (Racault et al., 2012). This form of definition is based on the population dynamics of the taxa, not on an intrinsic quality of their biology. This approach is valuable as specific aspects of blooming, such as global incidence and duration, can be quantified through the use of numerical indices. These indices can in turn be used to ask meaningful questions of the biology of the system, such as to how light and climatic indices influence the phenology and other large scale patterns of bloom formation (Racault et al., 2012).

The extra information afforded by using a quantitative definition based on indices of blooming in phytoplankton suggests that applying a similar approach to blooming in zooplankton could further our understanding. Bloom indices for zooplankton could be valuable in a range of different ways. For ecologists, quantitative indices for the magnitude of blooms would allow for descriptive comparisons of blooms in different groups, or trends in blooming in a particular species over time. Furthermore, the effects of differing degrees of blooming on food web interactions or the productivity of an area could be investigated, leading to a deeper understanding of how blooming impacts zooplankton systems.

Blooms of gelatinous zooplankton are also of interest to policy makers, as gelatinous zooplankton form one of the plankton lifeform indicators as part of the Marine Strategy Framework

Directive (MSFD) (Tett et al., 2015). In most cases, the negative interactions between gelatinous zooplankton and humans occur primarily during blooms (Masalimoni et al, 2000), therefore monitoring of the blooming of gelatinous zooplankton is of key importance. The creation of numerical bloom indices could provide further information to policy makers on whether management strategies are working effectively, on the progress of biological invasions (e.g. is a population of an invasive species actively blooming?).

The development of quantitative bloom indices could also be useful for asking more fundamental questions about the relationship between the gelatinous body form and blooming. Many gelatinous zooplankton form blooms, such as *Pelagia notiluca*, however some do not, such as the Stauromedusae. A range of factors contribute to bloom-like dynamics in the zooplankton including benthic processes, such as strobilation in scyphomedusae (Uye et al., 2006), some of which are of key importance to the populations of non-gelatinous taxa also. Despite this, the term bloom is applied exclusively to zooplankton that are gelatinous. One aim of this study is to investigate whether the population dynamics of gelatinous zooplankton differ quantitatively from those of other zooplankton, and whether other taxa also form blooms. As the gelatinous zooplankton are highly diverse in phylogeny, life history and functional ecology, the shared trait to determine whether an organism should be included within the group is a dilute body. With this is mind, by relating the bloom indices to carbon percentage for different species, it is possible to test whether the population dynamics of gelatinous zooplankton differ from those of other zooplankton. Using these relationships, it is possible to ask whether only gelatinous zooplankton form blooms, or whether this phenomenon is more widely distributed.

The aim of this chapter was to develop a number of indices to define blooms and determine whether bloom formation is related to carbon percentage. The aim was completed through the following objectives; first, to consider the population dynamics that may be characteristic of blooming; second, to suggest ways to capture these characteristics numerically; third, to use known bloom forming and more stable taxa to evaluate the indices; and fourth to relate the indices to carbon percentage and carbon mass to test whether more gelatinous taxa are more predisposed to form blooms.

5.2 - Methods

5.2.1 - Data sources

The data used in this chapter come from the L4 time series, described in detail in Chapter 2. Taxonomic resolution of identification was increased in 2009, particularly for the hydromedusae, and therefore only data from 2009-2015 inclusive were used in this analysis (319 time points, 638 net samples). Of the 188 taxa currently recorded, only those that had been consistently recorded since 2009 were included (127 taxa). Eggs were not included in the analysis.

5.2.2 - Development of bloom indices

Several qualities that are associated with blooming can be visualised by comparing changes in abundance over time for the two species, A and B, shown in Figure 5.1. Both species have the same total abundance over the period shown, although the population dynamics of the species differ. Species A would be described as more bloom-forming than species B, and below this quality is explored numerically. As this stage there is no attempt to classify the model species are gelatinous or otherwise, only to identify what numerical qualities are indicative of bloom formation. Many metagenic gelatinous zooplankton may fit the model of species B more closely as a result of continuous, or protracted, strobilation through the year (Houghton et al., 2007).

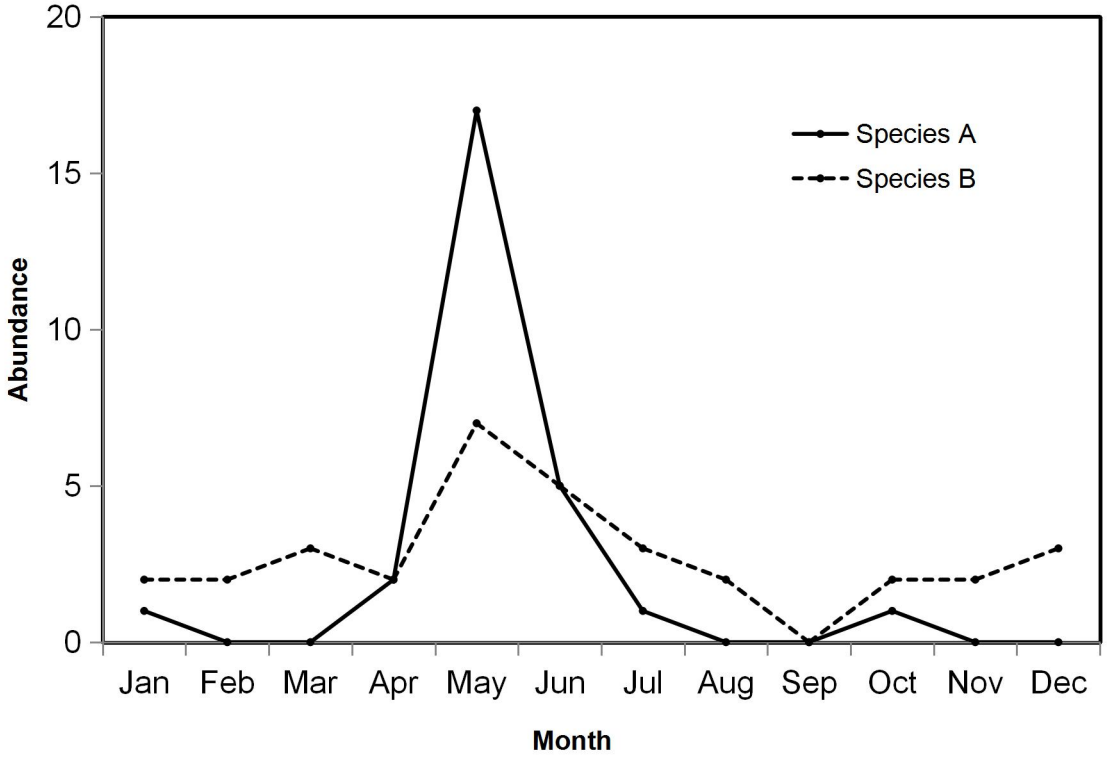


Figure 5.1 – *Schematic data of abundance of two species over the year to demonstrate how blooming can be quantified on the basis of abundance over time. Note that while the schematic shows changes over monthly timescales, the sampling at L4 is on a weekly basis, weather permitting.*

5.2.3 - Variability in abundance

Firstly, if a bloom is characterised by a period of high abundance relative to background, then this suggests that a key feature is higher total variability in abundance (a boom or bust pattern of abundance). The *coefficient of variation* is a measure of spread that can be used to compare variability of distributions with different means.

(eq. 5.1) Coefficient of variation = standard deviation (abundance) / mean (abundance)

In Figure 5.1, the *coefficient of variation* is 2.16 in species A and 0.64 in species B. Therefore, the first quality we can attribute to blooming organisms is high variability in abundance. Variability in abundance was compared across the 2009-2015 weekly time series and interannually.

To investigate variability across the time series the *coefficient of variation of abundance* was calculated for each species. Two indices were used to estimate interannual variability; the *ratio between the maximum and minimum mean annual abundance*, and the *coefficient of variation of mean annual abundances*. These indices were calculated including and excluding zeroes, as the large number of zeroes associated with species presence records tended to strongly decrease variability in rare species. Species that have more bloom-like population dynamics will have higher coefficients. If taxa with low carbon percentage have more bloom-like population dynamics then carbon percentage will be negatively related to; i) *coefficient of variation*, ii) *ratio between the maximum and minimum mean annual abundances* and iii) *coefficient of variation of mean annual abundances*.

5.2.4 - Temporal heterogeneity

Furthermore, the relatively high abundances that comprise blooms often increase and decrease rapidly; so species abundance tends to be concentrated into relatively short periods. In Figure 5.1, 65% of the total abundance of species A is concentrated in the maximum measurement compared to 27% in species B. Therefore, temporal heterogeneity in abundance, i.e. long periods of low (to zero) background abundance punctuated with short periods of high abundance is another quality associated with blooming.

Temporal heterogeneity could be considered as synonymous with temporal auto-correlation, the probability of the abundance at sample n+1 being similar to the abundance at sample n. However, given the patchy distribution and potential aggregation of some plankton species, random fluctuations that do not represent meaningful increases are common. For this reason, a temporal auto correlation function was not used as an index. Instead, temporal heterogeneity was investigated using two indices, the *number of non-zero records* and the *coefficient of the frequency distribution of abundance*.

The *number of non-zero records* was a count of all instances that a species had greater than zero abundance. The second index, *the frequency distribution of abundance*, was calculated for data that were first normalised to the maximum abundance for each species. The normalised data were then plotted as a histogram varying between 0 and 1 (maximum recorded abundance) in 0.01 bins. All frequency bins that had no recordings were omitted. For each species, linear models were generated between $\log_{10}$ index (the value of the bin) and frequency (Figure 5.2). If taxa with low carbon percentage have more bloom-like population dynamics then carbon percentage will be positively related to the *frequency distribution coefficient* and the *number of non-zero records*.

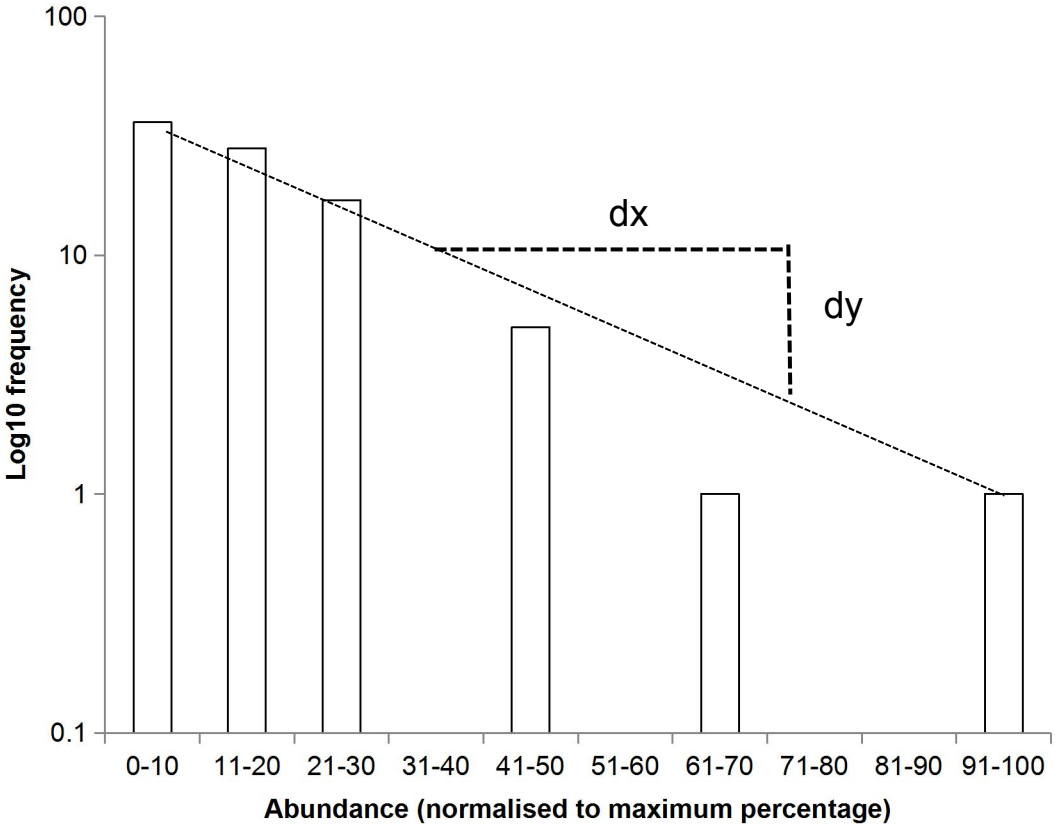


Figure 5.2 – *Schematic example of the frequency distribution coefficient, the slope of a linear model between abundance (as % of maximum abundance) and log_{10} frequency. In the actual analysis the x axis bins were of width 1% however this number of bins could not be clearly shown.*

5.2.5 - Population increase rate

Finally, taxa must be capable of high population growth rates to facilitate the rapid changes in population abundance associated with blooms. In Figure 5.1, the maximum slope of abundance increase is 8.5 individuals per month for species A and 3.5 individuals per month for species B. Rate of increase was quantified using the *interval between 25 and 50th cumulative percentile*s and an *increase rate index* that I devised. The 25th and 50th cumulative percentiles for each year were found by determining between which time points the cumulative abundance reached 25% and 50% of the maximum cumulative total annual abundance respectively, following the methods described to quantify phenology by Mackas et al. (2012). The interval was then calculated as the number of days between the 25th and 50th cumulative percentiles. This index can be heavily skewed in rare taxa, because if a taxon is infrequently recorded it could reach the 25th cumulative percentile and not be observed for several months before reaching the 50th. As a result these taxa would have abnormally long intervals, falsely suggesting slow gradual population growth. To avoid this, only taxa that were present in at least 30% of the samples (53 taxa) were included.

The *increase rate index* aimed to decrease the effect of patchy distributions by calculating the rate of change of abundance over several successive increases (Figure 5.3). This index was calculated on three point running mean data (where each data point is calculated as the mean of itself and the two adjacent data points), with half of the minimum value for each taxon added to avoid increases from a population of zero. The running mean was used to decrease the effects of patchiness and variability in sampling; in particular ensuring that small random decreases did not remove meaningful increase trends from the analysis. The *increase rate index* was calculated for two, three and four successive increases as;

(eq. 5.2) increase rate = (final abundance – starting abundance) / number of weeks

All increases were included in the analysis, even if multiple increases were present across overlapping subsets of the same range of data. For each species the mean, median and maximum increase was calculated for two, three and four successive increases. If taxa with low carbon percentage have more bloom-like population dynamics then carbon percentage will be negatively related to the *interval between the 25th and 50th cumulative percentiles* and positively related to the *increase rate index*.

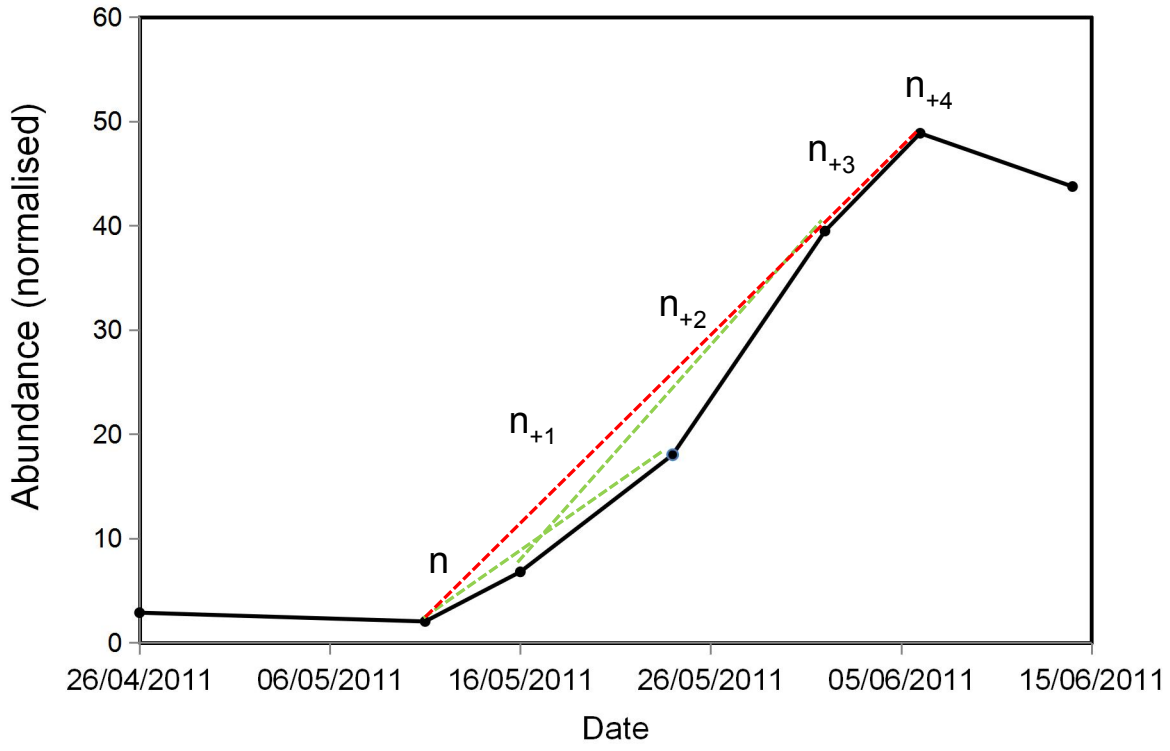


Figure 5.3 – *Schematic example of the increase rate index, calculated for four increases as (n+4 - n) / 4. The points on the black line are data, the red line shows the range over which the increase rate for four successive increases is calculated. The green lines show two valid two step increases across four successive points.*

5.2.6 - Testing bloom index performance

To determine the efficacy of the bloom indices, species that are known to form blooms should be compared with those that are known for having a stable population. *Pleurobrachia pileus* is a generalist zooplanktivore that spawns continuously throughout the year when food is sufficient (Fraser, 1970). This species is capable of paedogenesis, reproduction before reaching the adult

life form. In the case of *Pleurobrachia spp.*, reproduction can begin when the larvae reach diameters of only 0.4mm (Jaspers et al., 2012). These characteristics give *Pleurobrachia pileus* the potential for explosive population growth so this species was used as the example of a blooming species at L4. The efficacy of the bloom indices were tested by comparing the values for the bloom indices of *Pleurobrachia pileus* with another zooplanktonic taxon that shows a more stable population. *Oithona similis* is a cyclopoid copepod known to have relatively low rates of ingestion, growth, reproduction and mortality, to the extent that some authors have suggested this taxon may help stabilize plankton communities (Paffenhöfer, 1993). The contrast between the population dynamics of these species is demonstrated in Figure 5.4. The abundance of *Pleurobrachia pileus* is more densely concentrated into short sporadic periods, suggesting higher variability in abundance, population increase rate and temporal heterogeneity. These taxa were also selected for comparison as they are both relatively abundant at L4, an important quality for this assessment as some of the indices developed may be skewed by low abundance.

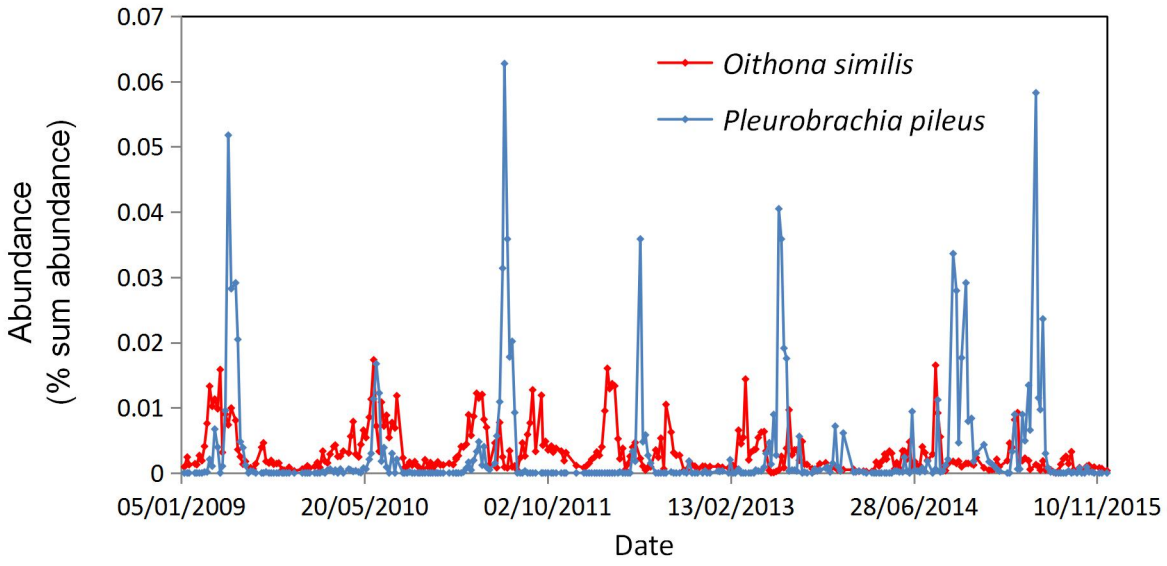


Figure 5.4 – *Abundance of* Oithona similis *(red) and* Pleurobrachia pileus *(blue) as a percentage of the total abundance of each species between 2009 and 2015.*

The secondary aim of this chapter was to investigate whether our varios indicators of bloom-like tendencies differed between gelatinous and non-gelatinous zooplankton. The outputs from each of these indices were used as dependent variables in general linear models based on the explanatory variables, carbon percentage and carbon mass. Carbon percentage of each taxon was estimated using the table of carbon percentage presented in Appendix I, and carbon mass following the methods also described in Chapter 2.

5.3 - Results

Species at L4 showed a range of patterns of abundance over time, with some species occurring only as short term blooms (e.g. *Evadne* spp.) and others occurring consistently throughout the year (e.g. *Oithona* spp.). In the case of blooming taxa, these blooms occurred at roughly similar times each year (e.g. *Pleurobrachia pileus*) or were more randomly distributed (e.g. *Goniopsyllus clausi*). *Beroe spp.* was the dominant taxa on the basis of biomass, however due to low number of recordings (present in nine samples) and potential overestimation due to fragmentation of the gelatinous body, it was omitted from these analyses. The taxa included vary widely in life history, biomass and total abundance. The full list of values of each index for each taxon is shown in Appendix III. The values for the chosen comparison species, *Pleurobrachia pileus* and *Oithona similis* are shown in Table 5.1. The values for the full list of species were combined with the estimates of carbon percentage, and used to create the General Linear Models (GLMs) shown in Table 5.2.

Table 5.1 – *Comparison of the values of blooms indices for* Pleurobrachia pileus *and* Oithona similis. *CV= coefficient of variation, CV NO 0 = coefficient of variation (no zeroes), Interval = the average interval between 25th and 50th cumulative percentile of annual total abundance, 2, 3, and 4 inc = maximum value for the increase rate index over 2, 3 and 4 weeks respectively, Interann CV = coefficient of variation of annual mean abundances, Non-0 = number of non-zero records, FDC = frequency distribution coefficient. Expected refers to whether the index value was predicted to be higher in* P. pileus *or* O. similis*, and actual refers to whether the index value was higher in* P. pileus *or* O. similis.

	CV	*CV NO 0*	*Interval*	*2 inc*	*3 inc*	*4 inc*	*Interann CV*	*Non-0*	*FDC*
P. pileus	3.19	1.85	14.00	249	731	758	0.63	126.00	-13.98
O. similis	1.09	1.09	46.71	7.84	11.4	17.3	0.34	318.00	-3.29
Expected	P>O	P>O	O>P	P>O	P>O	P>O	P>O	O>P	P>O
Actual	P>O	P>O	O>P	P>O	P>O	P>O	P>O	O>P	P>O

Table 5.2 – *Outputs of GLMs investigating the relationships between carbon percentage (C%), carbon mass (CM) and bloom indices. "No 0" indicates that records of abundance = 0 were excluded from the analysis as large numbers of abundance = 0 records can influence the calculation of some indices.*

Index	*df*	*p (C%)*	*p (CM)*	*Adj R2*	*slope C%*	*slope CM*
coeff of variation	124	0.067	0.84	0.011	-0.18	0.0009
coeff of variation (no 0)	114	0.21	0.99	0	-0.02	-0.000007
2 inc mean	109	0.066	0.51	0.02	-6.5	-0.1
2 inc median	109	0.15	0.84	0.002	-2.43	-0.01
2 inc max	109	0.19	0.58	0.001	-109	-1.9
3 inc mean	91	0.19	0.54	0.002	-19.3	-0.34
3 inc median	91	0.53	0.56	0	-0.91	-0.03
3 inc max	91	0.2	0.55	0.001	-213	-3.8
4 inc mean	68	0.16	0.63	0.006	-167	-4.2
4 inc median	68	0.52	0.48	0	-6.8	-0.55
4 inc max	68	0.15	0.6	0.01	-1047	-27.9
interannual (CV)	124	0.11	0.97	0.005	-0.024	-0.00002
interannual (min/max)	110	0.46	0.31	0	-1.23	-0.07
interannual (min/max, no 0)	110	0.07	0.86	0.01	-5.06	-0.02
interval (25-50)	44	0.34	0.4	0	0.93	-0.05
non-zero records	124	**0.00098**	0.39	0.07	6.5	-0.07
freq analysis	77	**0.0005**	0.13	0.14	0.61	-0.01

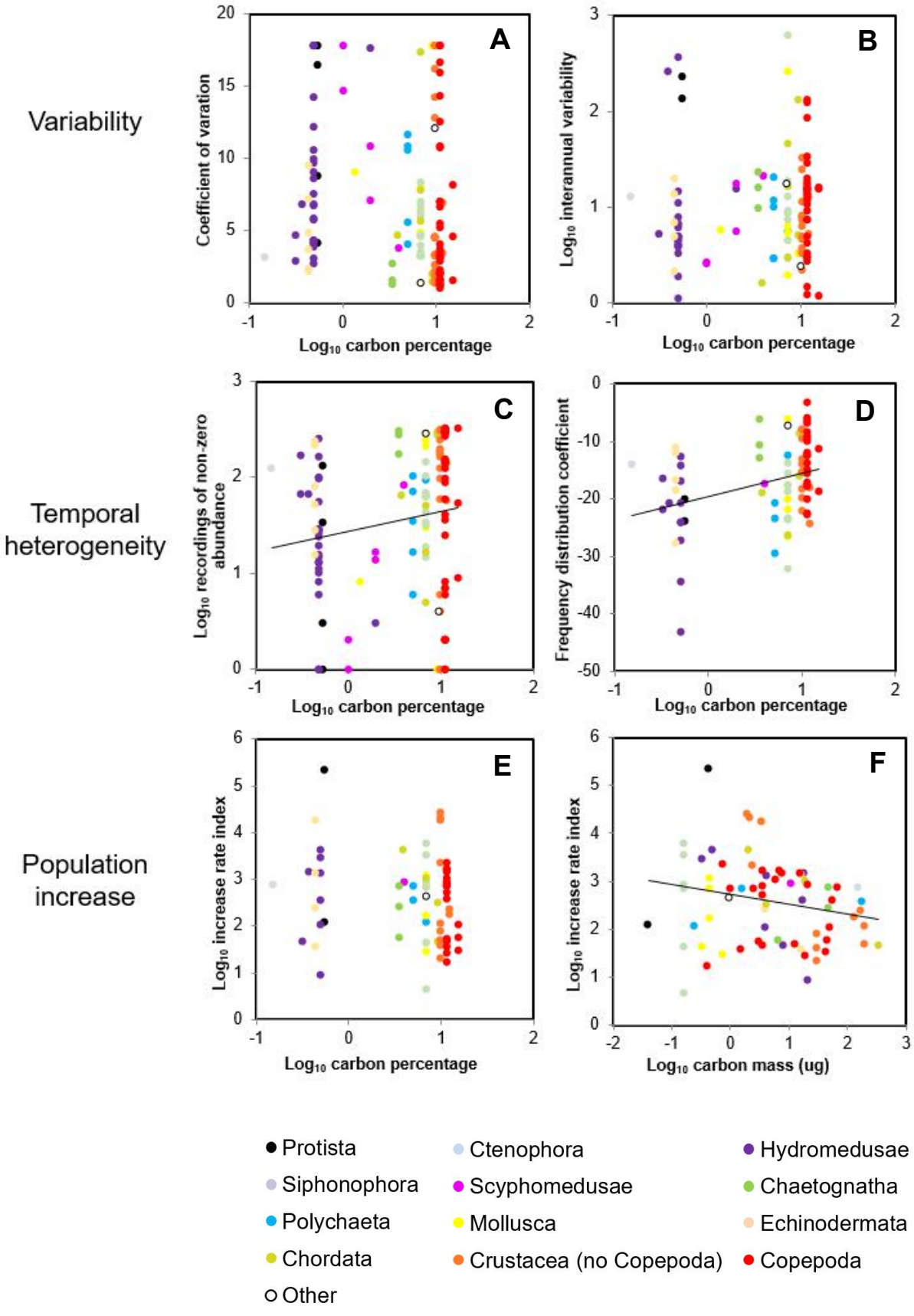

Variability
Temporal heterogeneity
Population increase
A
B
C
D
E
F
Coefficient of varation
Log10 interannual variability
Log10 recordings of non-zero abundance
Frequency distribution coefficient
Log10 increase rate index
Log10 carbon percentage
Log10 carbon mass (ug)
Protista
Ctenophora
Hydromedusae
Siphonophora
Scyphomedusae
Chaetognatha
Polychaeta
Mollusca
Echinodermata
Chordata
Crustacea (no Copepoda)
Copepoda
Other

Figure 5.5 – *Relationships between carbon percentage, carbon mass and bloom indices for zooplankton taxa at the L4 sampling site. A - coefficient of variation in abundance of zooplankton at L4 as a function of log_{10} carbon percentage (df = 124, p = 0.013, adj R^2 = 0.033, coefficient of variation = - 0.12 * log_{10} carbon percentage + 0.8), B – log_{10} interannual variability (maximum annual abundance / minimum annual abundance) as a function of log_{10} carbon percentage (df = 80, p = 0.07, adj R^2 = 0.01, log_{10} interannual variability = - 5.06 * log_{10} carbon percentage + 68.3), C – log_{10} number of non-zero abundance records as a function of log_{10} carbon percentage (df = 124, p = 0.001, adj R^2 = 0.07, number of non-zero records = 6.52 * carbon percentage – 58.1), D – coefficient of linear models between abundance and frequency as a function of log_{10} carbon percentage (df = 77, p = 0.0005, adj R^2 = 0.14, frequency distribution coefficient = 0.61 * carbon percentage - 20.1), E – log_{10} maximum increase rate index across four successive increases as a function of log_{10} carbon percentage (no statistically significant relationship detected), F – log_{10} maximum increase rate index across four successive increases as a function of log_{10} carbon mass (df = 68, p = 0.0002, adj R^2 = 0.16, log_{10} maximum increase rate index = - 0.46 * carbon percentage + 1.62).*

5.3.1 – Variability

5.3.1.1 – Testing of variability indices

P. pileus had higher values than *O. similis* for all three indices of population variability; *coefficient of variation*, *ratio between the maximum and minimum mean annual abundances* and *coefficient of variation of mean annual abundances*. This suggests that these indices could be effective for quantifying the variability associated with blooming in zooplankton.

5.3.1.2 – Effect of carbon percentage on variability indices

There was limited support for a relationship between carbon percentage and variability in abundance, but no relationship with carbon mass. No effect of either carbon mass or carbon percentage was observed on coefficient of variation at $p<0.05$. The full analysis including all data (Figure 5.5A, p = 0.067) and the analysis omitting zeroes and meroplanktonic taxa (p = 0.07) were approaching 5% significance levels. In both analyses, the slope with increasing carbon percentage was negative, offering limited support that more gelatinous taxa tend to be more variable at L4. There was a marginally significant (0.07) negative effect of carbon percentage on interannual variability (max / min annual abundance), potentially suggesting that gelatinous taxa may be more

variable than less gelatinous taxa (Figure 5.5B). However, the R^2 values for the relationships between variability and carbon mass and carbon percentage were very low, suggesting that other factors were more important in determining variability at L4.

5.3.2 - Temporal heterogeneity

5.3.2.1 – Testing of temporal heterogeneity indices

O. similis had higher values than *P. pileus* for the indices of temporal heterogeneity; *number of non-zero records* and *frequency distribution coefficient*. This follows the predictions made in the methods, suggesting that the indices used were capable of detecting the differences in temporal heterogeneity between the two species, and may be more widely applicable.

5.3.2.2 – Effect of carbon percentage on temporal heterogeneity indices

There was strong support for a relationship between temporal heterogeneity in abundance and carbon percentage, but no relationship with carbon mass. There was a highly significant positive relationship between carbon percentage and number of non-zero records, more gelatinous taxa were less frequently recorded at L4 (Figure 5.5C). Similarly, a highly significant positive relationship was observed between carbon percentage and the frequency distribution coefficient (Figure 5.5D), which suggests that the abundance of gelatinous taxa was more heterogeneously distributed through time than other taxa.

5.3.3 - Population increase rate

5.3.3.1 – Testing of population increase rate indices

As predicted, the *increase rate index* of *Pleurobrachia pileus* was higher and the *interval between the 25th and 50th cumulative percentiles* was shorter than that of *O. similis*. These indices

were capable of detecting the differences in the relative increase rates of these species, and may be effective more widely.

5.3.3.2 – Effect of carbon percentage on population increase rate indices

There was no significant relationship between increase rate indices and carbon percentage, but there was a significant negative relationship between carbon mass and increase rate (Figure 5.5E, F). The mean, median and maximum increase rates were calculated for two, three and four successive increases. To ensure that the transformation used on the data was not influencing the result a sensitivity analysis was performed. The original transformation, adding half the minimum abundance for each species, was substituted to adding 1 to abundance. No versions of the analysis could detect any significant relationship between increase rate and carbon percentage. In addition, the 25^{th} – 50^{th} cumulative interval was not affected either by carbon percentage or carbon mass.

5.4 – Discussion

5.4.1 – Variability in abundance

5.4.1.1 – Are the variability-based bloom indices effective?

The indices tested for variability in abundance were *coefficient of variation*, *ratio between the maximum and minimum mean annual abundances* and *coefficient of variation of mean annual abundances*. For these indices, *P. pileus* had higher values than *O. similis* as predicted. All of these indices were based on ratios and therefore scale to allow the comparison of taxa with different mean abundances. This is useful as many taxa are rare and therefore their mean abundance is lower than that of other more common species. It is worth noting that the *coefficient of variation* was calculated excluding zeros, the value for *P. pileus* decreased but the value for *O. similis* was relatively unchanged. This was the result of the high number of zero abundance

records in *P. pileus* relative to *O. similis* increasing variance. This difference was used in both the indices of temporal heterogeneity as another way to categorise bloom-like population dynamics. The indices based on interannual variability need several years of data to be useful, however the *coefficient of variation* could be used with potentially any period of repeated records. Its strength as an index will increase with additional records and should preferentially include at least one year to cover the full seasonal cycle.

5.4.1.2 – The relationship between carbon percentage and variability in abundance

There was limited evidence, both from the coefficient of variation and interannual variability, that more gelatinous taxa might be more variable in abundance at L4. One potential reason for this could be the influence of life history. Many gelatinous taxa have benthic stages such as polyps or hydroids (25 of 32 of taxa with carbon percentage <1%). The influence of a metagenic lifecycle with benthic polyps was highlighted in the bloom definition. Biomass is accumulated in the benthic stages of these organisms, and the release of planktonic larvae can increase populations faster than would be expected based on the existing planktonic population (Purcell et al., 2007). This benthic dependency is also observed in many of the less gelatinous taxa. However, the influence of benthic stages seem unlikely to be the primary cause of greater variation in abundance, as the average coefficient of variation of gelatinous taxa with benthic stages and without benthic stages was very similar (1.75 and 1.80 respectively). If the relationship between coefficient of variation and carbon percentage was driven by recruitment from the benthic stages of gelatinous zooplankton then a negative relationship between increase rate and carbon percentage would be expected; this is not observed.

5.4.2 - Temporal heterogeneity

5.4.2.1 – Are the temporal heterogeneity based bloom indices effective?

The indices used to investigate temporal heterogeneity were the *number of non-zero records* and the *frequency distribution coefficient*. For both indices, O. similis had higher values than *P. pileus*, as predicted. These indices are useful tools for comparing different species as they do not require the same amount of data as the others. It is possible to compare taxa with less than one year of data, and generate a more meaningful index than some of the others presented. However, these indices are potentially less effective than the others for use with rare species. For instance, the *number of non-zero records* in a taxon could be low as a result of only encountering that taxa during a short bloom. Alternatively, a low number of non-zero records could indicate that as a result of rarity, the species was recorded relatively few times over the course of the sampling period. This drawback, while lessened by normalisation, is also present in the *frequency distribution coefficient*. For this reason, I recommend that these indices are only used with relatively abundant taxa.

5.4.2.2 – Discussing the relationship between carbon percentage and temporal heterogeneity

There was a strong positive relationship between carbon percentage and number of non-zero records; taxa with higher carbon percentage were recorded more frequently. However, this index tends to be heavily skewed in species that form aggregations, as the probability of recording a specific taxon is affected by their distribution. To remedy this the frequency distribution analysis was also performed, with similar results. The frequency distribution of more gelatinous taxa tended to be steeper, implying the abundance of these species was concentrated into shorter periods, seen as spikes in the abundance profiles. This finding follows the predicted pattern, as gelatinous species are normally considered to be ephemeral (at least in their medusa phase) and exploit temporally and spatially patchy good conditions (Lucas and Dawson, 2014). For instance, many cnidarians and ctenophores have a generalist diet, allowing them to survive in a range of environments where food is both patchy and not diverse (Richardson et al., 2009). This contrasts

with several copepod taxa such as *Calanus helgolandicus* and *Oithona spp.*, which are noted for their relatively consistent abundance (and therefore shallow frequency distribution) throughout the year (Maud et al., 2015; Atkinson et al., 2015).

5.4.3 - Population increase rate

5.4.3.1 – Are the population increase based bloom indices effective?

Generating estimates of population increase rate using time series data is difficult because increases in recorded abundance are not necessarily representative of increases in abundance, it could be due to patchiness or active aggregation. The two indices used for population increase were the *interval between the 25th and 50th cumulative percentiles* and the *increase rate index*. The *interval* was shorter for *P. pileus* than *O. similis* as predicted. This was due to the abundance of *P. pileus* being concentrated into a shorter period than *O. similis.* The index was effective in these two taxa however it is highly sensitive to the annual total abundance, and for that reason this index should not be used with very rare taxa.

The increase rate index was devised as a way to estimate increase rate without being as sensitive to patchiness. The increase rate of *P. pileus* was expected to be higher than that of *O. similis*, with the difference increasing with the number of successive increases investigated. This was observed in the data, suggesting that this index may be an effective way of comparing relative abundance increase. There are however still potential issues with this method, such as consistent advection into sample area. This index is also highly sensitive to starting abundance, as it is based on the ratio between starting and finishing abundances, not the number of individuals increased per time point. Finally, this approach is somewhat reliant on a good time series, as the more reliable three and four successive increase indices need consistent present records, and several sets of successive increase are required to form reasonable comparisons.

5.4.3.2 – Discussing the relationship between carbon percentage and increase rate

One of the identified prerequisites for bloom formation was rapid increase in population (section 5.2.5). Therefore, if bloom-like dynamics are observed in gelatinous zooplankton but no other taxa then we might expect there to a negative relationship between carbon percentage and increase rate. While carbon mass was observed to have a strong negative effect on increase rate (Fig 5.9) consistent with higher growth rates and shorter generation times of smaller animals (Pianka, 1970), there was no relationship found between increase rate and carbon percentage. The highest population increase rates were observed in taxa with high reproductive outputs that did not reproduce sexually as planktonic adults e.g. the planktonic protist, *Noctiluca scintillans*. The cladocerans, *Evadne spp.* and *Podon spp*., were also within the top 5% of maximum population increase rates. These taxa are also capable of asexual reproduction through parthenogenesis (Mullin and Onbe, 1992; Kim and Onbe, 1989), and therefore are expected to have massive population increase potential relative to other metazoans. The other taxa that had high increase rates were meroplanktonic taxa, especially rhizocephalan nauplii. This is a result of these larvae being generated and released from adults on the seabed, and therefore not relying solely on the planktonic population to increase abundance. The only taxon that was holoplanktonic and was within the top 10 increase rates observed was Appendicularia, most likely *Oikopleura dioica*, known to have short generations times (Hopcroft and Roff, 1995) and extremely efficient feeding (King and Azam, 1980). Overall, increase rate appeared to be more a function of reproductive strategy, for example pulsed reproduction from the seabed controlling planktonic population increases, rather than carbon percentage.

5.4.4 – Are taxa with higher carbon percentages also blooming?

Taxa that are more gelatinous may be more variable in abundance and have shorter periods of significant presence in the zooplankton, but there was no evidence that these had a faster rate of population increase. Based on these observations, are taxa with lower carbon

percentage blooming at the L4 site, and would other zooplankton also be considered to be forming blooms?

Figure 5.6 shows that, relative to *Calanus helgolandicus*, *Pleurobrachia pileus* could be considered a blooming species. This is reflected in the values of the blooming indices, *P. pileus* has a steeper frequency distribution, higher coefficient of variation, higher interannual variability and higher maximum increase rate than *Calanus helgolandicus* (Appendix III).

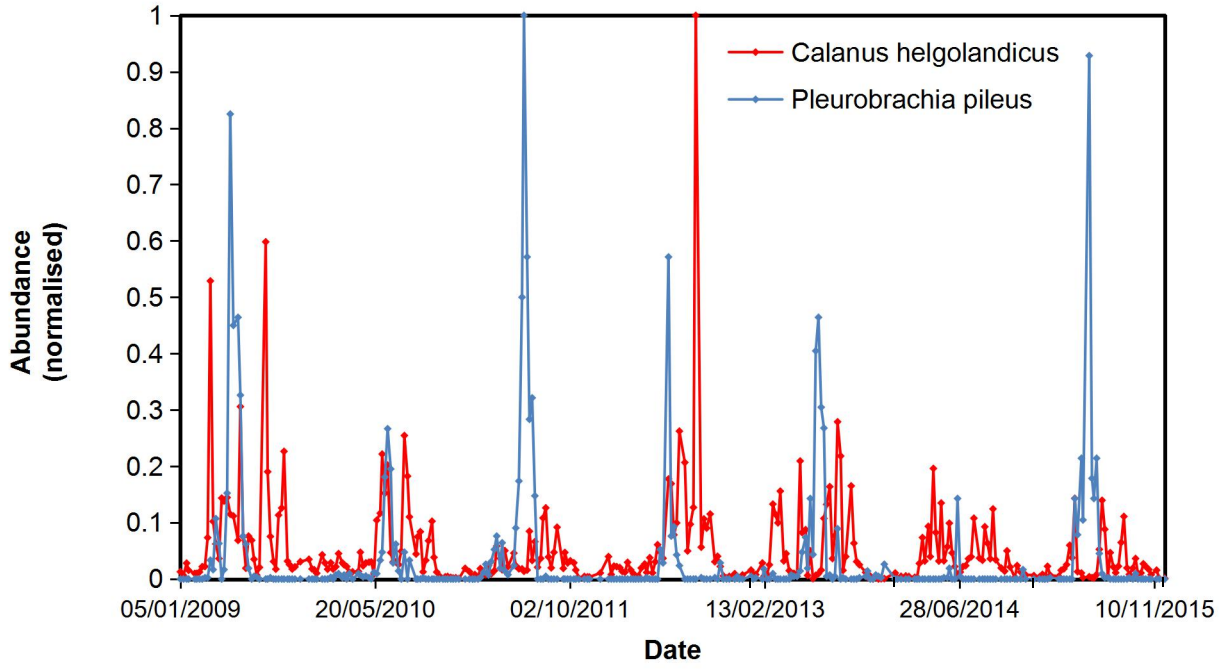


Figure 5.6 – *Three-point running mean abundance of* Calanus helgolandicus *and* Pleurobrachia pileus *at the L4 site between 05/01/2009 and 15/12/2015, normalised to the maximum abundance for each species.*

However, if *P. pileus* is compared to another calanoid copepod, *Temora longicornis*, we find that *T. longicornis* has a shallower frequency distribution (i.e. less temporally patchy) but has double the maximum increase rate. Does having a higher maximum increase rate than *P. pileus* qualify *T. longicornis* as a blooming species? Alternatively, is it not to be classified as forming a bloom as the abundance is more homogenously distributed through the year?

In Figure 5.7, *Temora longicornis* is compared to a siphonophore classically considered to form blooms, *Muggiaea atlantica* (Blackett et al., 2015). It is clear that these species have similar population dynamics, despite being at opposite ends of the carbon percentage spectrum. These examples demonstrate that the qualities I have defined as being associated with blooming do not always co-occur, and make generalisations difficult. Is it the variability in abundance, temporal patchiness, high population growth potential or all of these that define a species as “blooming”?

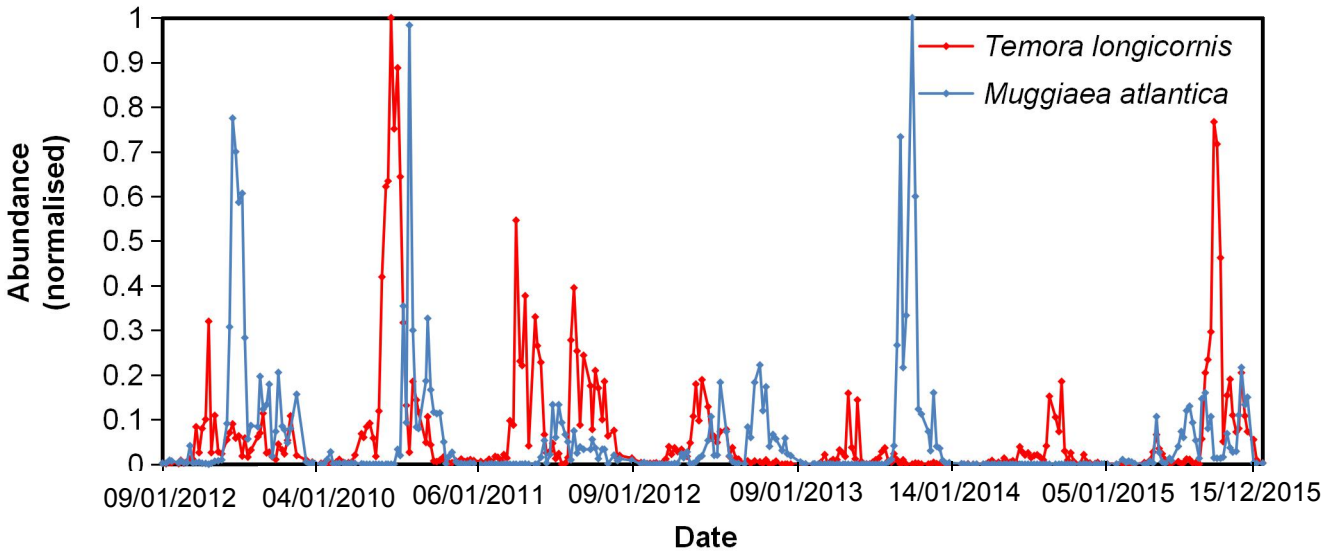


Figure 5.7 - *Three-point* running mean abundance of Temora longicornis and Muggiaea atlantica at the L4 site between 05/01/2009 and 15/12/2015, normalised to the maximum abundance for each species.

Based on these comparisons, it is unclear what demarks “blooms” of gelatinous zooplankton from transient high populations of non-gelatinous taxa. It is clear, however, that low carbon percentage is not a requirement for rapid increases in population. So why are blooms prevalent across such a diverse range of organisms?

The most significant relationship between carbon percentage and a bloom index was with temporal heterogeneity. The abundance of more gelatinous taxa was concentrated into shorter periods during the year. Conversely, the abundance of higher carbon percentage taxa was more

equally distributed through the year, and therefore may be expected to have lower biomass maxima. In fact, when ranked according to maximum estimated carbon biomass, the highest ranking taxa were copepods or other crustaceans (Figure 5.8).

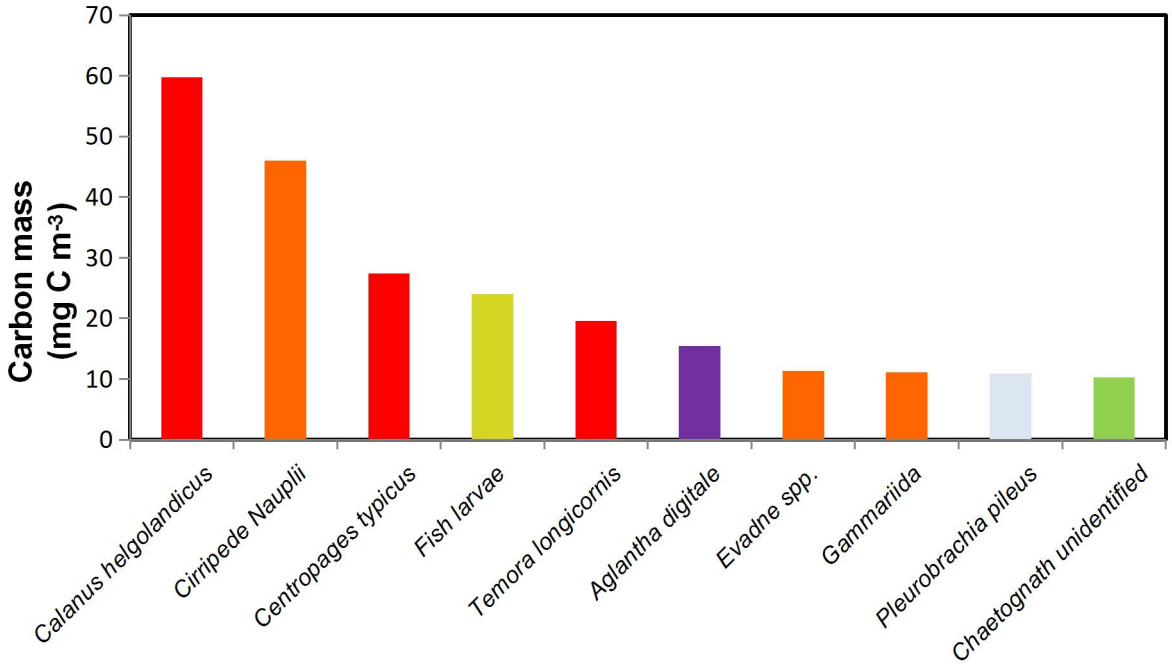


Figure 5.8 – *Ranked maximum recorded carbon biomasses (highest weekly value, mg C m^{-3}) for zooplankton taxa at L4 between 2009 and 2015. This plot excludes* Beroe spp.*, due to fragmentation and uncertainty over linear dimensions, precluding a robust biomass estimate.*

Despite the more sporadic nature of the gelatinous taxa, crustaceans had the highest maximum taxon-specific carbon biomass. However, if the species are ranked in terms of maximum wet mass, 9 of the highest 10 are gelatinous taxa (the other is cirripede nauplii), with the highest recorded wet mass in *Pleurobrachia pileus*. Despite the maximum carbon biomass of *P. pileus* being only 16% than that of *C. helgolandicus*, the maximum recorded wet biomass of *P. pileus* was still 18 times greater (Figure 5.9). This highlights the importance of considering both the carbon and wet masses of zooplankton, as these two measures of body size offer different stories regarding the relative importance of taxa at L4.

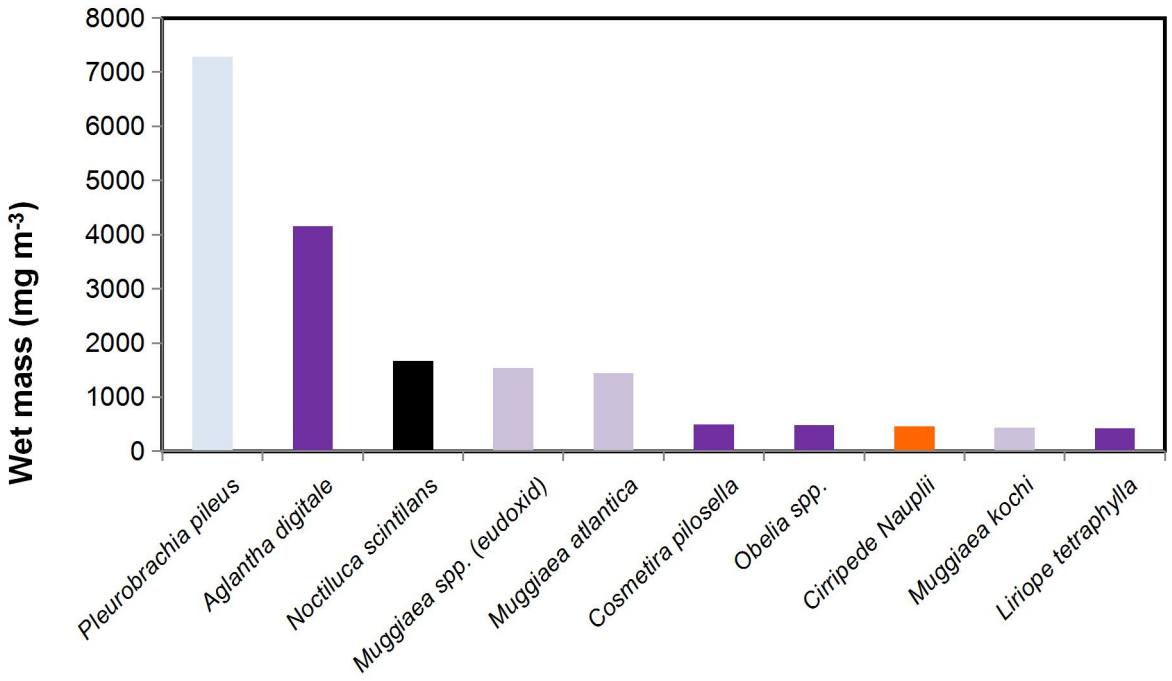


Figure 5.9 – *Ranked maximum recorded wet biomasses (highest weekly value, mg C m-3) for zooplankton taxa at L4 between 2009 and 2015.*

This comparison suggests an alternative hypothesis as to why blooming is described as such a characteristic feature across the gelatinous zooplankton. When a gelatinous species reaches moderate carbon biomass, they occupy a comparatively high volume as a result of their low carbon percentage. They are more noticeable than the same carbon mass of a more concentrated taxon such as copepods simply because they are large and take up more space (Figure 5.10).

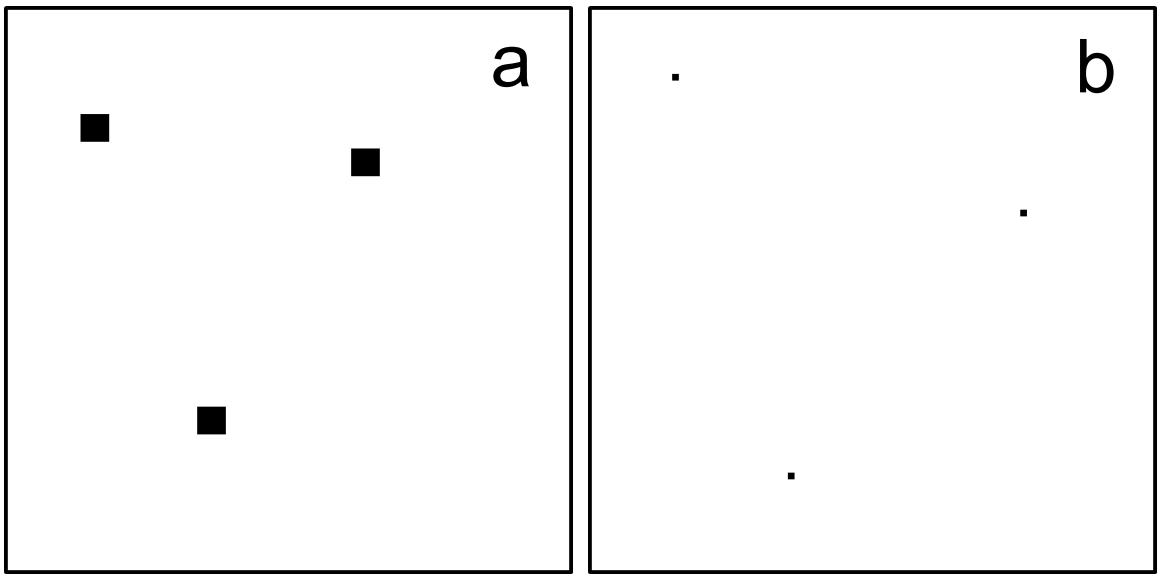


Figure 5.10 – *Two dimensional representation of one litre of sea water showing the volume occupied by a –* Pleurobrachia pileus *and b –* Calanus helgolandicus *during their respective wet biomass maxima shown in Figure 5.8. Despite the greater visibility of the* Pleurobrachia pileus*, the corresponding carbon mass of* Calanus helgolandicus *in panel b is six times greater than that of* Pleurobrachia pileus *in panel a.*

This form of visual sampling bias is amplified by physical aggregation in coastal areas. The UK media declared 2015 the “year of the jelly” as a result of mass strandings (especially of the large rhizostomid, *Rhizostoma octopus*) around the country (BBC News, 2015). These media reports were supported by ecological surveys in the south west of England (Hiscock and Earll, 2015). However, despite the relatively high reported populations, 2015 was unremarkable with respect to gelatinous populations at L4. The sampling regime at L4 is not designed to catch large gelatinous taxa however during this period additional zooplankton sampling was performed as part of the Marine Ecosystems Research Program (Hiscock and Earll, 2015). This sampling involved using a $1m^2$ net to sample a total of $55{,}000m^3$ of seawater across day and night cycles, throughout the year. Large gelatinous zooplankton were observed in inshore areas however very few were caught across the entire sampling period (1 adult *Chrysaora hysoscella*), despite the sampling closely adhering to established guidelines for catching these taxa (Raskoff, 2003). This demonstrates the stipulation made by Lucas and Dawson (2014) in the first definition given, that

not all high populations represent true blooms. It is also worth noting that most gelatinous taxa are not large, and that many small gelatinous do not form blooms following their definition.

This discussion is not intended to trivialise blooms, as the ecological and biogeochemical implications of bloom events are clearly significant. This discussion intends instead to address the extent to which low carbon percentage drives our interpretation of jellyfish blooms. When we encounter a jellyfish bloom it is often interpreted as an extraordinary concentration of biomass of a particular organism, but interpreting a bloom as a normal concentration of an extraordinary animal may be more appropriate.

CHAPTER 6 – Body size as a function of carbon mass and carbon percentage

6.1 - Introduction

Despite body size influencing all aspects of an organism's biology, it is an ambiguous term. Body size refers not to a single quality but to a range of variables that are related to different aspects of the physiology and ecology an organism. As a result of this, for information on the body size of an organism to be informative, it must be an appropriate measure for the question being investigated. For instance, when relating metabolic rate to body size, carbon or nitrogen mass is often most appropriate and the latter has been used widely (Brown et al., 2005, Kiorboe and Hirst, 2014). For investigating trends in metabolism, if we instead choose length as our measure of body size, we would find that organisms with highly elongated bodies might skew the relationship. We might expect the 40m long (but 3cm wide) siphonophore, *Praya dubia* to have a higher metabolic rate than that of a 25m long blue whale, despite the whale being many times greater in mass. Conversely, when considering whether a prey item is capable of being eaten by a gape-limited predator, length along the longest dimension will be of paramount importance, especially for taxa with long spines such as *Porcellana platycheles* larvae.

If all organisms were the same shape and composition then different measures would not be so necessary, however massive variation exists both inter and intraspecifically. While the variability between carbon mass and length as a result of shape change is readily accepted and even applied (Hirst et al., 2014), the variability between carbon mass and wet mass observed in zooplankton has not been considered in detail. This variability was summarised in the negative relationship between carbon mass and carbon percentage presented in chapter 3, and is explored in greater detail below.

As carbon mass and carbon percentage have different effects on organismal biology, investigating how taxa are distributed in this trait space might help to shed light on how the body size of plankton influences their biology and evolution. The aim of this chapter is to investigate the

form and implications of the relationship between carbon mass and carbon percentage through the following objectives;

- Determine the relationship between carbon mass and carbon percentage using the meta-analysis and L4 datasets.
- Investigate the spread around this relationship, focussing on the areas of trait space that are not populated with taxa.
- Discuss other taxa that are not gelatinous but show analogous decoupling between metabolic and ecological body size (i.e. pseudo-gelatinous taxa)
- Investigate how biomass is distributed in this trait space in a real assemblage using the L4 dataset

6.2 - What is the relationship between carbon percentage and carbon mass, and why is it important?

In Chapter 3, I found a negative relationship between carbon mass and carbon percentage (Figure 3.4). The only other study that has investigated this relationship is by Molina-Ramirez et al. (2015) exploring the relationship between carbon mass and wet mass of a range highly gelatinous taxa (cnidarians, ctenophores, salps and doliolids). These authors separated the taxa on the basis of feeding mode; carbon percentage decreased with increasing carbon mass in filter feeders (salps and doliolids), while in carnivores (cnidarians and ctenophores) carbon percentage was constant. The results in Chapter 3 followed the pattern of decreasing carbon percentage observed for the salps and doliolids in the study by Molina-Ramirez et al. (2015). However, in my study, carbon percentage decreased with increasing carbon mass across all taxa, regardless of feeding mode. This difference could be the result of including the full range of zooplankton in Chapter 3, in contrast to just highly gelatinous taxa in the study by Molina- Ramirez et al. (2015).

In the study by Molina-Ramirez et al. (2015), the linear relationships between carbon mass and wet mass were used to derive single values of carbon percentage for ctenophores (0.23% ±

0.14%) and cnidarians (1.77% ± 2.44%). In the meta-analysis presented in Chapter 3, carbon percentage within the cnidarians alone ranged from 0.02 and 2.22%, corresponding to a 110-fold difference in wet mass at equivalent carbon mass. While attributing a single value to a wide range of species can provide some simplification, it could lead to large errors. For instance, the range of carbon percentage seen in the cnidarians alone in Chapter 2 could correspond to a doubling in growth rate at the same carbon mass.

In the study by Molina-Ramirez et al. (2015), whether carbon percentage decreased with increasing carbon mass across species was dependent on feeding mode. Carnivores (defined as cnidarians and ctenophores) were found to have a fixed carbon percentage of 1.77% ± 2.44% at all carbon masses. Chapter 4 investigated the carbon percentage of *Aurelia aurita* throughout early development. On the basis of the findings of Molina-Ramirez et al. (2015) the carbon percentage of *Aurelia aurita* should not vary with carbon mass as it is a carnivore. However in chapter 3, it was observed that *Aurelia aurita* ephyrae diluted carbon centrations from 2.3% to 0.1% through ontogeny. This could be a result of Chapter 4 investigating intraspecific variability and the previous study by Molina Ramirez et al. (2015), interspecific variability. However, if the feeding mode hypothesis advanced by Molina-Ramirez et al. (2015) is correct then it should not matter whether the variation in carbon mass is interspecific or intraspecific. An alternative cause could be that the studies are investigating different scales, Chapter 4 investigated between 0.01 and 0.2 mg C in contrast to the range of between 0.01 and 100000 mg C in Molina Ramirez et al. (2015). Leaving aside contrasts with previous studies, Chapter 4 is the first investigation of how the carbon and wet masses interact to determine feeding and growth during development.

6.3 - Carbon percentage – carbon mass trait space

Figure 6.1 shows the relationship between carbon mass and carbon percentage and demonstrates the distribution of species in this trait space. Inspection of this figure shows that there are areas of trait space which appear to be without species. Throughout the thesis I have

discussed the potential benefits of viewing carbon percentage as a continuous trait. In this plot there is an interval between those taxa classically considered gelatinous and those not. However, this junction constitutes a tiny fraction of the range, between *Clione limacina* (2.49%) and *Sagitta spp.* (3.54%). Other open areas of the figure could either represent gaps in available data or indicate potential limits or boundaries in the trait space.

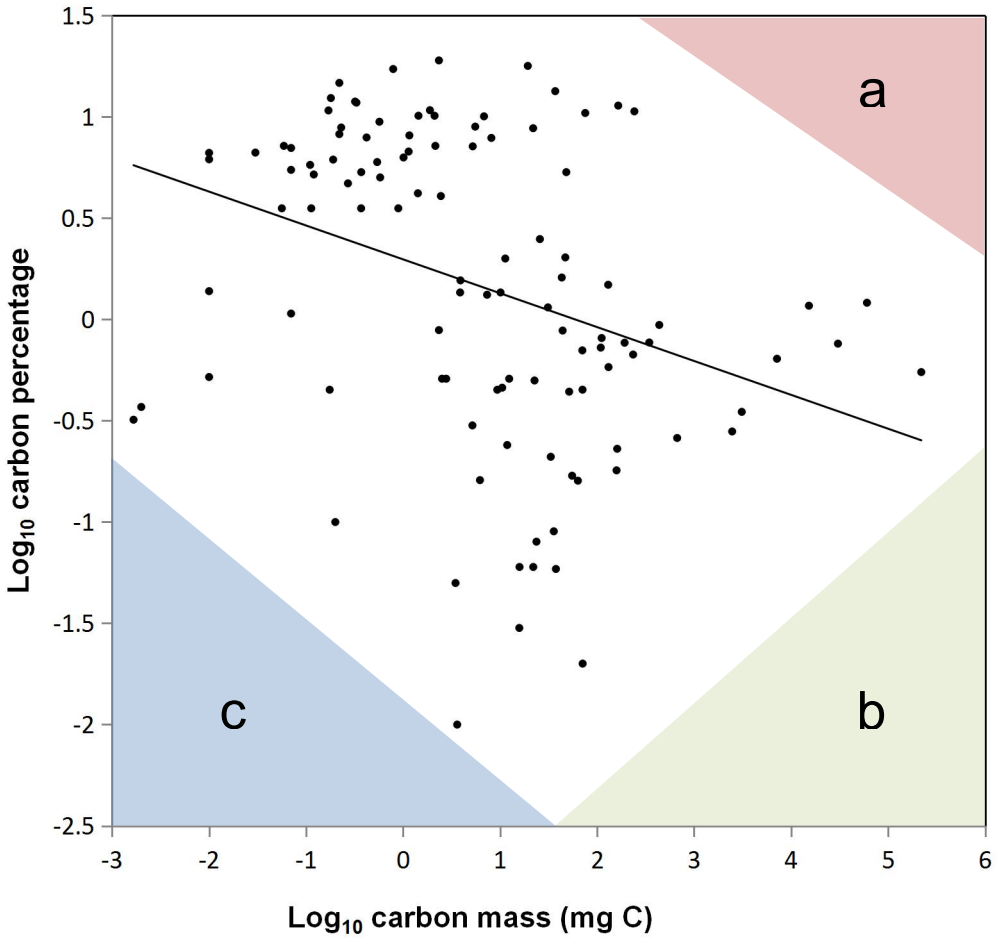


Figure 6.1 – *"Trait-space" plot showing Log_{10} carbon percentage of zooplankton ((carbon mass / wet mass)*100) as a function of log_{10} carbon mass (mg) as compiled from literature sources (see Appendix I), df = 106, p = 0.0003, R^2 = 0.12, log_{10} carbon percentage = 0.30 – 0.1672 log_{10} carbon mass. Vacant areas of trait space (colour shaded areas a,b,c) are described in the text below.*

6.3.1 - Area a: high carbon mass and high carbon percentage

The first area of empty trait space highlighted in Figure 6.1 (region *a* marked in red) indicates an absence of data for taxa with more than 5% carbon that exceed ~250 mg carbon. This maximum carbon mass is seen in adult *Euphausia superba* (approximately 65 mm maximum length: Atkinson et al., 2006), that are one of the largest epipelagic crustaceans. There are clearly pelagic, carbon-rich taxa with higher carbon masses, from fish to whales, but this body mass very roughly marks the transition from crustaceans to these nektonic life forms. This could be a result of the scope for growth scaling discussed above but there are alternative hypotheses, in particular buoyancy and oxygen requirement (Alexander, 1990; Verberk and Atkinson, 2013).

Large, high carbon percentage animals require supplementary methods to regulate buoyancy, such as constant swimming in krill (Kils, 1981). These methods, whether based on motion or regulation of a swim bladder carry an associated cost that could further favour the scope for growth of more gelatinous taxa at high carbon masses. In the case of highly gelatinous taxa, a much greater percentage of the body is sea water, and therefore the energetic cost of buoyancy regulation (sometimes through the exclusion of sulphate ions, Bidigare and Biggs, 1980) at a given body size is likely to be much lower than that of a high carbon percentage organism.

Oxygen transfer is another factor that could restrict the evolution of large, high carbon percentage zooplankton. Respiration rate is a function of carbon mass, so the respiratory requirement of high carbon mass animals is high (despite carbon specific respiration rate typically decreasing with increasing carbon mass (Kleiber, 1932; Brown et al. 2004; Glazier, 2006)). To be larger, organisms have had to develop means to increases the rate of oxygen transfer to meet the increased total respiratory requirement associated with large body size. All of these methods, including convolution of the body surface or a full respiratory systems increase the rate of oxygen transfer to exceed the rate that would be possible through passive diffusion across the body surface alone. The methods used to facilitate oxygen transfer depend on the taxon, however using

a simple geometric model it is possible to model the effect of variation in carbon percentage on tissue oxygen availability in a similar manner to feeding rate. Oxygen transfer is a function of surface area which is dependent on wet mass. Therefore, an organism with a lower carbon percentage will have a higher surface area to carbon mass ratio than a geometrically similar organism with higher carbon percentage. This suggests that decreasing carbon percentage increases carbon specific oxygen availability, potentially alleviating an oxygen limitation boundary. This is a considerable oversimplification, as organisms rarely grow isometrically (with considerable implication to metabolic scaling (Glazier et al., 2015)) and not all organisms are identical in shape. Furthermore, the most gelatinous taxa (cnidarians and ctenophores) maintain low core body oxygen percentage, such that diffusion gradients into the surface tissues are greater, and oxygen transfers through the tissues at a greater rate (Thuesen et al., 2005).

Irrespective of how carbon percentage affects respiratory requirements, the resilience of low carbon percentage taxa to hypoxia is well documented (Purcell et al., 2001; Decker et al., 2004; Thuesen et al., 2005; Elliot et al., 2012). Even allowing for morphological differences, it is clear that reduced carbon percentage has the potential to reduce the effects of oxygen limitation in both the context of hypoxic environments and determining maximum body size.

6.3.2 - Area b: high carbon mass and low carbon percentage

The organisms with the highest carbon masses are between 1.2% and 0.28% carbon, not at the minimum carbon percentage of approximately 0.05%, thus leaving area *b* blank (Figure 6.1, region b marked in green). It is possible that taxa that have lower carbon percentage cannot have carbon masses this high due to their physical fragility. While I cannot present conclusive data, taxa with lower carbon percentage tend to have particularly diaphanous bodies even for gelatinous taxa. Among the least gelatinous scyphomedusae are the rhizostomids with carbon percentage of up to 1.21%. These taxa are well known for their comparative rigidity, supporting their shape outside of

water, sporting common names such as the cannonball jellyfish and forming the basis of jellyfish fisheries (Brotz et al., 2016). In contrast, the lowest carbon percentages are observed in the lobate ctenophores, in particular the mesopelagic *Bathycyroe fosteri*. The bodies of these taxa are very fragile and readily fragment under minor physical stress (pers. obs.). However, large lobate ctenophores do exist, such as *Leucothea pulchra* (Matsumoto, 1988), capable of reaching lengths of 25 cm. This could suggest that the gap in the trait space may be in part due to inadequate sampling techniques for large, highly gelatinous taxa. The use of methods that involve minimal changes in water pressure or physical disturbance, such as those used with remotely operated vehicles might help to populate this area of trait space.

6.3.3 - Area c: low carbon mass and low carbon percentage

Finally, the lower left quadrant (Figure 6.1, region c in blue) is sparsely populated, indicating that there are relatively few taxa with both very low carbon percentage and carbon masses. This could indicate a lower limit, such that for a given carbon mass there is a minimum possible carbon percentage. In Chapter 3 we saw that ephyrae dilute from 2.3% carbon to 0.1% as they increase from 0.01 mg C to 0.17 mg, fitting within this potential boundary. This absence of taxa could also represent a potential sampling bias caused by the use of nets, or inappropriate mesh sizes (Raskoff et al., 2003). Several studies using a range of in-situ, visual sampling techniques have demonstrated the serial underestimation of small gelatinous taxa caused by net sampling (Luo et al., 2014; Cross et al., 2015)

6.4 - Pseudo gelatinous taxa

Data for pseudo gelatinous taxa seem to counter the trends documented in this thesis. Pseudo gelatinous taxa are defined here as any organism that artificially increases its effective body volume without directly increasing the wet mass of the body. There is a range of such organisms in the plankton, in particular appendicularians and thecosome pteropods. Both groups (from different phyla) use external mucosal structures for feeding, increasing their feeding potential.

A terrestrial analogue is the use of web by a spider to catch food. In all instances the animals increase their effective influence on the environment without increasing their carbon mass and therefore respiratory requirements. However, the creation and processing of these external structures is likely costly, contrasting with the seemingly low cost of reducing carbon percentage.

A conceptual difficulty here lies in what is defined as the carbon and wet masses of the organism. An appendicularian is wholly dependent on the mucosal house for feeding so completely excluding the house from measurements of mass is not representative of the organism as whole. However, the house is not attached to the animal and is not living. Likewise, it seems incorrect to calculate carbon specific feeding rate including the carbon that makes up the house, as it is not metabolically active. This is analogous to issues over whether to include storage lipid in estimates of carbon specific metabolic rate (Vidal and Whitledge, 1982). However if wet mass specific feeding rate is calculated on the basis of the animal alone, the result will be anomalous and not reflect the trophic strategy or morphology of the animal. This difficulty was also highlighted in a further contrast between this thesis and the study of Molina Ramirez et al. (2015). In their study, cnidarians included the cystonect siphonophore *Physalia physalis* and the chondrophore *Velella velella*. While these taxa belong to different groups in the Phylum Cnidaria, they are functionally united by the presence of a rigid float (similar to cartilage) that maintains their position in the neuston. This float is largely metabolic inactive (Larimer and Ashby, 1962) and is not involved in prey capture, therefore including the metabolically inactive float in calculations of carbon mass of the animal is analogous to examples described above. If we include the float in our estimate of carbon mass and make the implicit assumption that carbon mass is indicative of the amount of metabolically active tissue, then we could run into errors. This also explains why *Physalia physalis* had a carbon percentage that was significantly greater than that of any other cnidarian (9.02%, Molina-Ramirez et al., 2015). There are examples where including and excluding both internal and external structures can be unrepresentative of carbon or wet mass, so a more subtle form of definition may be needed. One example could be the separation between structure and reserve advanced by the dynamic energy budget model (Kooijman, 2010; Sousa et al., 2010). While for

many organisms, whole body measurements of carbon and wet mass will be most appropriate, the exceptions will often demonstrate interesting evolutionary strategies such as those detailed above.

6.5 - Carbon mass and carbon percentage at the L4 study site

The figure and discussion above indicate the potential trait space of carbon mass and carbon percentage. Therefore, it could be instructive to compare how this potential trait space corresponds to a real assemblage. For this, individual carbon mass, carbon percentage and taxon biomass were calculated for each taxon at the L4 sampling site (Figure 6.2).

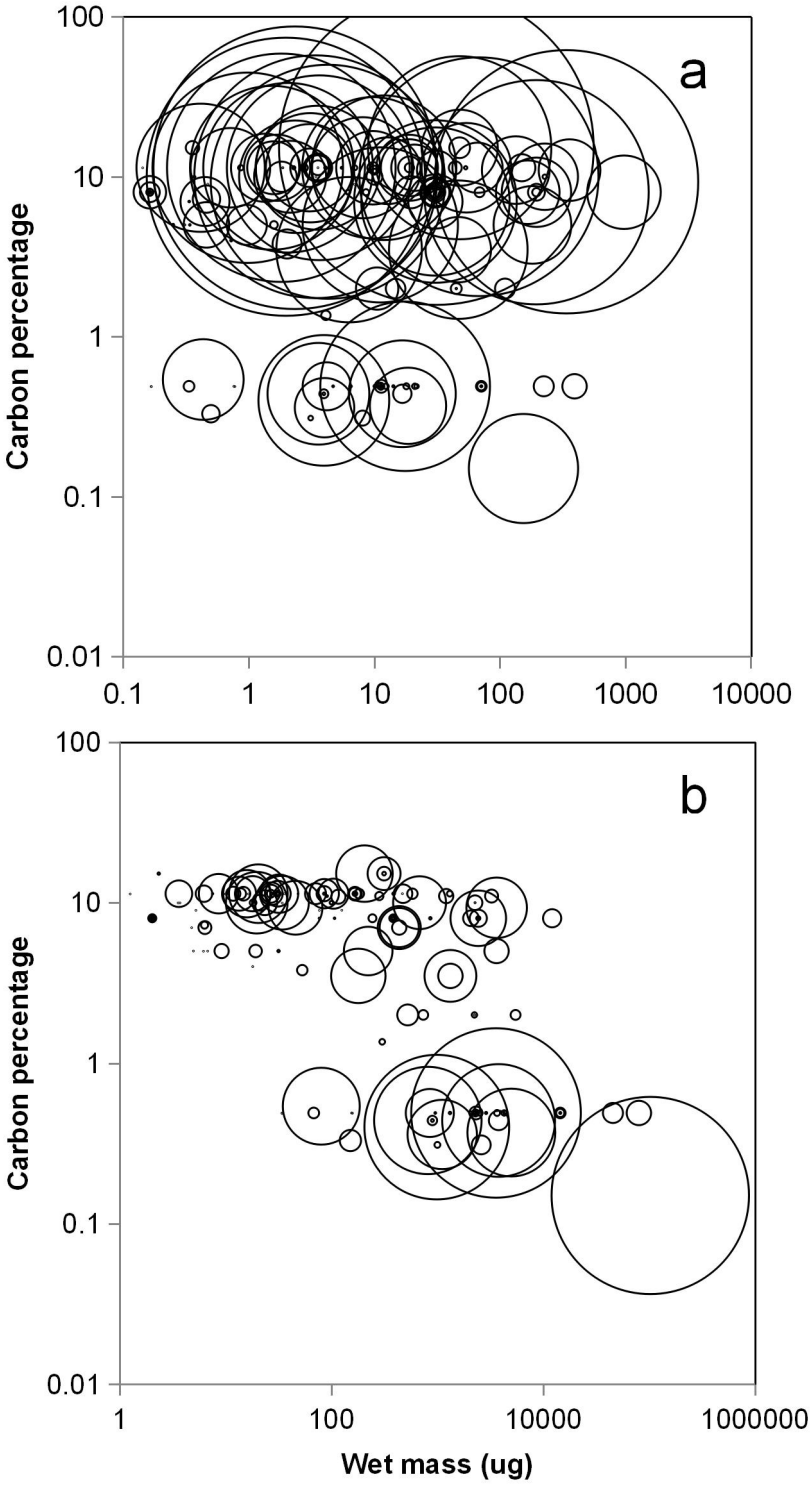

a
b
Carbon percentage
Carbon percentage
Wet mass (ug)
100
10
1
0.1
0.01
0.1
1
10
100
1000
10000
1
100
10000
1000000

Figure 6.2 – *Distribution of mean zooplankton biomass across axes of log_{10} carbon percentage and log_{10} individual carbon mass (a) or log_{10} individual wet mass (b) at the L4 sampling site between 1988 and 2016. Mean biomass (mg C m^{-3} for panel a and mg WM m^{-3} for panel b) for each species was obtained by averaging across all sampling time points. Larger bubbles indicate higher mean taxon biomass. Carbon masses were measured and carbon percentages were assigned as described in Chapter 5.*

Firstly, the trait distribution at L4 follows that defined in Figure 3.4 with carbon mass increasing with decreasing carbon percentage. The majority of the carbon mass at L4 is found between 6.4 and 12.6% carbon, including the majority of the calanoid copepods. Within this carbon percentage range, between 1 and 10 µg C is particularly biomass laden, including *Acartia clausi*, *Centropages spp* and *Para/Clauso/Cteno/Pseudocalanus.*

The distribution of mean wet mass across a trait space of wet mass and carbon percentage is shown in Figure 6.2b. *Beroe* spp. were omitted due to potential identification and recording issues. This distribution differs from that of Figure 6.2a, with mean wet mass more evenly distributed across the range. There is less biomass in the intermediate gelatinous range (0.8% < x < 6.4%) despite this range including ecologically important taxa such as chaetognaths. Greater mean wet mass is observed towards to the more gelatinous end of the spectrum, as moderate carbon masses in this area correspond to disproportionately high wet masses. The greatest mean carbon mass was found in an intermediate carbon mass bracket (<10 mg C), but the greatest mean wet mass was found in the maximum wet mass bracket (>100000 mg WM). This suggests that when gelatinous taxa dominate in wet mass terms it is because of relatively fewer larger individuals, rather than many small individuals. When the community is assessed in carbon mass terms (6.2a) the crustacean taxa are dominant but in wet mass terms (6.2b) the more gelatinous taxa are more significant, following the pattern seen in Chapter 5. The direct effect of carbon

percentage on feeding and growth rates and the radical difference between zooplankton assemblages viewed from carbon and wet mass terms highlights the importance of carbon percentage to understanding plankton biology.

6.6 - Conclusion

This chapter has demonstrated that the relationship between carbon mass and carbon percentage can suggest how different constraints shape zooplanktonic taxa. A whole range of different parameters can influence the size of organisms, including buoyancy and oxygen availability. The adoption of a more gelatinous body may increase the maximum carbon mass possible for an organism to live a planktonic lifestyle. More gelatinous taxa are closer to seawater in density and therefore potentially expend less energy on buoyancy regulation than denser organisms. Similarly, organisms with a more gelatinous body will have lower respiratory demands at the same wet mass, potentially allowing them to survive areas of lower oxygen concentration. While these examples are tied specifically to the environment experienced by zooplankton, the variability seen here has wider analogous significance. More generally, variation in the relationship between carbon and wet mass represents a decoupling between metabolic and physiological body size. This decoupling occurs in a wide variety of organisms from all environments, including spiders. When the decoupling between metabolic and physiological body size is appreciated, ecosystems can be viewed through either lens, highlighting the importance of using the appropriate index of body size for the question being investigated.

CHAPTER 7 – Concluding discussion

7.1 - Introduction

This thesis has examined the merit of using carbon percentage as a trait for understanding different aspects of zooplankton biology, over a range of scales and using different approaches involving experiments, time series analysis and meta-analysis. This chapter begins by summarising the results of Chapters 2, 3 and 4 to detail our current understanding of how carbon percentage affects vital rates. From there the population level implications of carbon percentage are discussed, alongside how the trait can be integrated into ecological models. Finally, an example from the L4 time series will be used to demonstrate how carbon percentage can be used as an ecological indicator in further work.

7.2 - Carbon percentage as a predictor variable for biological rates

To establish any relationships between carbon percentage and biological rates, I first needed to determine whether treating carbon percentage as a continuous variable reflects this trait in natural systems. This was investigated in Chapter 3 by plotting the carbon percentage of a wide range of zooplankton species. The distribution of species across this spectrum was not homogenous but was sufficient to allow carbon percentage to be treated as a continuous variable, and so carbon percentage was used as a predictor variable throughout the thesis. While a central gap between thaliaceans and chaetognaths did exist (Kiørboe, 2013), this gap was small compared to the full range, or even the variability within the Cnidaria alone. This variation is significant as the range of carbon percentage within classical gelatinous taxa alone (cnidarians, ctenophores and tunicates) was sufficient to have on effect on growth rate (Figure 3.5).

The key processes that determine organismal energy budgets are respiration, feeding, assimilation and growth. As described in the introduction, Acuña et al. (2011) demonstrated that respiration was dependent on carbon mass, and therefore is not directly affected by carbon

percentage. As a result, this thesis has focussed at an organismal level on feeding and growth rates.

7.2.1 - Feeding rates

Feeding was investigated in Chapter 4 by incubating *Aurelia aurita* ephyrae in saturating concentrations of *Artemia* nauplii. Ingestion rate was related to bell diameter, potentially as a result of prey capture being focussed on the lappet tips (Sullivan et al., 1997). As the ephyrae increased in carbon mass they decreased in carbon percentage. In the model, this dilution increased diameter, and therefore increase in feeding rate over time, faster than would have been possible if the ephyrae did not dilute during development. The increase in diameter associated with the dilution was equivalent to a 28% increase in feeding rate at the same carbon mass (Chapter 4).

Only a single species was investigated in Chapter 4, so the effect of carbon percentage on feeding across different species might be different. The effect of carbon percentage on feeding rate across zooplankton species was not directly investigated although inferences can be made using the results of Chapter 4. Specific feeding methods tend to decrease in efficiency with increasing body volume (Kiørboe, 2011). This suggests that wet mass- specific feeding rate will tend to decrease with the increasing wet mass, whether the mass was produced maintaining the same carbon percentage or by dilution. Therefore, carbon percentage will have no effect on wet mass specific feeding rate.

However, the situation is reversed for carbon mass. If an organism increases in wet mass by dilution while keeping carbon mass constant, it will experience a higher carbon specific feeding rate than an organism that does not exhibit this increase. This is a result of the organism increasing in wet mass (and therefore feeding rate) without increasing in carbon mass, leading to a greater amount of food per unit carbon of the organism. A higher carbon-specific feeding rate

means a greater scope for growth, potentially increasing fitness. Scope for growth is an estimate of metabolic profit, calculated as carbon ingested minus respiratory costs. As ingestion rate is function of wet mass and respiration rate is a function of carbon mass, scope for growth will be highly dependent on the interaction of carbon and wet mass, here expressed as carbon percentage.

7.2.2 - Growth rates

The effect of carbon percentage on growth rate was investigated across species in Chapter 3 and within a single species in Chapter 4. The effect of carbon percentage on intraspecific growth rate was unclear (Chapter 4). As carbon mass and carbon percentage were highly correlated it was not possible to distinguish between the effects of these two variables. It was observed that the wet mass scaling exponent for growth in the ephyrae in Chapter 3 (b = 0.62) was lower than that of many crustacean zooplankton based on intraspecific studies (b = 1, Hirst and Forster, 2013), so it is possible the process of dilution has an associated cost.

The effect of carbon percentage on growth rate between species was more pronounced than within species (Chapter 3). For maximum and mean growth rates, decreasing carbon percentage had a positive effect on growth rate. Across the range of zooplankton in the meta-analysis in Chapter 3, the effect of carbon percentage and carbon mass on growth was of a similar magnitude. Thus a change in carbon percentage of two orders of magnitude (e.g. from 15% in *Calanus helgolandicus* to 0.1% in *Aurelia aurita*) has an equivalent effect on growth rate to a decrease by two orders of magnitude in carbon mass. This increase in growth rate associated with decreasing carbon percentage could be the result of increased carbon specific feeding rate, as modelled mechanistically in Chapter 4.

One of the key results in Chapter 3 was a growth equation unifying the effects of carbon mass and carbon percentage. The strength of a unified growth equation is that it allows all zooplankton to be modelled with a single equation, without overlooking the effects of variation of carbon percentage on growth. Additionally, this approach can provide coverage for groups for which empirical growth data may not be available. It is far more straightforward to obtain the carbon and wet masses of an organism than to measure growth rate, so for rare species this could represent an effective approximation. Carbon mass is a necessity to predict any vital rate but in cases where wet mass is not easily quantified, the carbon percentage of a wide range of zooplankton taxa are provided in Appendix I. It should be noted however that food availability and temperature also influence growth rate, and the growth rate equation provided represents maximum food saturated growth rate at 15^{o}C.

7.3 - Population dynamics

The combined effects of carbon mass and carbon percentage on population level processes were tested in Chapter 5. Gelatinous zooplankton are well known for forming blooms and one aim here was to determine to what extent the organismal level traits described in other chapters drove bloom formation. It was predicted that the increase in feeding and growth rates described in the preceding chapters might increase the population growth potential of gelatinous zooplankton, translating to higher maximum population increase rate and variability. However, interpreting the data is not straightforward. Variability in abundance was inversely related to carbon percentage, such that more gelatinous taxa tended to be more variable across a range of time scales. However, there was no relationship between carbon percentage and population increase rate. This suggests that despite the apparent energy budget benefits of lowered carbon percentage, other process such as low carbon mass, parthenogenesis and benthic resting stages were also important in determining population increase rate and likely bloom formation. In fact, the maximum rate of carbon biomass increase of some copepod taxa (such as *Temora longicornis*) exceeded that of the more gelatinous taxa. Indeed, most gelatinous taxa are small and do not form blooms.

However, the maximum wet biomass (mg WM m^{-3}) was much higher in in more gelatinous taxa, resulting in highly visible populations over a short period. This could help to explain why rapid population increases in gelatinous zooplankton are considered significant and termed blooms, while increases in carbon mass of equal magnitude in less gelatinous taxa are not. It is worthy of note that many of the bloom forming gelatinous zooplankton that are of anthropogenic importance, such as *Pelagia noctiluca* and *Mnemiopsis leidyi*, are not recorded at L4. It is possible that these larger animals, and others such as the very large rhizostomids, rely on the scope for growth advantage described in the preceding chapters to maintain rapid growth at such large carbon masses.

7.4 - Addition of carbon percentage to trait based models

Despite the demonstrated significance of highly gelatinous taxa in planktonic ecosystems, carbon percentage is rarely considered in models of zooplankton ecology and was not mentioned in a recent review of zooplankton traits (Hébert et al., 2017). Tellingly, gelatinous zooplankton are often omitted from plankton or ecosystem models, possibly as a result of the differences between vital rates of highly gelatinous and less gelatinous taxa (Zhao et al., 2008; Everett et al., 2017; Kenitz et al., 2017). While the impact of highly gelatinous taxa varies between systems, omitting these taxa will reduce the utility of these ecosystem models. For instance, highly gelatinous taxa constitute the majority of the wet biomass at L4, as shown in Figure 6.3b.

The approach adopted in this thesis offers an alternative, substituting the dichotomy of cnidarians, ctenophores and salps *vs* all other zooplankton with a more quantitative description based on body composition (and the associated effects). This approach to dealing with the effects of carbon percentage is similar to how other traits have been integrated into trait based modelling. Instead of classifying species on the basis of phylogeny, taxa are classified on their functional characteristics, and scored on the basis of these traits. One example is mixotrophy. Many protists are to some extent mixotrophic, so using a categorical approach of phototroph or heterotroph

overlooks useful variation (Flynn and Mitra, 2009; Flynn et al., 2012). By quantifying the extent of mixotrophy for a given group, the benefits and trade-offss can also be modelled in quantitative way.

A similar approach can be used with carbon percentage, but it is easier to measure and quantify, especially when compared to some other routinely used zooplankton traits, such as feeding mode. Alongside ease of use, carbon percentage has been demonstrated to have effects of a similar magnitude to that of carbon mass (Chapter 2), the fundamental biological trait (Andersen, 2016). The traits of body mass and biovolume are considered independently in a recent review (Hébert et al., 2017), ignoring the importance of carbon percentage as an integrator of these multiple measures of size. Carbon mass (or more generally body size) is the primary trait used in many models, and indeed, some models focus on size alone. In size based models, the effects of low carbon percentage may cause highly gelatinous taxa to behave differently than other less gelatinous zooplankton, and may require them to be treated separately if considered at all. This causes increased model complexity but can be mitigated by the addition of carbon percentage as a trait. Carbon percentage summarises the decoupling between wet mass and carbon mass seen in the plankton, and unites it along a single axis. Values for this variable can be obtained through measurement, or by consulting Appendix I of this thesis. Indeed, many particle analysers or automated approaches to zooplankton enumeration use volume or equivalent spherical diameter, which can be taken as an effective approximation of wet mass for most zooplankton. This complements the information necessary to estimate vital rates of zooplankton without having to separate taxa on the basis of phylogeny.

7.5 - Carbon percentage as an ecological indicator

In the preceding chapters, carbon percentage has been used on a species or individual basis to ask questions about energy budgets and development. However, carbon percentage can also be used as a descriptive index, at different organisational levels. In a similar way to size

spectra, uniting individual traits into a single expression can give useful information about the assemblage as a whole.

For instance, it is generally accepted that gelatinous taxa are more common during the summer months, reflected in the abundance of media coverage regarding jellyfish strandings through the summer months (BBC News, 2016a; 2016b). By using carbon percentage to calculate the wet mass of each zooplankter, summing them and dividing the sum carbon mass by this number, it is possible to estimate the carbon percentage of the assemblage as a whole. Using this single value, we can investigate the ratio of highly gelatinous taxa relative to other zooplankton through the year, and determine whether gelatinous taxa are more numerous in summer (Figure 5.4).

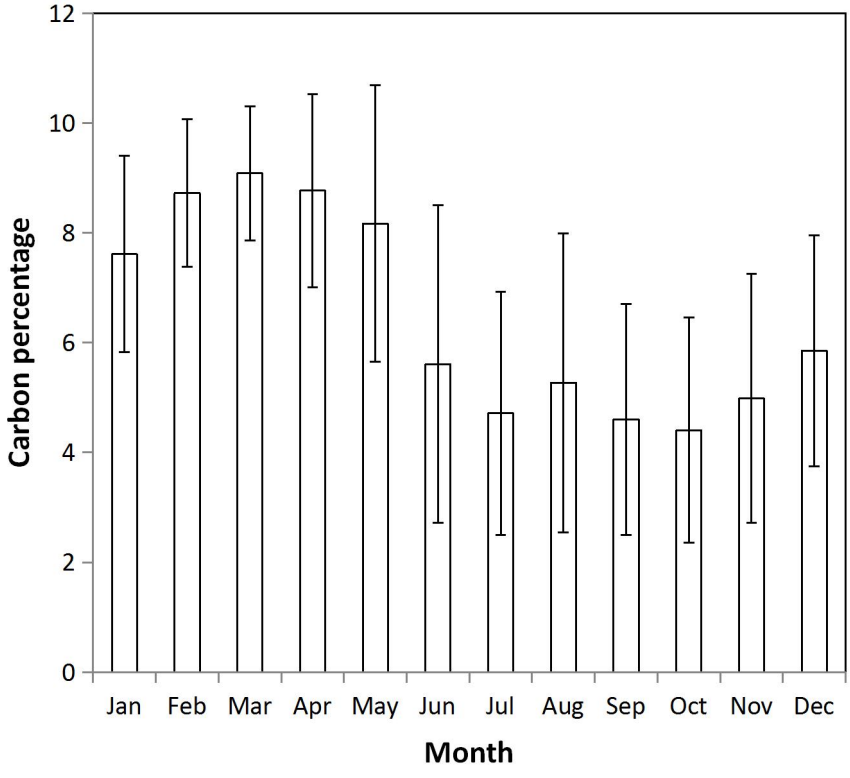


Figure 7.1 – *Monthly average assemblage carbon percentage at the L4 sampling site between 1988 and 2016. Assemblage carbon percentage was calculated as the sum of abundance of each taxon multiplied by their carbon mass, divided by the sum of the abundance of each taxon multiplied by their wet mass. Assemblage carbon percentage at each time point was sorted by month, and then averaged.*

According to this index, assemblage carbon percentage is both lowest and most variable in autumn at L4. This index can be used at different temporal scales to ask different questions, for instance, when applied to the full L4 time series between 1988 and 2016, there is a trend of decreasing assemblage carbon percentage over time (Figure 7.2). Further analysis suggests that this is the result of assemblage carbon percentage decreasing in autumn (Figure 7.3).

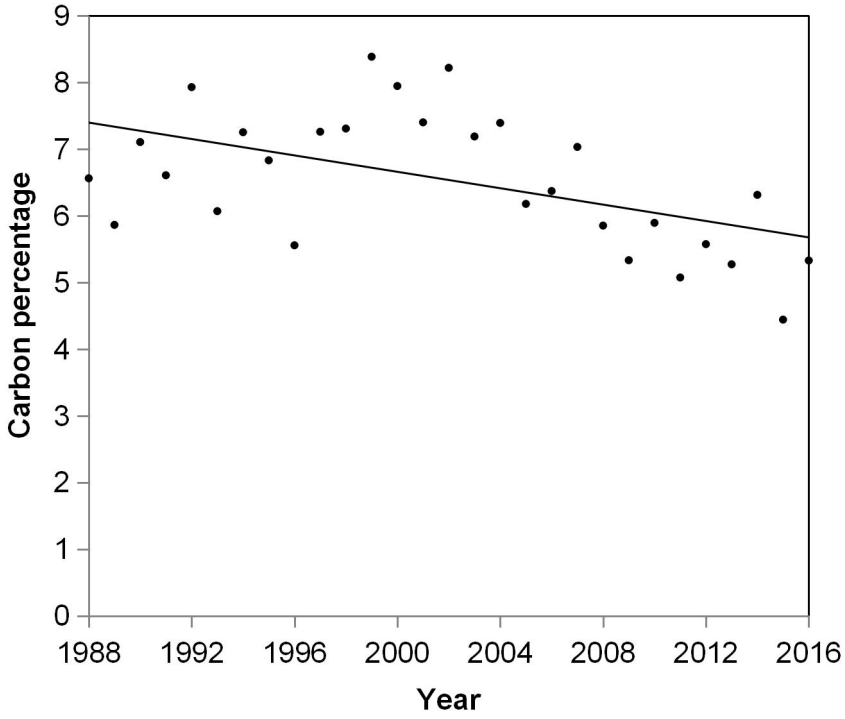


Figure 7.2 – *Assemblage carbon percentage (averaged by year) at the L4 sampling site recorded weekly between 1988 and 2016. Carbon percentages assigned as described in Chapter 4, df = 28, p = 0.0037, R^2 = 0.26, carbon percentage = - 0.0615 year + 129.68. Ctenophores were omitted due to potential preservation and recording issues.*

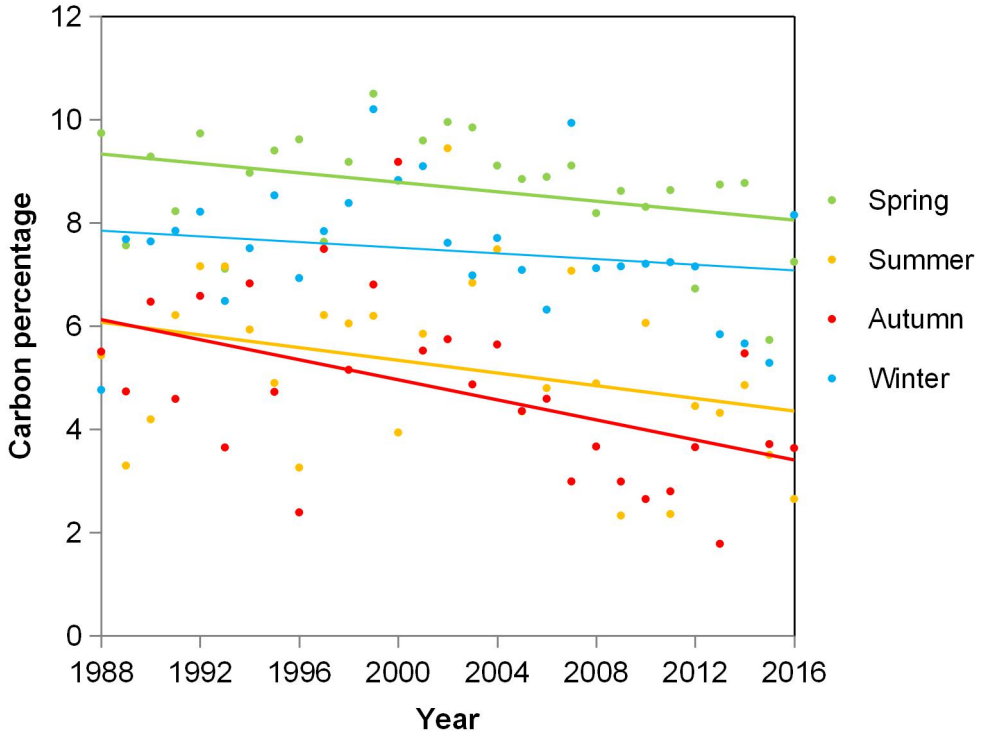


Figure 7.3 – *Trends in assemblage carbon percentage at the L4 sampling site between 1988 and 2016 in different seasons (winter = Jan, Feb, Mar, spring = Apr, May, Jun, summer = July, Aug, Sep, autumn = Oct, Nov, Dec). Spring carbon percentage = - 0.0457 year + 100.21, p = 0.052, R^2 = 0.13. Summer carbon percentage = - 0.0615 year + 128.3, p = 0.104, R^2 = 0.095. Autumn carbon percentage = - 0.0971 year + 199.2, p = 0.007, R^2 = 0.24. Winter carbon percentage = 0.0275 year + 62.422, p = 0.33, R^2 = 0.036. As above, ctenophores were omitted due to potential identification and recording issues.*

This plot shows that the trend of decreasing carbon percentage with time is strongest during autumn. This could help to explain why autumn was also the most variable season in the above plot of assemblage carbon percentage as a function of month. The intention is not to make compelling evidence that gelatinous zooplankton are increasing at L4, but rather demonstrate that carbon percentage can be a valuable way to summarise a zooplankton assemblage. Used in this way, carbon percentage could be used as a monitoring tool as an alternative to the currently used Marine Strategy Framework Directive (MSFD) lifeforms approach (Tett et al., 2015) to investigate the effects of fishing pressure, climate change and increased coastal development on zooplankton assemblages. While all indices have positive and negative qualities, assemblage carbon percentage could be particularly useful for comparing across multiple time series where different species are recorded.

7.6 - Closing remarks

Size is seen as the “master” trait because it determines such a wide variety of factors associated with organismal biology (Andersen, 2016). All physiological and ecological processes are in some way related to the size of the organism. For most organisms, different metrics of body size are broadly interchangeable. However; the seemingly exceptional characteristics of highly gelatinous zooplankton demonstrate that body size is a complex trait that is routinely oversimplified. Examination of the differences between highly gelatinous taxa and other zooplankton helped to show that different metrics of body size refer to different characteristics. Carbon mass represents metabolic body size, the amount of an organism that is actively involved in physiological processes such as respiration and excretion. Wet mass represents the effective influence of an organism, the amount of the surrounding environment that interacts with the organism at a given time. Wet mass also dictates the size of an organism relative to other organisms, a critical factor in determining food webs. Viewed this way, wet mass can be considered as an “ecological body size”.

The unique physical characteristics of the marine environment allow zooplankton to decouple these two metrics of body size, such that a single size metric is insufficient to fully define the range of characteristics commonly associated with body size. This decoupling allows organisms to adopt combinations of metabolic and ecological body size that otherwise would not be possible. This can have profound effects on organismal energy budgets and even population dynamics.

While previous studies have categorically separated jellyfish from other zooplankton, this thesis has endeavoured to show that the difference is a quantitative one based on these different metrics of body size. Furthermore, this thesis has demonstrated some of the ways that this can impact organismal energy budgets irrespective of phylogenetic affiliation, and has provided reasons why a lowered carbon percentage is seen in such a wide range of phyla. This approach of adopting carbon percentage as continuous trait to describe the decoupling of metabolic and

ecological body size can form a significant step toward a comprehensive picture of how taxa function and interact in the plankton. Using this information, we can better understand the differences and similarities between zooplanktonic taxa, and better predict how they might respond to our changing oceans.

References

Acuña, J.L. (2001) Pelagic tunicates: Why gelatinous? *American Naturalist* **158** 100-106.

Acuña, J.L., Lopez-Urrutia, A. and Colin, S. (2011) Faking giants: The evolution of high prey clearance rates in jellyfishes. *Science* **333** 1627-1629.

Addad, S., Exposito, J. Y., Faye, C., Ricard-Blum, S., and Lethias, C. (2011) Isolation, characterization and biological evaluation of jellyfish collagen for use in biomedical applications. *Marine Drugs* **9** 967-983.

Alexander, R.M. (1990) Size, speed and buoyancy adaptations in aquatic animals. *American Zoologist* **30** 189-196.

Alldredge, A.L. (1984) The quantitative significance of gelatinous zooplankton as pelagic consumers. In *Flows of energy and materials in marine ecosystems* (pp. 407-433). Springer US.

Alldredge, A.L. and Madin, L.P. (1982) Pelagic tunicates: unique herbivores in the marine plankton. *Bioscience* **32** 655-663.

Andersen, K. H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S. and Olsson, K. (2016) Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science* **8** 217-241.

Andersen, K.H, Aksnes, D.L., Berge, T., Fiksen, Ø., and Visser, A. (2015a) Modelling emergent trophic strategies in plankton. *Journal of Plankton Research* **37** 862-868.

Andersen, K.H., Berge, T., Goncalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C. et al. (2015b) Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science* **8** 3.1-3.25.

Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R.I. and Mitchell-Olds, T. (2012) Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, p.rspb20121051.

Arai, M.N., (2012) *A functional biology of Scyphozoa*. Springer Science & Business Media.

Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R.E., Murphy, E.J., et al. (2006) Natural growth rates in Antarctic krill (*Euphausia superba)*: II. Predictive models based on food, temperature, body length, sex and maturity stage. *Limnology and Oceanography* **51** 973-987.

Båmstedt, U., Wild, B. and Martinussen, M. (2001) Significance of food type for growth of ephyrae *Aurelia aurita* (Scyphozoa). *Marine Biology* **139** 641-650.

BBC News (2015) *Jellyfish at record high, says Marine Conservation Society*. [ONLINE] Available at: http://www.bbc.co.uk/news/uk-england-devon-33988083. [Accessed 27 April 2017].

BBC News (2016a) *Stinging jellyfish spotted on Scots beach*. [ONLINE] Available at: http://www.bbc.co.uk/news/uk-scotland-36916594. [Accessed 11 April 2017]

BBC News (2016b) *Thousands of jellyfish wash up on Cornish beach.* [ONLINE] Available at: http://www.bbc.co.uk/news/uk-england-cornwall-36793950. [Accessed 11 April 2017]

Belsley, D., Kuh, E. and Welsch, R. (1980) *Regression diagnostics*. Wiley.

Bidigare, R.R. and Biggs, D.C. (1980) The role of sulfate exclusion in buoyancy maintenance by siphonophores and other oceanic gelatinous zooplankton. *Comparative Biochemistry and Physiology* **66A** 467-471.

Blackett, M., Lucas, C.H., Harmer, R.A. and Licandro, P. (2015). Population ecology of *Muggiaea atlantica* (Cnidaria, Siphonophora) in the Western English Channel. *Marine Ecology Progress Series* **535** 129-144.

Bone, Q. (*ed.*) (1998) *The biology of pelagic tunicates.* Oxford University Press, Oxford.

Brotz, L. and Pauly, D. (2016) Studying jellyfish fisheries: toward accurate national catch reports and appropriate methods for stock assessments. *Jellyfish: Ecology, Distribution Patterns and Human Interactions.* Nova Publishers, Hauppauge, NY.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85** 1771-1789.

Burnham, K.P. and Anderson, D.R. (2002) *Model selection and multimodel inference: A practical information-theoretic approach.* Springer, New York.

Canepa, A., Fuentes, V., Sabatés, A., Piraino, S., Boero, F. and Gili, J.M. (2014) *Pelagia noctiluca* in the Mediterranean Sea. In *Jellyfish blooms* (pp. 237-266). Springer Netherlands.

Clarke, A. and Peck, L.S. (1991) The physiology of polar marine zooplankton. *Polar Research* **10** 355-370.

Clarke, A., Holmes, L.J. and Gore, D.J. (1992) Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. *Journal of Experimental Marine Biology and Ecology* **155** 55-68.

Cole, M., Lindeque, P.K., Fileman, E., Halsband, C. and Galloway, T. (2015) The impact of microplastics on feeding, function and fecundity in the copepod Calanus helgolandicus. *Environmental Science & Technology* **49** 1130-1137.

Condon, R.H, Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R., Mianzan, H.W., Bogeberg, M. et al. (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences U.S.A.* **110** 1000-1005.

Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B. and Mills, C.E. (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. *BioScience* **62** 160-169.

Cross, J., Nimmo-Smith, W.A.M., Hosegood, P.J. and Torres, R. (2015) The role of advection in the distribution of plankton populations at a moored 1-D coastal observatory. *Progress in Oceanography* **137** 342-359.

D'Ambra, I., Graham, W.M., Carmichael, R.H. and Hernandez, F.J. (2015) Fish rely on scyphozoan hosts as a primary food source: evidence from stable isotope analysis. *Marine Biology* **162** 247-252.

Decker, M.B., Breitburg, D.L. and Purcell, J.E. (2004) Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Marine Ecology Progress Series* **280** 163-172.

Delannoy, C.M., Houghton, J.D. Fleming, N.E., and Ferguson, H.W. (2011). Mauve Stingers (*Pelagia noctiluca*) as carriers of the bacterial fish pathogen *Tenacibaculum maritimum*. *Aquaculture* **311** 255-257.

Dong, J., Jiang, L.X., Tan, K. F., Liu, H.Y., Purcell, J. E., Li, P. J., and Ye, C.C. (2009) Stock enhancement of the edible jellyfish (*Rhopilema esculentum* Kishinouye) in Liaodong Bay, China: a review. *Hydrobiologia* **616** 113-118.

Dong, Z., Liu, D. and Keesing, J.K. (2010) Jellyfish blooms in China: dominant species, causes and consequences. *Marine Pollution Bulletin* **60** 954-963.

Doyle, T. K., De Haas, H., Cotton, D., Dorschel, B., Cummins, V., Houghton, J. D., and Hays, G.C. (2008). Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research* **30** 963-968.

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S. I., Robinson, K., and Madin, L. (2013) Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment* **11** 91-97.

Dunn, C.W., Leys, S.P. and Haddock, S.H. (2015) The hidden biology of sponges and ctenophores. *Trends in Ecology & Evolution* **30** 282-291.

Dunn, C.W., Pugh, P.R. and Haddock, S.H. (2005) Molecular phylogenetics of the siphonophora (Cnidaria), with implications for the evolution of functional specialization. *Systematic Biology* **54** 916-935.

Edwards, M. and Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430** 881.

Elliott, D.T., Pierson, J.J. and Roman, M.R. (2012) Relationship between environmental conditions and zooplankton community structure during summer hypoxia in the northern Gulf of Mexico. *Journal of Plankton Research* **34** 602-613.

Eloire, D., Somerfield, P.J., Conway, D.V.P., Halsband-Lenk, C., Harris, R. and Bonnet, D. (2010) Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. *Journal of Plankton Research* **32** 657–679.

Everett, J.D., Baird, M.E., Buchanan, P., Bulman, C., Davies, C., Downie, R., Griffiths, C., Heneghan, R., Kloser, R., Laiolo, L. and Lara Lopez, A. (2017) Modelling what we sample and sampling what we model: challenges for zooplankton model assessment. *Frontiers in Marine Science* **4** 77.

FAO (1999) *Fisheries, Aquaculture Information*, Statistics Service FishStatPlus.

Fenner, P.J. and Hadok, J.C. (2002) Fatal envenomation by jellyfish causing Irukandji syndrome. *Medical Journal of Australia* **177** 362-363.

Finenko, G.A., Kideys, A.E., Anninsky, B.E., Shiganova, T.A., Roohi, A., Tabari, M.R., Rostami, H. and Bagheri, S. (2006) Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. *Marine Ecology Progress Series* **314** 171-185.

Flynn, K.J. and Mitra, A. (2009) Building the “perfect beast”: modelling mixotrophic plankton. *Journal of Plankton Research* **31** 965-992.

Flynn, K.J., Stoecker, D.K., Mitra, A., Raven, J.A., Glibert, P.M., Hansen, P.J., Granéli, E. and Burkholder, J.M. (2012) Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *Journal of Plankton Research* **35** 3-11.

Fosså, J.H. (1992). Mass occurrence of *Periphylla periphylla* (Scyphozoa, Coronatae) in a Norwegian fjord. *Sarsia* **77** 237-251.

Fossette, S., Gleiss, A.C., Chalumeau, J., Bastian, T., Armstrong, C.D., Vandenabeele, S., Karpytchev, M. and Hays, G.C. (2015) Current-oriented swimming by jellyfish and its role in bloom maintenance. *Current Biology* **25** 342-347.

Frandsen, K. and Riisgard, H. (1997) Size dependent respiration and growth of jellyfish, *Aurelia aurita*. *Sarsia* **82** 307-312.

Frandsen, K.T. and Riisgård, H.U., (1997) Size dependent respiration and growth of jellyfish, Aurelia aurita. *Sarsia* **82** 307-312.

Fraser, J.H. (1970) The ecology of the ctenophore Pleurobrachia pileus in Scottish waters. *ICES Journal of Marine Science* **33**149-168.

Fuentes, V.L., Angel, D.L., Bayha, K.M., Atienza, D., Edelist, D., Bordehore, C., Gili, J.M. and Purcell, J.E. (2010) Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia* **645** 23-37.

Fuentes, V.L., Angel, D.L., Bayha, K.M., Atienza, D., Edelist, D., Bordehore, C., and Purcell, J.E. (2010) Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia* **645** 23-37.

Gemmell, B.J., Costello, J.H., Colin, S.P. Stewart, C.J., Dabiri, J.O.,Tafti, D. and Priya, S. (2013) Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. *Proceedings of the National Academy of Sciences USA* **110** 17904-17909.

Gibbons, M.J. and Richardson, A.J. (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. *Journal of Plankton Research* **35** 929-938.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. and Charnov, E.L. (2002) Effects of size and temperature on metabolic rate. *Science* **293** 2248-2251.

Glazier, D.S. (2006) The 3/4-power law is not universal: evolution of isometric, ontogenetic metabolic scaling in pelagic animals. *BioScience* **56** 325-332.

Glazier, D.S., Hirst, A.G. and Atkinson, D. (2015) Shape shifting predicts ontogenetic changes in metabolic scaling in diverse aquatic invertebrates. *Proceedings of the Royal Society of London B: Biological Sciences* **282** 20142302.

Graham, W. M., Pagès, F. and Hamner, W. M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* **451** 199-212.

Haddock, S. H. (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Coelenterate Biology,* Springer, Dordrecht.

Hamner, W.M. and Dawson, M.N., (2009) A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. *Hydrobiologia* **616** 161-191.

Hamner, W.M., Madin, L.P., Alldredge, A.L., Gilmer, R.W. and Hamner, P.P. (1975) Underwater observations of gelatinous zooplankton: sampling problems, feeding biology, and behaviour. *Limnology and Oceanography* **20** 907-917.

Hansen, P.J., Bjørnsen, P.K., and Hansen, B.W. (1997) Zooplankton grazing and growth: scaling within the 2–2000 μm body size range. *Limnology and Oceanography* **42** 687-704.

Hansson, L.J. (1997) Effect of temperature on growth rate of *Aurelia aurita* (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. *Marine Ecology Progress Series* **161** 145-153.

Hansson, L.J. and Norrman, B. (1995) Release of dissolved organic carbon (DOC) by the scyphozoan jellyfish *Aurelia aurita* and its potential influence on the production of planktonic bacteria. *Marine Biology* ***121*** 527-532.

Haraldsson, M., Tönnesson, K., Tiselius, P., Thingstad, T.F. and Aksnes, D.L. (2012) Relationship between fish and jellyfish as a function of eutrophication and water clarity. *Marine Ecology Progress Series* **471** 73-85.

Harbison, G.R. (1992) The gelatinous inhabitants of the ocean interior. *Oceanus* **35** 18-23.

Harbison, G.R., Biggs, D.C. and Madin, L.P. (1977). The associations of Amphipoda Hyperiidea with gelatinous zooplankton—II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep Sea Research* **24** 465-488.

Harris, R. (2010) The L4 time series: the first 20 years. *Journal of Plankton Research* **32** 577–583.

Harris, R.P., Irigoien, X., Head, R.N., Rey, C., Hygum, B.H., Hansen, B.W., Niehoff, B., Meyer-Harms, B. and Carlotti, F., (2000) Feeding, growth and reproduction in the genus *Calanus*. *ICES Journal of Marine Science* **57** 1708-1726.

Harrison, N.M. (1984) Predation on jellyfish and their associates by seabirds. *Limnology and Oceanography* **29** 1335-1337.

Hébert, M-P., Beisner, B. E. and Maranger, R. (2017) Linking zooplankton community structure to ecosystem functioning: towards an effect-trait framework. *Journal of Plankton Research* **39** 3-12

Hendrickx, J. (2012). *perturb: Tools for evaluating collinearity*. R package version 2.05. http://CRAN.R-project.org/package=perturb

Hirst, A.G. (2012) Intra-specific scaling of mass to length in pelagic animals: ontogenetic shape change and its implications. *Limnology and Oceanography* **57** 1579-1590.

Hirst, A.G. and Forster, J. (2013) When growth models are not universal: evidence from marine invertebrates. *Proceedings of the Royal Society of London B: Biological Sciences* **280** 20131546.

Hirst, A.G., Roff, J.C. and Lampitt, R.S. (2003) A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Advances in Marine Biology* **44** 1-142.

Hiscock, K., Earll, B. (2015) *South West Marine Ecosystems in 2015*. [ONLINE] Available at: http://swmecosystems.co.uk/wp-content/uploads/2017/03/SWME-2015-collated_reports_FINAL_December.doc [Accessed 12 May 2017]

Hopcroft, R.R. and Roff, J.C. (1995) Zooplankton growth rates: extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *Journal of Plankton Research* **17** 205-220.

Hopcroft, R.R., and Roff, J.C., (1995). Zooplankton growth rates: extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *Journal of Plankton Research* **17** 205-220.

Hosia, A., and Båmstedt, U. (2007). Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, Western Norway. *Marine Ecology Progress Series* **351** 113-127.

Houghton, J.D., Doyle, T.K., Wilson, M.W., Davenport, J. and Hays, G.C. (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* **87** 1967-1972.

Ikeda, T. (2013) Synthesis towards a global-bathymetric model of metabolism and chemical composition of mysid crustaceans. *Journal of Experimental Marine Biology and Ecology* **445** 79-87.

Ikeda, T. (2014) Synthesis toward a global model of metabolism and chemical composition of medusae and ctenophores. *Journal of Experimental Marine Biology and Ecology* **456** 50-64.

Ikeda, T. and Takahashi, T. (2012) Synthesis towards a global-bathymetric model of metabolism and chemical composition of marine pelagic chaetognaths. *Journal of Experimental Marine Biology and Ecology* **424** 78-88.

Jaspers, C., Haraldsson, M., Bolte, S., Reusch, T.B., Thygesen, U.H. and Kiørboe, T. (2012) Ctenophore population recruits entirely through larval reproduction in the central Baltic Sea. *Biology Letters* p.rsbl20120163.

Kawahara, M., Ohtsu, K. and Uye, S.I. (2013) Bloom or non-bloom in the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae): roles of dormant podocysts. *Journal of Plankton Research* **35** 213-217.

Kawahara, M., Uye, S.I., Ohtsu, K. and Iizumi, H. (2006) Unusual population explosion of the giant jellyfish *Nemopilema nomurai (*Scyphozoa: Rhizostomeae) in East Asian waters. *Marine Ecology Progress Series* **307** 161-173.

Kenitz, K.M., Visser, A.W., Mariani, P. and Andersen, K.H. (2017) Seasonal succession in zooplankton feeding traits reveals trophic trait coupling. *Limnology and Oceanography* DOI: 10.1002/lno.10494

Kils, U. (1981) *The swimming behavior, swimming performance and energy balance of Antarctic krill, Euphausia superba* (No. 3). SCAR and SCOR, Scott Polar Research Institute.

Kim, S. W., and Onbé, T. (1989). Observations on the biology of the marine cladoceran *Podon schmackeri*. *Journal of Crustacean Biology* **9** 54-59.

King, K.R., Hollibaugh, J.T., and Azam, F. (1980). Predator-prey interactions between the larvacean Oikopleura dioica and bacterioplankton in enclosed water columns. *Marine Biology* **56** 49-57.

Kiørboe, T. (2011) How zooplankton feed: mechanisms, traits and trade-offs. *Biological Reviews* **86** 311-339.

Kiørboe, T. (2013) Zooplankton body composition. *Limnology and Oceanography* **58** 1843-1850.

Kiørboe, T. and Hirst, A.G. (2014) Shifts in mass scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. *The American Naturalist* **183** 118-130.

Kleiber, M. (1932) Body size and metabolism. *Hilgardia* **6** 315-332

Kooijman, S.A.L.M. (2010) *Dynamic energy budget theory for metabolic organisation*. Cambridge University Press, Cambridge.

Kremer, P. and Reeve, M. (1989) Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. II Carbon budgets and growth model. *Journal of Plankton Research* **11** 553-574.

Lalli, C.M. and Gilmer, R.W. (1989) *Pelagic snails: the biology of holoplanktonic gastropod mollusks*. Stanford University Press.

Larimer, J.L. and Ashby, E.A. (1962) Float gases, gas secretion and tissue respiration in the Portuguese man-of-war, *Physalia*. *Journal of Cellular Physiology* **60** 41-47.

Larson, R.J. (1987) Respiration and carbon turnover rates of medusae from the NE Pacific. *Comparative Biochemistry and Physiology Part A: Physiology* **87** 93-100.

Lebrato, M., Pitt, K.A., Sweetman, A.K., Jones, D.O., Cartes, J.E., Oschlies, A., Condon, R.H., Molinero, J.C., Adler, L., Gaillard, C. and Lloris, D. (2012) Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia* **690** 227-245.

Libralato, S., Christensen, V. and Pauly, D. (2006) A method for identifying keystone species in food web models. *Ecological Modelling* **195** 153-171.

Licandro, P., Conway, D.V.P., Yahia, M.D., De Puelles, M.F., Gasparini, S., Hecq, J.H. and Kirby, R.R. (2010). A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters* rsbl20100150.

Litchman, E., Ohman, M.D. and Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. *Journal of Plankton Research* **35** 473-484.

Little, W.S. and Copley, N.J. (2003) *Silhouette DIGITIZER Version 1.0 Users Guide*. Woods Hole Technical Report.

Lucas C.H. and Dawson M.N. (2014) What are jellyfishes and thaliaceans and why do they bloom? In: Pitt, K.A. and Lucas, C.H. (eds) *Jellyfish blooms* (p 9−44). Springer, Dordrecht.

Lucas, C.H., Pitt, K.A., Purcell, J.E., Lebrato, M. and Condon, R.H. (2011) What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. *Ecology* **92** 1704-1704.

Luo, J.Y., Grassian, B., Tang, D., Irisson, J.O., Greer, A.T., Guigand, C.M., McClatchie, S. and Cowen, R.K. (2014) Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. *Marine Ecology Progress Series* **510** 129-149.

Lynam, C.P. and Brierley, A.S. (2007) Enhanced survival of 0-group gadoid fish under jellyfish umbrellas. *Marine Biology* **150** 1397-1401.

Lynam, C.P., Gibbons, M.J., Axelsen, B.E., Sparks, C.A., Coetzee, J., Heywood, B.G. and Brierley, A.S. (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology* **16** 492.

Lynam, C.P., Heath, M.R., Hay, S.J. and Brierley, A.S. (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series* **298** 157-167.

Mackas, D.L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D., Mazzocchi, M.G., Batten, S., Richardson, A.J., Johnson, C. and Head, E. (2012) Changing zooplankton seasonality

in a changing ocean: comparing time series of zooplankton phenology. *Progress in Oceanography* **97** 31-62.

Mackas, D.L., Greve, W., Edwards, M., Chiba, S., Tadokoro, K., Eloire, D. and Head, E. (2012) Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. *Progress in Oceanography* **97** 31-62.

Madin, L.P. (1982) Production, composition and sedimentation of salp fecal pellets in oceanic waters. *Marine Biology* **67** 39-45.

Marcos-López, M., Mitchell, S.O. and Rodger, H.D (2016) Pathology and mortality associated with the mauve stinger jellyfish *Pelagia noctiluca* in farmed Atlantic salmon *Salmo salar* L. *Journal of Fish Diseases* **39** 111-115.

Matsumoto, G.I. (1988) A new species of lobate ctenophore, *Leucothea pulchra* sp. nov., from the California Bight. *Journal of Plankton Research* **10** 301-311.

Maud, J.L., Atkinson, A., Hirst, A.G., Lindeque, P.K., Widdicombe, C.E., Harmer, R.A., McEvoy, A. and Cummings, D.G. (2015) How does *Calanus helgolandicus* maintain its population in a changing climate? Analysis of a 25-year time series from the English Channel. *Progress in Oceanography* **137** 513-523.

Milisenda, G., Rosa, S., Fuentes, V.L., Boero, F., Guglielmo, L., Purcell, J.E. and Piraino, S. (2014). Jellyfish as prey: frequency of predation and selective foraging of Boops boops (Vertebrata, Actinopterygii) on the mauve stinger *Pelagia noctiluca* (Cnidaria, Scyphozoa). *PLoS One* **9** e94600.

Miranda, L.S., Morandini, A.C. and Marques, A.C. (2012) Do Staurozoa bloom? A review of stauromedusan population biology. *Hydrobiologia* **690** 57-67.

Molina-Ramirez, A., Caceres, C., Romero-Romero, S., Bueno, J., Ignacio Gonzalez-Gordillo, J., Irigoien, X., Sostres, J., Bode, A., et al. (2015) Functional differences in the allometry of the water, carbon and nitrogen content of gelatinous organisms. *Journal of Plankton Research.* **35** 989-1000.

Møller, L.F. and Riisgård, H.U. (2007) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. *Marine Ecology Progress Series* **346** 167-177.

Moloney, C.L. and Field, J.G. (1991) The size-based dynamics of plankton food webs. I. A simulation model of carbon and nitrogen flows. *Journal of Plankton Research* **13** 1003-1038.

Mullin, M.M., and Onbé, T. (1992). Diel reproduction and vertical distributions of the marine cladocerans, *Evadne tergestina* and *Penilia avirostris*, in contrasting coastal environments. *Journal of Plankton Research* **14** 41-59.

Nissimov, J.I., Napier, J.A., Allen, M.J., Kimmance, S.A. (2015) Intragenus competition between coccolithoviruses: an insight on how a select few can come to dominate many. *Environmental Microbiology* **18** 133-145. 10.1111/1462-2920.12902

Oguz, T., Fach, B. and Salihoglu, B. (2008) Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea. *Journal of Plankton Research* **30** 1385-1397.

Olesen, N., Frandsen, K. and Riisgard, H.U., (1994) Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. *Marine Ecology Progress Series.* **105** 9-18.

Pauly, D., Graham, W., Libralato, S., Morissette, L., and Palomares, M. D. (2009) Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* **616** 67-85.

Peters, R.H., (ed.) (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge.

Pianka, E.R (1970) On r-and K-selection. *The American Naturalist* **104** 592-597.

Pitt, K.A., Duarte, C.M., Lucas, C.H., Sutherland, K.R., Condon, R.H., Mianzan, H., Purcell, J.E., Robinson, K.L., et al. (2013) Jellyfish body plans provide allometric advantages beyond low carbon percentage. *PLoS One* **8** e72683.

Platt, T., (1985) Structure of the marine ecosystem: its allometric basis. *Canadian Bulletin of Fisheries and Aquatic Sciences* **213** 55-64.

Pond, D.W., Harris, R.P., Head, R.N. and Harbour, D. (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, U.K. *Marine Ecology Progress Series* **143** 45-63.

Purcell, J.E. (1984) Predation on fish larvae by *Physalia physalis*, the Portuguese man of war. *Marine Ecology Progress Series* **19** 189-191.

Purcell, J.E. (2012) Jellyfish and Ctenophora blooms coincide with human proliferations and environmental perturbations. *Annual Review of Marine Science* **4** 209-235

Purcell, J.E. and Arai, M.N. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* **451** 27-44.

Purcell, J.E., Breitburg, D.L., Decker, M.B., Graham, W.M., Youngbluth, M.J. and Raskoff, K.A., (2001) Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. *Coastal and Estuarine Studies* **58** 77-100.

Purcell, J.E., Uye, S.I. and Lo, W.T. (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* **350** 153-174.

Quiñones, J., Monroy, A., Acha, E.M. and Mianzan, H. (2013) Jellyfish bycatch diminishes profit in an anchovy fishery off Peru. *Fisheries Research* **139** 47-50.

R Core Team (2014) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Racault, M.F., Le Quéré, C., Buitenhuis, E., Sathyendranath, S. and Platt, T., (2012) Phytoplankton phenology in the global ocean. *Ecological Indicators* **14** 152-163.

Raskoff, K.A., Purcell, J.E. and Hopcroft, R.R. (2005) Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. *Polar Biology* **28** 207-217.

Raskoff, K.A., Sommer, F.A., Hamner, W.M. and Cross, K.M. (2003) Collection and culture techniques for gelatinous zooplankton. *The Biological Bulletin* **204** 68-80.

Redfield, A. C. (1934). *On the proportions of organic derivatives in sea water and their relation to the composition of plankton* (pp. 176-92). University Press of Liverpool, Liverpool.

Richardson, A.J., Bakun, A., Hays, G.C. and Gibbons, M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution* **24** 312-322.

Roberts, R.J. (2001) Miscellaneous non-infectious diseases. *Fish Pathology* (pp. 367–379), WB Saunders, London.

Royall, R.M. (1997) *Statistical evidence: a likelihood paradigm*. New York, NY: Chapman and Hall.

Sappenfield, A.D., Tarhan, L.G. and Droser, M.L. (2016) Earth's oldest jellyfish strandings: a unique taphonomic window or just another day at the beach? *Geological Magazine* 2016 1-16.

Schmidt, K., Atkinson, A., Stübing, D., McClelland, J.W., Montoya, J.P. and Voss, M., (2003) Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. *Limnology and Oceanography* **48** 277-289.

Seo, H.C., Kube, M., Edvardsen, R.B., Jensen, M.F., Beck, A., Spriet, E., Gorsky, G., Thompson, E.M., Lehrach, H., Reinhardt, R. and Chourrout, D. (2001) Miniature genome in the marine chordate *Oikopleura dioica*. *Science* **294** 2506-2506.

Shiganova, T.A. and Bulgakova, Y.V. (2000) Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. *ICES Journal of Marine Science* **57** 641-648.

Smyth, T., Atkinson, A., Widdicombe, S., Frost, M., Allen, I., Fishwick, J., Quieros, A., Sims, D. and Barange, M. (2015) The Western Channel. *Progress in Oceanography* **137** 335-341

Sousa, T., Domingos, T., Poggiale, J.C. and Kooijman, S.A.L.M., (2010) Dynamic energy budget theory restores coherence in biology. *Philosophical Transactions of the Royal Society of Biology B* **365** 3413-3428.

Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Dando, P.R., Genner, M.J., Joint, I., Kendall, M.A., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N.,

Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W. and Hawkins, S.J. (2005) Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology* **47** 1-105.

Straile, D. (1997) Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnology and Oceanography* **42** 1375-1385.

Straile, D., (1997) Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnology and Oceanography* **42** 1375-1385.

Sullivan, B.K., Suchman, C.L. and Costello, J.H. (1997) Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. *Marine Biology* **130** 213-222.

Sullivan, L.J. and Gifford, D.J. (2007) Growth and feeding rates of the newly hatched ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research* **29** 949-965.

Sutherland, K.L., Madin, L.P. and Stocker, R. (2010) Filtration of submicrometer particles by pelagic tunicates. *Proceedings of the National Academy of Sciences USA* **107** 15129-15134.

Sweetman, A.K. and Chapman, A. (2011) First observations of jelly-falls at the seafloor in a deep-sea fjord. *Deep Sea Research Part I: Oceanographic Research Papers*, **58** 1206-1211.

Tett, P. (2015) Guide to the PLANKTON INDEX method and software, v. 3.01.

Thuesen, E.V., Rutherford, L.D., Brommer, P.L., Garrison, K., Gutowska, M.A. and Towanda, T. (2005) Intragel oxygen promotes hypoxia tolerance of scyphomedusae. *Journal of Experimental Biology* **208** 2475-2482.

Troedsson, C., Bouquet, J.M., Aksnes, D.L. and Thompson, E.M. (2002) Resource allocation between somatic growth and reproductive output in the pelagic chordate *Oikopleura dioica* allows opportunistic response to nutritional variation. *Marine Ecology Progress Series* **243** 83-91.

UNESCO (1968) Zooplankton sampling. *Monographs on Oceanographic Methodology*, Paris.

Uye, S.I. (2008) Blooms of the giant jellyfish *Nemopilema nomurai*: a threat to the fisheries sustainability of the East Asian Marginal Seas. *Plankton and Benthos Research* **3** 125-131.

Uye, S.I. (2014) The giant jellyfish *Nemopilema nomurai* in East Asian marginal seas. In *Jellyfish Blooms* (pp. 185-205) ed. Pitt, K.A, Lucas, C.H., Springer, Netherlands.

Verberk, W.C. and Atkinson, D. (2013) Why polar gigantism and Palaeozoic gigantism are not equivalent: effects of oxygen and temperature on the body size of ectotherms. *Functional Ecology* **27** 1275-1285.

Vidal, J. and Whitledge, T.E. (1982) Rates of metabolism of planktonic crustaceans as related to body weight and temperature of habitat. *Journal of Plankton Research* **4** 77-84.

Weltzein, F.A., Hemre, G.I., Evjemo, J.O., Olsen, Y. and Fyhn, H.J. (2000) β-Hydroxybutyrate in developing nauplii of brine shrimp (*Artemia franciscana* K.) under feeding and non-feeding conditions. *Comparative Biochemistry and Physiology* **125B** 63-69

Wirtz, K. (2012) Who is eating whom? Morphology and feeding type determine the size relation between planktonic predators and their ideal prey. *Marine Ecology Progress Series* **445** 1-12

Yang, L.H. and Rudolf, V.H.W. (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* **13** 1-10.

You, K., Ma, C., Gao, H., Li, F., Zhang, M., Qiu, Y., and Wang, B. (2007) Research on the jellyfish (*Rhopilema esculentum* Kishinouye) and associated aquaculture techniques in China: current status. *Aquaculture International* **15** 479-488.

Zhao, J., Ramin, M., Cheng, V. and Arhonditsis, G.B. (2008) Plankton community patterns across a trophic gradient: the role of zooplankton functional groups. *Ecological Modelling* **213** 417-436.

Appendix I – Carbon percentage

Compilation of published values for carbon percentage (C%) values of zooplanktonic taxa.

Group	Species	C%	Compilation	Reference
Amphipoda	Cyphocaris challengeri	10.14	Kiorboe, 2013	18
Amphipoda	Parathemisto japonica	8.87	Kiorboe, 2013	18
Amphipoda	Parathemisto libellula	6.75	Kiorboe, 2013	9
Amphipoda	Platyscelus serratulus	9.47	Kiorboe, 2013	18
Amphipoda	Primno abyssalis female	7.16	Kiorboe, 2013	8
Amphipoda	Themisto japonica female	8.11	Kiorboe, 2013	8
Anthoathecata	Cladonema californicum	0.81	Kiorboe, 2013	14
Anthoathecata	Euphysa tentaculata	0.32	Pitt et al. 2013	15
Anthoathecata	Rathkea octopunctata	1.38	Pitt et al. 2013	15
Anthoathecata	Sarsia princeps	0.37	Pitt et al. 2013	15
Anthoathecata	Sarsia princeps	0.16	Kiorboe, 2013	13
Anthoathecata	Stomotoca atra	0.41	Kiorboe, 2013	13
Beroid	Beroe ovata	0.16	Pitt et al. 2013	7
Beroid	Beroe sp.	0.23	Kiorboe, 2013	7
Beroid	Beroe sp.	0.21	Pitt et al. 2013	7
Calanoida	Calanus acutus	6.85	Kiorboe, 2013	3
Calanoida	Calanus cristatus	10.14	Kiorboe, 2013	18
Calanoida	Calanus finmarchicus	14.73	Kiorboe, 2013	9
Calanoida	Calanus glacialis female	11.77	Kiorboe, 2013	9
Calanoida	Calanus hyperboreus	19.02	Kiorboe, 2013	9
Calanoida	Calanus pacificus	12.40	Kiorboe, 2013	18
Calanoida	Calanus plumchrus	17.25	Kiorboe, 2013	18
Calanoida	Calanus propinquus	12.92	Kiorboe, 2013	3
Calanoida	Candacia aetiopica	6.67	Kiorboe, 2013	18
Calanoida	Candacia columbiae	6.16	Kiorboe, 2013	18
Calanoida	Disseta palumbi	4.70	Kiorboe, 2013	18
Calanoida	Eucalanus bungii	5.99	Kiorboe, 2013	18
Calanoida	Euchirella rostromagna	7.01	Kiorboe, 2013	3
Calanoida	Gaetanus tenuispinus	5.56	Kiorboe, 2013	3
Calanoida	Labidocera acutifrons	5.20	Kiorboe, 2013	18
Calanoida	Metridia longa female	10.77	Kiorboe, 2013	9
Calanoida	Metridia okhotensis	11.91	Kiorboe, 2013	18
Calanoida	Paraeuchaeta birostrata	10.80	Kiorboe, 2013	18
Calanoida	Pleuromamma xiphias	5.80	Kiorboe, 2013	18
Calanoida	Pontellina plumata	6.65	Kiorboe, 2013	18
Calanoida	Rhincalanus nasutus	7.03	Kiorboe, 2013	18
Cephalopoda	Psychroteuthis sp.	13.41	Kiorboe, 2013	7
Chaetognatha	Aidanosagitta neglecta	2.79	Kiorboe, 2013	10
Chaetognatha	Caecosagitta macrocephala	5.97	Kiorboe, 2013	10
Chaetognatha	Eukrohnia bathypelagica	2.94	Kiorboe, 2013	10
Chaetognatha	Eukrohnia fowleri	4.19	Kiorboe, 2013	10
Chaetognatha	Eukrohnia hamata	2.69	Kiorboe, 2013	3
Chaetognatha	Parasagitta elegans	4.46	Kiorboe, 2013	10
Chaetognatha	Pseudosagitta scrippsae	1.28	Kiorboe, 2013	10
Chaetognatha	Sagitta elegans	4.07	Kiorboe, 2013	9
Chaetognatha	Sagitta gazellae	1.35	Kiorboe, 2013	3
Chaetognatha	Sagitta marri	3.72	Kiorboe, 2013	3

Chaetognatha	Sagitta nagae	5.03	Kiorboe, 2013	18
Chaetognatha	Solidosagitta zetesios	4.19	Kiorboe, 2013	10
Coronatae	Atolla wyvillei	0.77	Pitt et al. 2013	2
Coronatae	Periphylla periphylla	0.64	Pitt et al. 2013	24
Cydippid	Agmayeria tortugensis	0.94	Pitt et al. 2013	1
Cydippid	Callianira antarctica	0.36	Kiorboe, 2013	14
Cydippid	Mertensia sp.	0.46	Kiorboe, 2013	7
Cydippid	Pleurobrachia pileus	0.15	Kiorboe, 2013	14
Cydippid	Pleurobrachia sp.	0.18	Kiorboe, 2013	14
Decapoda	Chorismus antarcticus	10.66	Kiorboe, 2013	7
Decapoda	Lucifer reynaudii	5.48	Kiorboe, 2013	18
Euphausiacea	Euphausia crystallorophias	8.80	Kiorboe, 2013	7
Euphausiacea	Euphausia pacifica	8.96	Kiorboe, 2013	18
Euphausiacea	Euphausia superba	11.38	Kiorboe, 2013	7
Euphausiacea	Tessarabrachion oculatus	10.07	Kiorboe, 2013	18
Euphausiacea	Thysanoessa inermis	17.87	Kiorboe, 2013	9
Gymnosomata	Clione limacina	1.36	Kiorboe, 2013	9
Leptothecata	Eutonina indicans	0.34	Kiorboe, 2013	13
Leptothecata	Mitrocoma cellularia	0.10	Kiorboe, 2013	9
Leptothecata	Phialidium gregarium	0.37	Kiorboe, 2013	13
Leptothecata	Phialidium lomae	0.25	Kiorboe, 2013	13
Leptothecata	Phialidium sp.	1.07	Pitt et al. 2013	16
Lobata	Bathocyroe fosteri	0.01	Pitt et al. 2013	1
Lobata	Bolinopsis infundibulum	0.07	Kiorboe, 2013	14
Lobata	Eurhamphaea vexilligera	0.03	Pitt et al. 2013	12
Lobata	Mnemiopsis leidyi	0.06	Pitt et al. 2013	11
Lobata	Mnemiopsis mccradyi	0.08	Pitt et al. 2013	20
Lobata	Ocryopsis maculata	0.09	Pitt et al. 2013	12
Lobata	Ocyropsis spp.	0.05	Pitt et al. 2013	12
Mysidacea	Antarctomysis maxima	10.46	Kiorboe, 2013	7
Mysidacea	Meterythrops microphthalma	7.88	Kiorboe, 2013	8
Mysidacea	Siriella aequiremis	7.92	Kiorboe, 2013	18
Narcomedusae	Aeginura grimaldii	0.30	Pitt et al. 2013	1
Narcomedusae	Pegantha sp.	0.44	Molina-Ramirez et al., 2015	17
Narcomedusae	Solmissus incisus	0.06	Pitt et al. 2013	1
Ostracoda	Conchoecia antipoda	4.76	Kiorboe, 2013	3
Polychaeta	Tomopteris carpenteri	5.34	Kiorboe, 2013	3
Polychaeta	Vanadis antarctica	5.11	Kiorboe, 2013	3
Rhizostomae	Catostylus mosaicus	1.17	Kiorboe, 2013	19
Rhizostomae	Cotylorhiza tuberculata	0.55	Pitt et al. 2013	14
Rhizostomae	Mastigias papua	0.67	Kiorboe, 2013	22
Rhizostomae	Nemopilema nomurai	0.55	Kiorboe, 2013	23
Rhizostomae	Rhizostoma octopus	0.35	Pitt et al. 2013	14
Rhizostomae	Rhizostoma pulmo	0.98	Kiorboe, 2013	14
Rhizostomae	Rhopilema esculentum	1.21	Kiorboe, 2013	23
Rhizostomae	Rhopilema hispidum	0.76	Pitt et al. 2013	23
Scyphomedusae	Chrysaora hysocella	0.18	Pitt et al. 2013	14
Semaeostomae	Aurelia aurita	0.10	Pitt et al. 2013	15
Semaeostomae	Chrysaora fuscescens	0.28	Pitt et al. 2013	21
Semaeostomae	Chrysaora hysoscella	0.18	Kiorboe, 2013	14
Semaeostomae	Chrysaora quinquecirrha	0.48	Kiorboe, 2013	14
Semaeostomae	Cyanea capillata	0.45	Kiorboe, 2013	13
Semaeostomae	Pelagia noctiluca	0.35	Kiorboe, 2013	14
Semaeostomae	Poralia rufescens	0.02	Kiorboe, 2013	1
Siphonophora	Abyla sp.	0.51	Molina-Ramirez et al.,	17

			2015	
Siphonophora	Abylopsis tetragona	0.42	Pitt et al. 2013	14
Siphonophora	Apolemia sp.	1.56	Molina-Ramirez et al., 2015	17
Siphonophora	Athorybia sp.	0.16	Molina-Ramirez et al., 2015	17
Siphonophora	Calycopsis borchgrevinki	0.50	Pitt et al. 2013	2
Siphonophora	Diphyes antarctica	0.45	Kiorboe, 2013	7
Siphonophora	Muggiaea atlantica	0.44	Kiorboe, 2013	14
Siphonophora	Prayidae sp.	1.32	Pitt et al. 2013	17
Siphonophora	Sphaeronectes gracilis	0.56	Kiorboe, 2013	14
Thaliacea	Cyclosalpa affinis	0.10	Kiorboe, 2013	13
Thaliacea	Doliolum denticulatum	3.87	Kiorboe, 2013	14
Thaliacea	Iasis zonaria	1.61	Molina-Ramirez et al., 2015	17
Thaliacea	Ihlea racovitzai	0.88	Molina-Ramirez et al., 2015	17
Thaliacea	Pegea confederata	1.15	Molina-Ramirez et al., 2015	17
Thaliacea	Pyrosoma atlanticum	1.43	Kiorboe, 2013	14
Thaliacea	Salpa cylindrica	0.56	Kiorboe, 2013	14
Thaliacea	Salpa democratica	1.59	Kiorboe, 2013	5
Thaliacea	Salpa fusiformis	0.44	Kiorboe, 2013	14
Thaliacea	Salpa maxima	1.42	Kiorboe, 2013	14
Thaliacea	Salpa thompsoni aggregate	0.19	Kiorboe, 2013	4
Thaliacea	Salpa thompsoni solitary	0.18	Kiorboe, 2013	6
Thaliacea	Thalia democratica	0.87	Kiorboe, 2013	14
Thaliacea	Thalia rhomboides	1.48	Pitt et al. 2013	17
Thaliacea	Thethys vagina	0.45	Pitt et al. 2013	17
Thecosomata	Clio pyramidata	6.31	Kiorboe, 2013	18
Thecosomata	Limacina helicina	8.23	Kiorboe, 2013	9
Thecosomata	Limacina inflata	6.18	Kiorboe, 2013	18
Trachymedusae	Aglantha digitale	0.52	Kiorboe, 2013	15
Trachymedusae	Botrynema brucei	0.24	Pitt et al. 2013	2
Trachymedusae	Colobonema sericeum	0.81	Pitt et al. 2013	1
Trachymedusae	Eperetmus typus	0.34	Pitt et al. 2013	13
Trachymedusae	Gonionemus vertens	0.63	Kiorboe, 2013	13

References

1. Bailey, T.G., Youngbluth, M.J. and Owen, G.P. (1995) Chemical composition and metabolic rates of gelatinous zooplankton from midwater and benthic boundary layer environments off Cape Hatteras, North Carolina, USA. *Marine Ecology Progress Series* 122 121-134.
2. Clarke, A., Holmes, L.J. and Gore, D.J. (1992) Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. *Journal of Experimental Marine Biology and Ecology 155* 5-68.
3. Donnelly, J., Torres, J.T., Hopkins, T.L. and Lancraft, T.M. (1994) Chemical composition of Antarctic zooplankton during austral fall and winter. *Polar Biology* 14 171–183.
4. Doyle, T. K., Houghton, J. D. R. McDevitt, R. Davenport and J. Hays, G. C. (2007) The energy density of jellyfish: Estimates from bomb-calorimetry and proximate-composition. *Journal of Experimental Marine Biology and Ecology* 343 239–252.
5. Heron, A. C., McWilliam, P. S. and Pont, G. D. (1988) Length-weight relation in the salp Thalia democratica and potential of salps as a source of food. *Marine Ecology Progress Series* 42 125–132.

6. Iguchi, N. and Ikeda, T. (2004) Metabolism and elemental composition of aggregate and solitary forms of Salpa thompsoni (Tunicata: Thaliacea) in waters off the Antarctic Peninsula during austral summer 1999. *Journal of Plankton Research 26* 1025–1037.
7. Ikeda, T. and Bruce, B. (1986) Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November–December). *Marine Biology* 92 545–555.
8. Ikeda, T. and Hirakawa, K. (1998) Metabolism and body composition of zooplankton from the mesopelagic zone of southern Japan Sea. *Plankton Biology and Ecology* 45 31–44.
9. Ikeda, T. and Skjoldal, H.R. (1989) Metabolism and elemental composition of zooplankton from the Barents Sea during early arctic summer. *Marine Biology* 100 173–183.
10. Ikeda, T. and Takahashi, T. (2012) Synthesis towards a global-bathymetric model of metabolism and chemical composition of marine pelagic chaetognaths. *Journal of Experimental Marine Biology and Ecology* 424 78–88.
11. Kremer, P. (1975) Excretion and body composition of the ctenophore *Mnemiopsis leidyi* (A. Agassiz): comparisons and consequences. *10th European Symposium on Marine Biology* 2 351-362.
12. Kremer, P., Canino, M.F. and Gilmer, R.W. (1986) Metabolism of epipelagic tropical ctenophores. *Marine Biology* 90 403-412.
13. Larson, R. J. (1986) Water content, organic content, and carbon and nitrogen composition of medusa from the Northeast Pacific. *Journal of Experimental Marine Biology and Ecology* 99 107–120.
14. Lucas, C. H., K. A. Pitt, J. E. Purcell, M. Lebrato and Condon, R.H. (2011) What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. *Ecology* 92 1704.
15. Matsakis, S. and Conover, R.J. (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during Spring. *Canadian Journal of Fisheries and Aquatic Sciences* 48 1419-1430.
16. Matsakis, S. and Nival, P. (1989) Elemental composition and food intake of *Phialidium* hydromedusae in the laboratory. *Journal of Experimental Marine Biology and Ecology* 130 277-290.
17. Molina-Ramirez et al. (2015) Functional differences in allometry of the water, carbon and nitrogen content of gelatinous organisms. *Journal of Plankton Research* 37 989-1000.
18. Omori, M. (1969) Weight and chemical composition of some important oceanic zooplankton in the North Pacific. *Marine Biology* 3 4–10.
19. Pitt unpubl.
20. Reeve, M.R. and Baker, L.D. (1975) Production of two planktonic carnivores (chaetognath and ctenophore) in South Florida inshore waters. *Fisheries Bulletin* 73 238-248.
21. Shenker, J.M. (1985) Carbon content of the neritic scyphomedusa *Chrysaora fuscescens*. *Journal of Plankton Research* 7 169-173
22. Uye in Lucas et al. (2011) What's in a jellyfish? Proximate and elementary compositions and biometric relationships for use in biogeochemical studies. *Ecology* 92 1704.
23. Uye unpubl.
24. Youngbluth, M.J., Båmstedt, U. (2001) Distribution, abundance, behaviour and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. *Hydrobiologia* 451 321-333

Appendix II – Growth rates

Compilation of published zooplanktonic growth rates. C% = carbon percentage, Temp = temperature, *g* = specific growth rate, Temp *g* = g adjusted to 15^{o}C using a Q_{10} of 2.8, Mass *g* = specific growth rate adjusted to a carbon mass of 1 mg C. Temperature and mass adjustments as detailed in Chapter 2.

Record	Phylum	Group	Species	Source	C%	Mass (mg C)	Temp (C)	g (d-1)	Temp g (d-1)
1	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	9.80E-04	21	0.25	1.35E-01
2	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	4.53E-03	21	0.25	1.35E-01
3	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	1.33E-02	21	0.25	1.35E-01
4	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	3.20E-02	21	0.25	1.35E-01
5	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	5.93E-02	21	0.25	1.35E-01
6	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	9.79E-02	21	0.25	1.35E-01
7	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	1.57E-01	21	0.08	4.47E-02
8	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	2.38E-01	21	0.04	2.37E-02
9	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	9.80E-04	26	0.35	1.13E-01
10	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	4.53E-03	26	0.35	1.13E-01
11	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	1.33E-02	26	0.35	1.13E-01
12	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	3.20E-02	26	0.35	1.13E-01
13	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	5.93E-02	26	0.35	1.13E-01
14	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	9.79E-02	26	0.35	1.13E-01
15	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	1.57E-01	26	0.07	2.38E-02
16	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	2.38E-01	26	0.01	2.26E-03
17	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	9.80E-04	31	0.41	7.89E-02
18	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	4.53E-03	31	0.41	7.89E-02
19	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	1.33E-02	31	0.41	7.89E-02
20	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	3.20E-02	31	0.41	7.89E-02
21	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	5.93E-02	31	0.41	7.89E-02
22	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	9.79E-02	31	0.11	2.12E-02

23	Chaetognatha	Chaetognatha	*Sagitta hispida*	41	3.54	1.57E-01	31	0.04	7.89E-03
24	Chaetognatha	Chaetognatha	*Sagitta hispida*	43	3.54	2.78E-02	16	0.08	7.13E-02
25	Chaetognatha	Chaetognatha	*Sagitta hispida*	43	3.54	1.30E-02	21	0.12	6.63E-02
26	Chaetognatha	Chaetognatha	*Sagitta hispida*	43	3.54	3.68E-02	21	0.14	7.28E-02
27	Chaetognatha	Chaetognatha	*Sagitta hispida*	43	3.54	3.81E-02	26	0.00	6.44E-04
28	Chaetognatha	Chaetognatha	*Sagitta hispida*	43	3.54	3.35E-02	26	0.12	3.80E-02
29	Crustacea	Copepoda	Acartia clausi	29	11.89	1.32E-04	15	0.25	2.48E-01
30	Crustacea	Copepoda	Acartia clausi	29	11.89	1.13E-03	15	0.31	3.08E-01
31	Crustacea	Copepoda	Acartia tonsa	4	11.89	2.10E-04	17	0.45	3.66E-01
32	Crustacea	Copepoda	Acartia tranteri	27	11.89	6.00E-04	12.2	0.13	1.79E-01
33	Crustacea	Copepoda	Acartia tranteri	27	11.89	6.00E-04	15.8	0.21	1.90E-01
34	Crustacea	Copepoda	Acartia tranteri	27	11.89	6.00E-04	20.8	0.31	1.68E-01
35	Crustacea	Copepoda	Calanus chilensis	13	12.96	3.99E-03	13	0.14	1.70E-01
36	Crustacea	Copepoda	Calanus chilensis	13	12.96	3.99E-03	18	0.16	1.16E-01
37	Crustacea	Copepoda	Calanus finmarchicus	6	14.73	4.70E-04	8	0.25	5.16E-01
38	Crustacea	Copepoda	Calanus finmarchicus	6	14.73	2.55E-02	8	0.20	4.07E-01
39	Crustacea	Copepoda	Calanus glacialis	12	12.96	6.56E-02	10	0.05	7.70E-02
40	Crustacea	Copepoda	Calanus glacialis	12	12.96	5.94E-02	3	0.05	1.82E-01
41	Crustacea	Copepoda	Calanus helgolandicus	38	19.02	6.69E-04	15	0.41	4.10E-01
42	Crustacea	Copepoda	Calanus helgolandicus	38	19.02	2.50E-03	15	0.41	4.10E-01
43	Crustacea	Copepoda	Calanus helgolandicus	38	19.02	1.46E-02	15	0.33	3.30E-01
44	Crustacea	Copepoda	Calanus helgolandicus	38	19.02	1.56E-02	15	0.20	1.95E-01
45	Crustacea	Copepoda	Calanus helgolandicus	38	19.02	3.29E-02	15	0.20	2.00E-01
46	Crustacea	Copepoda	Calanus marshallae	40	12.96	4.00E-04	10	0.05	8.37E-02
47	Crustacea	Copepoda	Calanus marshallae	40	12.96	8.00E-03	10	0.18	2.95E-01
48	Crustacea	Copepoda	Calanus marshallae	40	12.96	1.00E-01	10	0.02	4.02E-02
49	Crustacea	Copepoda	Calanus pacificus	50	17.25	3.60E-03	15.5	0.41	3.92E-01
50	Crustacea	Copepoda	Calanus pacificus	50	17.25	8.80E-03	15.5	0.35	3.37E-01
51	Crustacea	Copepoda	Calanus pacificus	50	17.25	2.40E-02	15.5	0.28	2.63E-01
52	Crustacea	Copepoda	Calanus pacificus	50	17.25	5.60E-02	15.5	0.15	1.41E-01
53	Crustacea	Copepoda	Calanus pacificus	50	17.25	3.60E-03	12	0.33	4.55E-01
54	Crustacea	Copepoda	Calanus pacificus	50	17.25	8.80E-03	12	0.29	3.97E-01
55	Crustacea	Copepoda	Calanus pacificus	50	17.25	2.40E-02	12	0.22	2.99E-01

56	Crustacea	Copepoda	Calanus pacificus	50	17.25	5.60E-02	12	0.13	1.78E-01
57	Crustacea	Copepoda	Calanus pacificus	50	17.25	3.60E-03	8	0.19	3.86E-01
58	Crustacea	Copepoda	Calanus pacificus	50	17.25	8.80E-03	8	0.17	3.51E-01
59	Crustacea	Copepoda	Calanus pacificus	50	17.25	2.40E-02	8	0.16	3.37E-01
60	Crustacea	Copepoda	Calanus pacificus	50	17.25	5.60E-02	8	0.12	2.43E-01
61	Crustacea	Copepoda	Calanus sinicus	49	12.96	4.47E-04	10.3	0.22	3.50E-01
62	Crustacea	Copepoda	Calanus sinicus	49	12.96	4.47E-04	13	0.31	3.76E-01
63	Crustacea	Copepoda	Calanus sinicus	49	12.96	4.47E-04	15	0.38	3.80E-01
64	Crustacea	Copepoda	Calanus sinicus	49	12.96	4.47E-04	17.5	0.48	3.72E-01
65	Crustacea	Copepoda	Calanus sinicus	49	12.96	4.47E-04	20.2	0.60	3.51E-01
66	Crustacea	Copepoda	Calanus sinicus	49	12.96	1.98E-03	10.3	0.54	8.81E-01
67	Crustacea	Copepoda	Calanus sinicus	49	12.96	1.98E-03	13	0.74	9.07E-01
68	Crustacea	Copepoda	Calanus sinicus	49	12.96	1.98E-03	15	0.89	8.92E-01
69	Crustacea	Copepoda	Calanus sinicus	49	12.96	1.98E-03	17.5	1.10	8.50E-01
70	Crustacea	Copepoda	Calanus sinicus	49	12.96	1.98E-03	20.2	1.33	7.77E-01
71	Crustacea	Copepoda	Calanus sinicus	49	12.96	7.75E-03	10.3	0.31	5.01E-01
72	Crustacea	Copepoda	Calanus sinicus	49	12.96	7.75E-03	13	0.38	4.72E-01
73	Crustacea	Copepoda	Calanus sinicus	49	12.96	7.75E-03	15	0.44	4.39E-01
74	Crustacea	Copepoda	Calanus sinicus	49	12.96	7.75E-03	17.5	0.51	3.93E-01
75	Crustacea	Copepoda	Calanus sinicus	49	12.96	7.75E-03	20.2	0.58	3.41E-01
76	Crustacea	Copepoda	Calanus sinicus	49	12.96	3.00E-02	10.3	0.09	1.41E-01
77	Crustacea	Copepoda	Calanus sinicus	49	12.96	3.00E-02	13	0.12	1.41E-01
78	Crustacea	Copepoda	Calanus sinicus	49	12.96	3.00E-02	15	0.14	1.37E-01
79	Crustacea	Copepoda	Calanus sinicus	49	12.96	3.00E-02	17.5	0.17	1.28E-01
80	Crustacea	Copepoda	Calanus sinicus	49	12.96	3.00E-02	20.2	0.20	1.17E-01
81	Crustacea	Copepoda	Centropages hamatus	15	11.89	1.79E-04	17	0.26	2.15E-01
82	Crustacea	Copepoda	Centropages hamatus	15	11.89	1.55E-03	17	0.29	2.34E-01
83	Crustacea	Copepoda	Centropages hamatus	29	11.89	1.79E-04	15	0.28	2.82E-01
84	Crustacea	Copepoda	Centropages hamatus	29	11.89	2.06E-03	15	0.34	3.35E-01
85	Crustacea	Copepoda	Centropages typicus	15	11.89	1.79E-04	17	0.35	2.81E-01
86	Crustacea	Copepoda	Centropages typicus	15	11.89	1.66E-03	17	0.38	3.06E-01
87	Crustacea	Copepoda	Eurytemora affinis	19	11.89	3.76E-04	5.5	0.06	1.57E-01
88	Crustacea	Copepoda	Eurytemora affinis	19	11.89	3.61E-04	10	0.13	2.16E-01

89	Crustacea	Copepoda	Eurytemora affinis	19	11.89	3.47E-04	15	0.25	2.53E-01
90	Crustacea	Copepoda	Eurytemora affinis	19	11.89	2.95E-04	20	0.28	1.66E-01
91	Crustacea	Copepoda	Eurytemora affinis	19	11.89	2.70E-04	25	0.36	1.29E-01
92	Crustacea	Copepoda	Eurytemora herdmani	12	11.89	1.09E-03	10	0.21	3.50E-01
93	Crustacea	Copepoda	Eurytemora herdmani	12	11.89	2.96E-03	3	0.06	1.89E-01
94	Crustacea	Copepoda	Eurytemora herdmani	12	11.89	7.47E-04	3	0.09	3.10E-01
95	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	5.00E-04	15	0.11	1.07E-01
96	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.60E-03	15	0.18	1.76E-01
97	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.32E-02	15	0.11	1.14E-01
98	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	2.00E-03	15	0.22	2.18E-01
99	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.08E-02	15	0.10	1.03E-01
100	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	5.00E-04	20	0.16	9.62E-02
101	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.60E-03	20	0.30	1.77E-01
102	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.32E-02	20	0.18	1.06E-01
103	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	2.00E-03	20	0.34	2.03E-01
104	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.08E-02	20	0.17	9.98E-02
105	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	5.00E-04	25	0.26	9.11E-02
106	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.60E-03	25	0.40	1.43E-01
107	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.32E-02	25	0.25	9.00E-02
108	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	2.00E-03	25	0.52	1.86E-01
109	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.08E-02	25	0.22	7.93E-02
110	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	5.00E-04	30	0.35	7.51E-02
111	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.60E-03	30	0.52	1.11E-01
112	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.32E-02	30	0.20	4.27E-02
113	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	2.00E-03	30	0.75	1.61E-01
114	Crustacea	Copepoda	Labidocera euchaeta	47	5.2	1.08E-02	30	0.15	3.24E-02
115	Crustacea	Copepoda	Oithona similis	46		8.90E-05	15	0.20	2.00E-01
116	Crustacea	Copepoda	Oithona similis	46		5.00E-04	15	0.07	7.40E-02
117	Crustacea	Copepoda	Oncaea mediterranea	39		2.19E-04	20	0.26	1.55E-01
118	Crustacea	Copepoda	Paracalanus sp.	49	11.89	4.60E-05	10.3	0.12	1.87E-01
119	Crustacea	Copepoda	Paracalanus sp.	49	11.89	4.60E-05	13	0.15	1.88E-01
120	Crustacea	Copepoda	Paracalanus sp.	49	11.89	4.60E-05	15	0.18	1.84E-01
121	Crustacea	Copepoda	Paracalanus sp.	49	11.89	4.60E-05	17.5	0.23	1.74E-01

122	Crustacea	Copepoda	Paracalanus sp.	49	11.89	4.60E-05	20	0.27	1.60E-01
123	Crustacea	Copepoda	Paracalanus sp.	49	11.89	6.32E-04	10.3	0.24	3.88E-01
124	Crustacea	Copepoda	Paracalanus sp.	49	11.89	6.32E-04	13	0.32	3.96E-01
125	Crustacea	Copepoda	Paracalanus sp.	49	11.89	6.32E-04	15	0.39	3.88E-01
126	Crustacea	Copepoda	Paracalanus sp.	49	11.89	6.32E-04	17.5	0.48	3.70E-01
127	Crustacea	Copepoda	Paracalanus sp.	49	11.89	6.32E-04	20	0.57	3.42E-01
128	Crustacea	Copepoda	Pseudocalanus elongatus	18	11.89	2.00E-04	12.5	0.18	2.33E-01
129	Crustacea	Copepoda	Pseudocalanus elongatus	18	11.89	4.80E-04	12.5	0.38	4.92E-01
130	Crustacea	Copepoda	Pseudocalanus elongatus	18	11.89	4.00E-03	12.5	0.19	2.46E-01
131	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	6.00E-04	15.5	0.25	2.39E-01
132	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	1.20E-03	15.5	0.25	2.34E-01
133	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	2.00E-03	15.5	0.23	2.17E-01
134	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	2.80E-03	15.5	0.20	1.91E-01
135	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	6.00E-04	12	0.23	3.07E-01
136	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	1.20E-03	12	0.22	2.93E-01
137	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	2.00E-03	12	0.21	2.82E-01
138	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	2.80E-03	12	0.20	2.71E-01
139	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	6.00E-04	8	0.16	3.20E-01
140	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	1.20E-03	8	0.16	3.19E-01
141	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	2.00E-03	8	0.15	3.14E-01
142	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	2.80E-03	8	0.15	3.02E-01
143	Crustacea	Copepoda	Pseudocalanus sp.	50	11.89	4.00E-03	8	0.13	2.73E-01
144	Crustacea	Copepoda	Pseudocalanus sp.	29	11.89	2.99E-04	15	0.15	1.50E-01
145	Crustacea	Copepoda	Pseudocalanus sp.	29	11.89	2.15E-03	15	0.20	1.95E-01
146	Crustacea	Copepoda	Pseudodiaptomus marinus	48	11.89	1.36E-04	20	0.23	1.38E-01
147	Crustacea	Copepoda	Pseudodiaptomus marinus	48	11.89	1.35E-03	20	0.36	2.12E-01
148	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	9.90E-05	6.6	0.10	2.47E-01
149	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	9.90E-05	10	0.18	3.08E-01
150	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	9.90E-05	15	0.34	3.36E-01

151	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	9.90E-05	20	0.52	3.13E-01
152	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	9.90E-05	22	0.61	2.96E-01
153	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	9.90E-05	28	0.89	2.34E-01
154	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	1.13E-03	6.6	0.10	2.40E-01
155	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	1.13E-03	10	0.20	3.33E-01
156	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	1.13E-03	15	0.40	4.03E-01
157	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	1.13E-03	20	0.68	4.06E-01
158	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	1.13E-03	22	0.81	3.94E-01
159	Crustacea	Copepoda	Sinocalanus tenellus	28	11.89	1.13E-03	28	1.28	3.35E-01
160	Crustacea	Copepoda	Temora longicornis	29	11.89	1.79E-04	15	0.26	2.57E-01
161	Crustacea	Copepoda	Temora longicornis	29	11.89	1.68E-03	15	0.34	3.38E-01
162	Crustacea	Copepoda	Temora longicornis	18	11.89	1.30E-04	12.5	0.21	2.72E-01
163	Crustacea	Copepoda	Temora longicornis	18	11.89	1.80E-03	12.5	0.34	4.40E-01
164	Crustacea	Copepoda	Temora longicornis	18	11.89	8.00E-03	12.5	0.31	4.01E-01
165	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.50E-02	8	0.13	2.69E-01
166	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	3.00E-02	8	0.13	2.57E-01
167	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	5.00E-02	8	0.12	2.45E-01
168	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.00E-01	8	0.11	2.28E-01
169	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.50E-01	8	0.11	2.16E-01
170	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	2.00E-01	8	0.10	2.08E-01
171	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	3.00E-01	8	0.10	1.95E-01
172	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	5.00E-01	8	0.09	1.75E-01
173	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	7.50E-01	8	0.08	1.54E-01
174	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.00E+00	8	0.07	1.38E-01
175	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.50E-02	12	0.19	2.63E-01
176	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	3.00E-02	12	0.18	2.45E-01
177	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	5.00E-02	12	0.17	2.33E-01
178	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.00E-01	12	0.15	2.10E-01
179	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.50E-01	12	0.15	1.97E-01
180	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	2.00E-01	12	0.14	1.87E-01
181	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	3.00E-01	12	0.13	1.70E-01
182	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	5.00E-01	12	0.11	1.47E-01
183	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	7.50E-01	12	0.09	1.25E-01

184	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.00E+00	12	0.08	1.08E-01
185	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.50E-02	15	0.25	2.47E-01
186	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	3.00E-02	15	0.23	2.31E-01
187	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	5.00E-02	15	0.22	2.22E-01
188	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.00E-01	15	0.21	2.07E-01
189	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.50E-01	15	0.20	1.97E-01
190	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	2.00E-01	15	0.19	1.88E-01
191	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	3.00E-01	15	0.17	1.74E-01
192	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	5.00E-01	15	0.15	1.52E-01
193	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	7.50E-01	15	0.13	1.29E-01
194	Crustacea	Crustacea	Calliopius laeviusculus	10	8.42	1.00E+00	15	0.11	1.09E-01
195	Crustacea	Crustacea	Euphausia pacifica	45	8.4	2.80E-03	8	0.10	2.04E-01
196	Crustacea	Crustacea	Euphausia pacifica	45	8.4	1.11E-02	8	0.11	2.32E-01
197	Crustacea	Crustacea	Euphausia pacifica	45	8.4	3.39E-02	8	0.04	8.22E-02
198	Crustacea	Crustacea	Euphausia pacifica	45	8.4	1.24E-01	8	0.02	4.93E-02
199	Crustacea	Crustacea	Euphausia pacifica	45	8.4	1.99E-01	8	0.02	4.11E-02
200	Crustacea	Crustacea	Euphausia pacifica	45	8.4	4.17E-01	8	0.02	3.08E-02
201	Crustacea	Crustacea	Euphausia pacifica	45	8.4	2.78E-03	12	0.08	1.13E-01
202	Crustacea	Crustacea	Euphausia pacifica	45	8.4	8.83E-03	12	0.15	2.04E-01
203	Crustacea	Crustacea	Euphausia pacifica	45	8.4	3.32E-02	12	0.07	8.99E-02
204	Crustacea	Crustacea	Euphausia pacifica	45	8.4	1.37E-01	12	0.04	5.31E-02
205	Crustacea	Crustacea	Euphausia pacifica	45	8.4	2.25E-01	12	0.03	4.36E-02
206	Crustacea	Crustacea	Euphausia pacifica	45	8.4	4.92E-01	12	0.02	3.27E-02
207	Crustacea	Crustacea	Euphausia pacifica	33	8.4	2.51E-01	10	0.02	3.35E-02
208	Crustacea	Crustacea	Euphausia pacifica	33	8.4	2.52E-01	10	0.02	3.18E-02
209	Crustacea	Crustacea	Euphausia pacifica	33	8.4	3.64E-01	10	0.02	2.68E-02
210	Crustacea	Crustacea	Euphausia pacifica	33	8.4	7.96E-01	10	0.01	1.34E-02
211	Crustacea	Crustacea	Euphausia pacifica	33	8.4	4.38E-01	10	0.01	1.34E-02
212	Crustacea	Crustacea	Euphausia pacifica	33	8.4	6.56E-01	10	0.01	8.37E-03
213	Crustacea	Crustacea	Euphausia pacifica	33	8.4	8.91E-01	10	0.01	1.17E-02
214	Crustacea	Crustacea	Euphausia pacifica	33	8.4	7.35E-01	10	0.00	6.69E-03
215	Crustacea	Crustacea	Euphausia pacifica	33	8.4	7.51E-01	10	0.00	5.02E-03
216	Crustacea	Crustacea	Euphausia superba	21	10.4	1.52E+01	0.75	0.01	3.69E-02

217	Crustacea	Crustacea	Euphausia superba	21	10.4	2.48E+01	0.75	0.01	2.91E-02
218	Crustacea	Crustacea	Euphausia superba	21	10.4	3.63E+01	0.75	0.01	2.78E-02
219	Crustacea	Crustacea	Euphausia superba	21	10.4	3.59E+01	0.75	0.00	2.13E-02
220	Crustacea	Crustacea	Euphausia superba	21	10.4	4.82E+01	0.75	0.00	2.04E-02
221	Crustacea	Crustacea	Euphausia superba	21	10.4	2.62E+01	0.75	0.00	1.82E-02
222	Crustacea	Crustacea	Euphausia superba	21	10.4	5.16E+01	0.75	0.00	1.69E-02
223	Crustacea	Crustacea	Euphausia superba	21	10.4	5.15E+01	0.75	0.00	1.47E-02
224	Crustacea	Crustacea	Euphausia superba	21	10.4	6.45E+01	0.75	0.00	1.17E-02
225	Crustacea	Crustacea	Euphausia superba	21	10.4	6.08E+01	0.75	0.00	8.67E-03
226	Crustacea	Crustacea	Euphausia superba	5	10.4	2.02E+01	2	0.01	2.52E-02
227	Crustacea	Crustacea	Euphausia superba	5	10.4	1.87E+01	2	0.01	3.51E-02
228	Crustacea	Crustacea	Euphausia superba	5	10.4	2.06E+01	2	0.01	2.40E-02
229	Crustacea	Crustacea	Homarus americanus	34	8.07	4.03E-01	22	0.20	9.73E-02
230	Crustacea	Crustacea	Homarus americanus	34	8.07	5.82E-01	22	0.11	5.45E-02
231	Crustacea	Crustacea	Homarus americanus	34	8.07	7.34E-01	22	0.13	6.37E-02
232	Crustacea	Crustacea	Homarus americanus	34	8.07	8.42E-01	22	0.07	3.45E-02
233	Crustacea	Crustacea	Homarus americanus	34	8.07	9.57E-01	22	0.04	1.85E-02
234	Crustacea	Crustacea	Homarus americanus	34	8.07	1.64E+00	22	0.12	5.89E-02
235	Crustacea	Crustacea	Hyas araneus	1	8.07	4.19E-02	12	0.10	1.36E-01
236	Crustacea	Crustacea	Hyas araneus	1	8.07	9.18E-02	12	0.06	8.44E-02
237	Crustacea	Crustacea	Hyas araneus	1	8.07	1.66E-01	12	0.06	8.44E-02
238	Crustacea	Crustacea	Hyas araneus	1	8.07	2.17E-01	12	0.02	2.18E-02
239	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.78E-02	12	0.22	3.04E-01
240	Crustacea	Crustacea	Hyas coarctatus	23	8.07	2.44E-02	12	0.09	1.28E-01
241	Crustacea	Crustacea	Hyas coarctatus	23	8.07	2.92E-02	12	0.09	1.17E-01
242	Crustacea	Crustacea	Hyas coarctatus	23	8.07	3.46E-02	12	0.09	1.16E-01
243	Crustacea	Crustacea	Hyas coarctatus	23	8.07	3.87E-02	12	0.03	3.54E-02
244	Crustacea	Crustacea	Hyas coarctatus	23	8.07	4.15E-02	12	0.05	6.13E-02
245	Crustacea	Crustacea	Hyas coarctatus	23	8.07	5.32E-02	12	0.13	1.74E-01
246	Crustacea	Crustacea	Hyas coarctatus	23	8.07	6.72E-02	12	0.11	1.44E-01
247	Crustacea	Crustacea	Hyas coarctatus	23	8.07	8.01E-02	12	0.07	9.40E-02
248	Crustacea	Crustacea	Hyas coarctatus	23	8.07	9.14E-02	12	0.06	8.58E-02
249	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.01E-01	12	0.04	4.90E-02

250	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.06E-01	12	0.01	1.77E-02
251	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.12E-01	12	0.07	9.53E-02
252	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.34E-01	12	0.11	1.50E-01
253	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.56E-01	12	0.04	5.58E-02
254	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.57E-01	12	0.05	6.67E-02
255	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.69E-01	12	0.03	3.95E-02
256	Crustacea	Crustacea	Hyas coarctatus	23	8.07	1.35E-01	12	0.12	1.57E-01
257	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	4.51E-02	17	0.07	5.86E-02
258	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	1.53E-01	17	0.03	2.12E-02
259	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	2.40E-01	17	0.01	8.14E-03
260	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	2.89E-01	17	0.01	4.07E-03
261	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	3.24E-01	17	0.00	3.26E-03
262	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	3.50E-01	17	0.00	1.63E-03
263	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	3.63E-01	17	0.00	8.14E-04
264	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	4.11E-02	17	0.06	5.21E-02
265	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	1.23E-01	17	0.02	1.95E-02
266	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	1.87E-01	17	0.01	8.14E-03
267	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	2.25E-01	17	0.01	4.07E-03
268	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	2.48E-01	17	0.00	2.44E-03
269	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	2.62E-01	17	0.00	8.14E-04
270	Crustacea	Crustacea	Metamysidopsis elongata	7	9.78	2.69E-01	17	0.00	8.14E-04
271	Crustacea	Crustacea	Themisto japonica	22	8.91	6.04E-03	1	0.06	2.46E-01

272	Crustacea	Crustacea	Themisto japonica	22	8.91	1.29E-02	1	0.04	1.87E-01
273	Crustacea	Crustacea	Themisto japonica	22	8.91	2.43E-02	1	0.04	1.49E-01
274	Crustacea	Crustacea	Themisto japonica	22	8.91	4.22E-02	1	0.03	1.21E-01
275	Crustacea	Crustacea	Themisto japonica	22	8.91	6.94E-02	1	0.02	1.01E-01
276	Crustacea	Crustacea	Themisto japonica	22	8.91	1.09E-01	1	0.02	8.45E-02
277	Crustacea	Crustacea	Themisto japonica	22	8.91	1.67E-01	1	0.02	7.19E-02
278	Crustacea	Crustacea	Themisto japonica	22	8.91	2.50E-01	1	0.01	6.09E-02
279	Crustacea	Crustacea	Themisto japonica	22	8.91	3.68E-01	1	0.01	5.20E-02
280	Crustacea	Crustacea	Themisto japonica	22	8.91	5.36E-01	1	0.01	4.44E-02
281	Crustacea	Crustacea	Themisto japonica	22	8.91	7.78E-01	1	0.01	3.76E-02
282	Crustacea	Crustacea	Themisto japonica	22	8.91	6.04E-03	7	0.12	2.82E-01
283	Crustacea	Crustacea	Themisto japonica	22	8.91	1.29E-02	7	0.09	2.15E-01
284	Crustacea	Crustacea	Themisto japonica	22	8.91	2.43E-02	7	0.08	1.71E-01
285	Crustacea	Crustacea	Themisto japonica	22	8.91	4.22E-02	7	0.06	1.39E-01
286	Crustacea	Crustacea	Themisto japonica	22	8.91	6.94E-02	7	0.05	1.16E-01
287	Crustacea	Crustacea	Themisto japonica	22	8.91	1.09E-01	7	0.04	9.71E-02
288	Crustacea	Crustacea	Themisto japonica	22	8.91	1.67E-01	7	0.04	8.91E-02
289	Crustacea	Crustacea	Themisto japonica	22	8.91	2.50E-01	7	0.03	7.00E-02
290	Crustacea	Crustacea	Themisto japonica	22	8.91	3.68E-01	7	0.03	5.97E-02
291	Crustacea	Crustacea	Themisto japonica	22	8.91	5.36E-01	7	0.02	5.08E-02
292	Crustacea	Crustacea	Themisto japonica	22	8.91	7.78E-01	7	0.02	4.31E-02
293	Crustacea	Crustacea	Themisto japonica	22	8.91	6.04E-03	15	0.24	2.37E-01
294	Crustacea	Crustacea	Themisto japonica	22	8.91	1.29E-02	15	0.18	1.80E-01
295	Crustacea	Crustacea	Themisto japonica	22	8.91	2.43E-02	15	0.14	1.44E-01
296	Crustacea	Crustacea	Themisto japonica	22	8.91	4.22E-02	15	0.12	1.17E-01
297	Crustacea	Crustacea	Themisto japonica	22	8.91	6.94E-02	15	0.10	9.71E-02
298	Crustacea	Crustacea	Themisto japonica	22	8.91	1.09E-01	15	0.08	8.16E-02
299	Crustacea	Crustacea	Themisto japonica	22	8.91	1.67E-01	15	0.07	6.91E-02
300	Crustacea	Crustacea	Themisto japonica	22	8.91	2.50E-01	15	0.06	5.87E-02
301	Crustacea	Crustacea	Themisto japonica	22	8.91	3.68E-01	15	0.05	5.00E-02
302	Crustacea	Crustacea	Themisto japonica	22	8.91	5.36E-01	15	0.04	4.26E-02
303	Crustacea	Crustacea	Themisto japonica	22	8.91	7.78E-01	15	0.04	3.61E-02
304	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	5.57E-04	20	0.75	4.47E-01

305	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	1.04E-02	20	0.98	5.88E-01
306	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	8.20E-02	20	0.30	1.81E-01
307	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	1.81E-01	20	0.09	5.14E-02
308	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	3.04E-01	20	0.10	6.09E-02
309	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	4.83E-01	20	0.03	1.77E-02
310	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	7.21E-01	20	0.09	5.40E-02
311	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	1.01E+00	20	0.01	4.29E-03
312	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	4.95E-05	13	0.01	1.22E-02
313	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	7.18E-05	13	0.27	3.27E-01
314	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	2.92E-04	13	0.42	5.14E-01
315	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	1.73E-03	13	0.54	6.68E-01
316	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	9.64E-03	13	0.49	6.00E-01
317	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	6.73E-02	13	0.71	8.73E-01
318	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	2.22E-01	13	0.06	7.41E-02
319	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	3.52E-01	13	0.07	8.38E-02
320	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	4.80E-01	13	0.03	3.42E-02
321	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	7.17E-01	13	0.07	9.07E-02
322	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	3.35E-05	13	0.22	2.69E-01
323	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	1.45E-04	13	0.65	8.00E-01
324	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	1.01E-03	13	0.65	8.02E-01
325	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	6.84E-03	13	0.42	5.17E-01
326	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	4.99E-02	13	0.36	4.47E-01
327	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	2.15E-01	13	0.13	1.54E-01
328	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	3.79E-01	13	0.07	7.99E-02
329	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	5.11E-01	13	0.09	1.14E-01
330	Ctenophora	Cydippida	Pleurobrachia bachei	42	0.15	6.54E-01	13	0.01	1.75E-02
331	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	1.53E-02	14.2	0.33	3.54E-01
332	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	1.43E-01	14.2	0.22	2.42E-01
333	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	4.47E-01	14.2	0.12	1.35E-01
334	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	8.75E-01	14.2	0.04	4.43E-02
335	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	1.52E+00	14.2	0.05	5.37E-02
336	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	2.16E+00	14.2	0.02	2.66E-02
337	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	3.33E-02	14.2	0.11	1.24E-01

338	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	1.30E-01	14.2	0.22	2.38E-01
339	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	5.11E-01	14.2	0.15	1.59E-01
340	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	1.16E+00	14.2	0.06	6.74E-02
341	Ctenophora	Cydippida	Pleurobrachia bachei	20	0.15	1.66E+00	14.2	0.02	2.58E-02
342	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	5.00E-03	16.5	0.08	7.25E-02
343	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	1.50E-02	16.5	0.26	2.19E-01
344	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	3.50E-02	16.5	0.30	2.55E-01
345	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	5.00E-03	20	0.70	4.17E-01
346	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	1.50E-02	20	0.51	3.05E-01
347	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	3.50E-02	20	0.33	1.98E-01
348	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	5.00E-03	23.5	0.56	2.33E-01
349	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	1.50E-02	23.5	0.49	2.03E-01
350	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	3.50E-02	23.5	0.27	1.13E-01
351	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	5.00E-03	26.5	0.69	2.11E-01
352	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	1.50E-02	26.5	0.60	1.83E-01
353	Chordata	Doliolida	Dolioletta gegenbauri	16	0.3	3.50E-02	26.5	0.47	1.43E-01
354	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	3.52E-03	20	0.09	5.41E-02
355	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	3.83E-03	20	0.08	4.89E-02
356	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	4.45E-03	20	0.22	1.29E-01
357	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	5.59E-03	20	0.24	1.44E-01
358	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	6.88E-03	20	0.17	1.03E-01
359	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	8.31E-03	20	0.21	1.24E-01
360	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	1.02E-02	20	0.20	1.19E-01
361	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	1.25E-02	20	0.21	1.24E-01
362	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	1.68E-02	20	0.08	4.64E-02
363	Chordata	Doliolida	Dolioletta gegenbauri	11	0.3	2.15E-02	20	0.10	6.18E-02
364	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	1.38E+00	11.6	0.11	1.54E-01
365	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	2.81E+00	11.6	0.09	1.33E-01
366	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	5.58E+00	11.6	0.10	1.45E-01
367	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	1.04E+01	11.6	0.08	1.09E-01
368	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	1.66E+01	11.6	0.06	7.96E-02
369	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	2.39E+01	11.6	0.05	6.77E-02
370	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	3.04E+01	11.6	0.02	2.90E-02

371	Cnidaria	Hydromedusae	Aequorea victoria	2	0.75	3.38E+01	11.6	0.01	1.42E-02
372	Cnidaria	Hydromedusae	Aequorea vitrina	35	0.75	1.68E-01	15	0.17	1.69E-01
373	Cnidaria	Hydromedusae	Aequorea vitrina	35	0.75	7.97E-01	15	0.10	9.94E-02
374	Cnidaria	Hydromedusae	Aequorea vitrina	35	0.75	7.97E-01	15	0.06	5.59E-02
375	Cnidaria	Hydromedusae	Aequorea vitrina	35	0.75	1.68E+00	15	0.05	5.00E-02
376	Cnidaria	Hydromedusae	Aequorea vitrina	35	0.75	2.42E+00	15	0.05	5.00E-02
377	Cnidaria	Hydromedusae	Aequorea vitrina	35	0.75	5.15E+00	15	0.06	6.00E-02
378	Cnidaria	Hydromedusae	Cladonema californicum	8	0.81	5.22E-03	18	0.35	2.56E-01
379	Cnidaria	Hydromedusae	Cladonema californicum	8	0.81	1.88E-02	18	0.24	1.73E-01
380	Cnidaria	Hydromedusae	Cladonema californicum	8	0.81	5.15E-02	18	0.12	8.86E-02
381	Cnidaria	Hydromedusae	Cladonema californicum	8	0.81	1.12E-01	18	0.12	8.53E-02
382	Cnidaria	Hydromedusae	Cladonema californicum	8	0.81	1.83E-01	18	0.05	3.52E-02
383	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	4.74E-02	12	0.29	3.92E-01
384	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	1.10E-01	12	0.15	2.05E-01
385	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	1.69E-01	12	0.12	1.66E-01
386	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	2.23E-01	12	0.08	1.08E-01
387	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	2.45E-01	12	0.08	1.08E-01
388	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	3.65E-01	12	0.07	1.01E-01
389	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	3.80E-01	12	0.04	6.01E-02
390	Cnidaria	Hydromedusae	Sarsia tubulosa	9	0.25	6.52E-01	12	0.04	5.02E-02
391	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	3.96E+00	24	0.17	6.92E-02
392	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	9.89E+00	24	1.41	5.58E-01
393	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.56E+01	24	1.39	5.50E-01
394	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.53E+01	24	0.58	2.29E-01
395	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	3.56E+01	24	0.27	1.06E-01
396	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	6.20E+01	24	0.16	6.39E-02
397	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.05E+02	24	0.35	1.40E-01
398	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.44E+02	24	0.36	1.41E-01
399	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.70E+02	24	0.75	2.96E-01
400	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.26E+02	24	0.17	6.79E-02
401	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.75E+02	24	0.15	6.11E-02
402	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	3.07E+02	24	0.09	3.72E-02
403	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.68E+00	17	0.58	4.70E-01

404	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.23E+00	17	0.07	5.94E-02
405	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.61E+00	17	0.29	2.33E-01
406	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	3.62E+00	17	0.18	1.45E-01
407	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	7.38E+00	17	0.00	1.16E-07
408	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.01E+01	17	0.63	5.10E-01
409	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.61E+01	17	0.33	2.68E-01
410	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.03E+01	17	0.16	1.29E-01
411	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.37E+01	17	0.16	1.29E-01
412	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	3.11E+01	17	0.43	3.51E-01
413	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	4.19E+01	17	0.21	1.69E-01
414	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	5.81E+01	17	0.42	3.45E-01
415	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	7.51E+01	17	0.08	6.58E-02
416	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	8.89E+01	17	0.30	2.41E-01
417	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.13E+02	17	0.24	1.94E-01
418	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.45E+02	17	0.23	1.89E-01
419	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	1.86E+02	17	0.23	1.88E-01
420	Ctenophora	Lobata	Bolinopsis mikado	24	0.07	2.31E+02	17	0.21	1.72E-01
421	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	1.86E-01	25.4	0.31	1.05E-01
422	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	2.42E-01	25.4	0.43	1.47E-01
423	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	2.98E-01	25.4	0.17	5.81E-02
424	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	4.80E-01	25.4	1.96	6.72E-01
425	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	7.36E-01	25.4	0.03	1.03E-02
426	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	7.59E-01	25.4	0.04	1.41E-02
427	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	8.41E-01	25.4	0.05	1.78E-02
428	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	1.07E+00	25.4	0.16	5.57E-02
429	Ctenophora	Lobata	Mnemiopsis leidyi	17	0.1	1.60E+00	25.4	0.11	3.93E-02
430	Ctenophora	Lobata	Mnemiopsis leidyi	44	0.1	1.10E-02	26	0.68	2.19E-01
431	Ctenophora	Lobata	Mnemiopsis leidyi	44	0.1	1.10E-02	26	0.92	2.96E-01
432	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.21E-03	26	0.50	1.60E-01
433	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.20E-02	26	0.73	2.37E-01
434	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.83E-02	26	0.72	2.32E-01
435	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	9.57E-02	26	0.54	1.75E-01
436	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	3.44E-01	26	0.14	4.54E-02

437	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	8.38E-01	26	0.33	1.06E-01
438	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.28E+00	26	0.48	1.53E-01
439	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.54E+00	26	0.24	7.59E-02
440	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.51E+00	26	0.11	3.55E-02
441	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	3.21E+00	26	0.06	1.88E-02
442	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.98E+00	26	0.37	1.21E-01
443	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	6.96E+00	26	0.09	2.94E-02
444	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	8.13E+00	26	0.04	1.45E-02
445	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	9.61E+00	26	0.09	3.02E-02
446	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	9.74E+00	26	0.16	5.30E-02
447	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.26E+01	26	0.08	2.58E-02
448	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.91E+01	26	0.09	2.87E-02
449	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	7.52E-03	31	0.66	1.27E-01
450	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	3.59E-02	31	0.44	8.38E-02
451	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	5.49E-02	31	1.35	2.60E-01
452	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.63E-01	31	0.49	9.46E-02
453	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.81E-01	31	0.24	4.54E-02
454	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	8.82E-01	31	0.23	4.36E-02
455	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.39E+00	31	0.24	4.54E-02
456	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.87E+00	31	0.31	5.91E-02
457	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.93E+00	31	0.20	3.83E-02
458	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.52E-03	21	0.33	1.78E-01
459	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	3.89E-03	21	1.45	7.83E-01
460	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	9.87E-03	21	0.38	2.08E-01
461	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.76E-02	21	0.38	2.04E-01
462	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.99E-02	21	1.09	5.90E-01
463	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.53E-02	21	0.93	4.99E-01
464	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	7.69E-02	21	0.21	1.14E-01
465	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.94E-01	21	0.35	1.91E-01
466	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	3.67E-01	21	0.15	7.91E-02
467	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.06E-01	21	0.07	3.79E-02
468	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	6.14E-01	21	0.24	1.32E-01
469	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.19E+00	21	0.29	1.56E-01

470	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.73E+00	21	0.10	5.53E-02
471	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.07E+00	21	0.21	1.11E-01
472	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	2.64E+00	21	0.48	2.56E-01
473	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	3.38E+00	21	0.07	3.68E-02
474	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	4.55E+00	21	0.24	1.27E-01
475	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	6.87E+00	21	0.07	3.74E-02
476	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	9.74E+00	21	0.14	7.73E-02
477	Ctenophora	Lobata	Mnemiopsis mccradyi	41	0.085	1.21E+01	21	0.06	3.44E-02
478	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	1.57E-01	26	0.78	2.52E-01
479	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	3.27E-01	26	0.64	2.08E-01
480	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	5.99E-01	26	0.40	1.29E-01
481	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	4.13E-01	26	0.38	1.24E-01
482	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	2.56E+00	26	0.53	1.69E-01
483	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	1.82E+00	26	0.34	1.08E-01
484	Ctenophora	Lobata	Mnemiopsis mccradyi	30	0.085	3.69E+00	21	0.24	1.29E-01
485	Ctenophora	Nuda	Beroe ovata	26	0.16	8.16E+01	26	0.21	6.68E-02
486	Ctenophora	Nuda	Beroe ovata	26	0.16	9.05E+01	26	0.00	2.64E-08
487	Ctenophora	Nuda	Beroe ovata	26	0.16	9.65E+01	26	0.13	4.11E-02
488	Ctenophora	Nuda	Beroe ovata	26	0.16	1.13E+02	26	0.18	5.87E-02
489	Ctenophora	Nuda	Beroe ovata	26	0.16	1.31E+02	26	0.12	3.79E-02
490	Ctenophora	Nuda	Beroe ovata	26	0.16	1.47E+02	26	0.11	3.61E-02
491	Ctenophora	Nuda	Beroe ovata	26	0.16	1.64E+02	26	0.11	3.44E-02
492	Ctenophora	Nuda	Beroe ovata	26	0.16	1.77E+02	26	0.05	1.59E-02
493	Ctenophora	Nuda	Beroe ovata	26	0.16	1.82E+02	26	0.00	9.11E-04
494	Ctenophora	Nuda	Beroe ovata	26	0.16	1.91E+02	26	0.10	3.12E-02
495	Ctenophora	Nuda	Beroe ovata	26	0.16	5.25E+01	26	0.19	5.98E-02
496	Ctenophora	Nuda	Beroe ovata	26	0.16	5.50E+01	26	0.09	3.01E-02
497	Ctenophora	Nuda	Beroe ovata	26	0.16	6.97E+01	26	0.38	1.23E-01
498	Ctenophora	Nuda	Beroe ovata	26	0.16	1.02E+02	26	0.38	1.21E-01
499	Ctenophora	Nuda	Beroe ovata	26	0.16	1.27E+02	26	0.06	1.96E-02
500	Ctenophora	Nuda	Beroe ovata	26	0.16	1.34E+02	26	0.06	1.85E-02
501	Ctenophora	Nuda	Beroe ovata	26	0.16	1.38E+02	26	0.00	1.64E-09
502	Ctenophora	Nuda	Beroe ovata	26	0.16	5.35E+01	26	0.00	7.48E-08

503	Ctenophora	Nuda	Beroe ovata	26	0.16	5.35E+01	26	0.00	6.73E-08
504	Ctenophora	Nuda	Beroe ovata	26	0.16	5.82E+01	26	0.17	5.40E-02
505	Ctenophora	Nuda	Beroe ovata	26	0.16	5.60E+01	26	0.09	2.95E-02
506	Ctenophora	Nuda	Beroe ovata	26	0.16	6.57E+01	26	0.23	7.29E-02
507	Ctenophora	Nuda	Beroe ovata	26	0.16	7.88E+01	26	0.14	4.41E-02
508	Ctenophora	Nuda	Beroe ovata	26	0.16	8.43E+01	26	0.00	1.61E-08
509	Ctenophora	Nuda	Beroe ovata	26	0.16	8.71E+01	26	0.06	2.09E-02
510	Ctenophora	Nuda	Beroe ovata	26	0.16	9.30E+01	26	0.07	2.13E-02
511	Ctenophora	Nuda	Beroe ovata	26	0.16	9.97E+01	26	0.07	2.32E-02
512	Chordata	Salpida	Thalia democratica	11	0.87	6.29E-03	20	0.34	2.01E-01
513	Chordata	Salpida	Thalia democratica	11	0.87	8.04E-03	20	0.16	9.28E-02
514	Chordata	Salpida	Thalia democratica	11	0.87	1.01E-02	20	0.31	1.86E-01
515	Chordata	Salpida	Thalia democratica	11	0.87	1.32E-02	20	0.22	1.31E-01
516	Chordata	Salpida	Thalia democratica	11	0.87	1.53E-02	20	0.06	3.86E-02
517	Chordata	Salpida	Thalia democratica	11	0.87	1.60E-02	20	0.03	1.54E-02
518	Chordata	Salpida	Thalia democratica	11	0.87	3.53E-03	20	0.04	2.31E-02
519	Chordata	Salpida	Thalia democratica	11	0.87	3.68E-03	20	0.04	2.57E-02
520	Chordata	Salpida	Thalia democratica	11	0.87	4.15E-03	20	0.20	1.19E-01
521	Chordata	Salpida	Thalia democratica	11	0.87	5.02E-03	20	0.18	1.08E-01
522	Chordata	Salpida	Thalia democratica	11	0.87	5.86E-03	20	0.13	7.73E-02
523	Chordata	Salpida	Thalia democratica	11	0.87	6.73E-03	20	0.15	8.76E-02
524	Cnidaria	Scyphomedusae	Aurelia aurita	36	0.2	1.99E-02	15	0.25	2.51E-01
525	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	1.24E-03	6	0.24	5.98E-01
526	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	1.99E-03	9.5	0.20	3.58E-01
527	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	3.03E-03	12	0.32	4.32E-01
528	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	1.77E-03	15	0.25	2.48E-01
529	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	4.79E-03	18	0.39	2.88E-01
530	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	1.48E-03	15	0.25	2.54E-01
531	Cnidaria	Scyphomedusae	Aurelia aurita	3	0.2	4.65E-03	18	0.41	2.97E-01
532	Cnidaria	Scyphomedusae	Aurelia aurita	14	0.2	3.82E-02	15	0.24	2.38E-01
533	Cnidaria	Scyphomedusae	Aurelia aurita	14	0.2	3.84E-02	15	0.21	2.08E-01
534	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	9.78E-03	10	0.07	1.12E-01
535	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	1.22E-02	12	0.10	1.35E-01

536	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	2.07E-02	15	0.17	1.74E-01
537	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	2.48E-02	17	0.20	1.63E-01
538	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	3.29E-02	21	0.24	1.30E-01
539	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	2.66E-02	22.5	0.21	9.69E-02
540	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	2.07E-02	24.5	0.17	6.53E-02
541	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	1.08E-02	26	0.08	2.63E-02
542	Cnidaria	Scyphomedusae	Aurelia labiata	51	0.2	1.17E-02	28	0.09	2.42E-02
543	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	37	0.53	9.32E-03	23	0.74	3.25E-01
544	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	2.39E+00	27.5	0.09	2.57E-02
545	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	6.39E+00	27.5	0.04	1.06E-02
546	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	1.06E+01	27.5	0.05	1.41E-02
547	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	1.50E+01	27.5	0.01	2.78E-03
548	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	1.72E+01	27.5	0.01	2.92E-03
549	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	1.93E+01	27.5	0.00	1.31E-03
550	Cnidaria	Scyphomedusae	Chrysaora quinquecirrha	31	0.53	2.02E+01	27.5	0.00	8.51E-04
551	Cnidaria	Scyphomedusae	Nemopilema nomurai	25	0.55	1.08E+01	25	0.07	2.63E-02
552	Cnidaria	Scyphomedusae	Nemopilema nomurai	25	0.55	2.17E+01	25	0.05	1.87E-02
553	Cnidaria	Scyphomedusae	Nemopilema nomurai	25	0.55	4.74E+01	25	0.09	3.21E-02
554	Cnidaria	Scyphomedusae	Nemopilema nomurai	25	0.55	1.10E+02	25	0.06	2.25E-02
555	Cnidaria	Scyphomedusae	Pelagia noctiluca	32	0.35	1.95E-01	27.5	0.08	2.34E-02
556	Cnidaria	Scyphomedusae	Pelagia noctiluca	32	0.35	2.80E-01	27.5	0.02	5.32E-03
557	Cnidaria	Scyphomedusae	Pelagia noctiluca	32	0.35	1.85E-01	27.5	0.09	2.41E-02
558	Cnidaria	Scyphomedusae	Pelagia noctiluca	32	0.35	1.33E-01	27.5	0.10	2.82E-02
559	Cnidaria	Scyphomedusae	Pelagia noctiluca	32	0.35	2.21E-01	27.5	0.04	1.19E-02
560	Cnidaria	Scyphomedusae	Pelagia noctiluca	32	0.35	1.40E-01	27.5	0.06	1.60E-02

Record	Mass g (d-1)	Food offered
1	2.38E-02	Fed so that no more than 50% of copepod prey were removed
2	3.50E-02	Fed so that no more than 50% of copepod prey were removed
3	4.57E-02	Fed so that no more than 50% of copepod prey were removed
4	5.70E-02	Fed so that no more than 50% of copepod prey were removed
5	6.65E-02	Fed so that no more than 50% of copepod prey were removed

6	7.54E-02	Fed so that no more than 50% of copepod prey were removed
7	2.82E-02	Fed so that no more than 50% of copepod prey were removed
8	1.66E-02	Fed so that no more than 50% of copepod prey were removed
9	2.00E-02	Fed so that no more than 50% of copepod prey were removed
10	2.93E-02	Fed so that no more than 50% of copepod prey were removed
11	3.83E-02	Fed so that no more than 50% of copepod prey were removed
12	4.77E-02	Fed so that no more than 50% of copepod prey were removed
13	5.56E-02	Fed so that no more than 50% of copepod prey were removed
14	6.31E-02	Fed so that no more than 50% of copepod prey were removed
15	1.50E-02	Fed so that no more than 50% of copepod prey were removed
16	1.58E-03	Fed so that no more than 50% of copepod prey were removed
17	1.40E-02	Fed so that no more than 50% of copepod prey were removed
18	2.05E-02	Fed so that no more than 50% of copepod prey were removed
19	2.68E-02	Fed so that no more than 50% of copepod prey were removed
20	3.34E-02	Fed so that no more than 50% of copepod prey were removed
21	3.90E-02	Fed so that no more than 50% of copepod prey were removed
22	1.18E-02	Fed so that no more than 50% of copepod prey were removed
23	4.97E-03	Fed so that no more than 50% of copepod prey were removed
24	2.91E-02	Recently hatched Artemia added daily
25	2.24E-02	Recently hatched Artemia added daily
26	3.19E-02	Recently hatched Artemia added daily
27	2.85E-04	Recently hatched Artemia added daily
28	1.63E-02	Recently hatched Artemia added daily
29	2.66E-02	Laboratory high food (see Hirst & Bunker 2002)
30	5.65E-02	Laboratory high food (see Hirst & Bunker 2002)
31	4.41E-02	Laboratory high food (see Hirst & Bunker 2002)
32	2.80E-02	Laboratory high food (see Hirst & Bunker 2002)
33	2.97E-02	Laboratory high food (see Hirst & Bunker 2002)
34	2.64E-02	Laboratory high food (see Hirst & Bunker 2002)
35	4.26E-02	Laboratory high food (see Hirst & Bunker 2002)
36	2.92E-02	Laboratory high food (see Hirst & Bunker 2002)
37	7.60E-02	Laboratory high food (see Hirst & Bunker 2002)
38	1.63E-01	Laboratory high food (see Hirst & Bunker 2002)

39	3.90E-02	Laboratory high food (see Hirst & Bunker 2002)
40	9.00E-02	Laboratory high food (see Hirst & Bunker 2002)
41	6.59E-02	Laboratory high food (see Hirst & Bunker 2002)
42	9.17E-02	Laboratory high food (see Hirst & Bunker 2002)
43	1.15E-01	Laboratory high food (see Hirst & Bunker 2002)
44	6.89E-02	Laboratory high food (see Hirst & Bunker 2002)
45	8.52E-02	Laboratory high food (see Hirst & Bunker 2002)
46	1.18E-02	Laboratory high food (see Hirst & Bunker 2002)
47	8.81E-02	Laboratory high food (see Hirst & Bunker 2002)
48	2.26E-02	Laboratory high food (see Hirst & Bunker 2002)
49	9.60E-02	Laboratory high food (see Hirst & Bunker 2002)
50	1.03E-01	Laboratory high food (see Hirst & Bunker 2002)
51	1.04E-01	Laboratory high food (see Hirst & Bunker 2002)
52	6.86E-02	Laboratory high food (see Hirst & Bunker 2002)
53	1.11E-01	Laboratory high food (see Hirst & Bunker 2002)
54	1.22E-01	Laboratory high food (see Hirst & Bunker 2002)
55	1.18E-01	Laboratory high food (see Hirst & Bunker 2002)
56	8.67E-02	Laboratory high food (see Hirst & Bunker 2002)
57	9.46E-02	Laboratory high food (see Hirst & Bunker 2002)
58	1.08E-01	Laboratory high food (see Hirst & Bunker 2002)
59	1.33E-01	Laboratory high food (see Hirst & Bunker 2002)
60	1.18E-01	Laboratory high food (see Hirst & Bunker 2002)
61	5.10E-02	Laboratory high food (see Hirst & Bunker 2002)
62	5.47E-02	Laboratory high food (see Hirst & Bunker 2002)
63	5.53E-02	Laboratory high food (see Hirst & Bunker 2002)
64	5.41E-02	Laboratory high food (see Hirst & Bunker 2002)
65	5.11E-02	Laboratory high food (see Hirst & Bunker 2002)
66	1.86E-01	Laboratory high food (see Hirst & Bunker 2002)
67	1.91E-01	Laboratory high food (see Hirst & Bunker 2002)
68	1.88E-01	Laboratory high food (see Hirst & Bunker 2002)
69	1.79E-01	Laboratory high food (see Hirst & Bunker 2002)
70	1.64E-01	Laboratory high food (see Hirst & Bunker 2002)
71	1.49E-01	Laboratory high food (see Hirst & Bunker 2002)

72	1.40E-01	Laboratory high food (see Hirst & Bunker 2002)
73	1.30E-01	Laboratory high food (see Hirst & Bunker 2002)
74	1.17E-01	Laboratory high food (see Hirst & Bunker 2002)
75	1.01E-01	Laboratory high food (see Hirst & Bunker 2002)
76	5.87E-02	Laboratory high food (see Hirst & Bunker 2002)
77	5.88E-02	Laboratory high food (see Hirst & Bunker 2002)
78	5.70E-02	Laboratory high food (see Hirst & Bunker 2002)
79	5.34E-02	Laboratory high food (see Hirst & Bunker 2002)
80	4.85E-02	Laboratory high food (see Hirst & Bunker 2002)
81	2.49E-02	Laboratory high food (see Hirst & Bunker 2002)
82	4.65E-02	Laboratory high food (see Hirst & Bunker 2002)
83	3.26E-02	Laboratory high food (see Hirst & Bunker 2002)
84	7.13E-02	Laboratory high food (see Hirst & Bunker 2002)
85	3.25E-02	Laboratory high food (see Hirst & Bunker 2002)
86	6.18E-02	Laboratory high food (see Hirst & Bunker 2002)
87	2.18E-02	Laboratory high food (see Hirst & Bunker 2002)
88	2.98E-02	Laboratory high food (see Hirst & Bunker 2002)
89	3.45E-02	Laboratory high food (see Hirst & Bunker 2002)
90	2.18E-02	Laboratory high food (see Hirst & Bunker 2002)
91	1.66E-02	Laboratory high food (see Hirst & Bunker 2002)
92	6.35E-02	Laboratory high food (see Hirst & Bunker 2002)
93	4.41E-02	Laboratory high food (see Hirst & Bunker 2002)
94	5.12E-02	Laboratory high food (see Hirst & Bunker 2002)
95	1.60E-02	Laboratory high food (see Hirst & Bunker 2002)
96	3.52E-02	Laboratory high food (see Hirst & Bunker 2002)
97	3.86E-02	Laboratory high food (see Hirst & Bunker 2002)
98	4.61E-02	Laboratory high food (see Hirst & Bunker 2002)
99	3.32E-02	Laboratory high food (see Hirst & Bunker 2002)
100	1.44E-02	Laboratory high food (see Hirst & Bunker 2002)
101	3.55E-02	Laboratory high food (see Hirst & Bunker 2002)
102	3.61E-02	Laboratory high food (see Hirst & Bunker 2002)
103	4.30E-02	Laboratory high food (see Hirst & Bunker 2002)
104	3.22E-02	Laboratory high food (see Hirst & Bunker 2002)

105	1.36E-02	Laboratory high food (see Hirst & Bunker 2002)
106	2.86E-02	Laboratory high food (see Hirst & Bunker 2002)
107	3.05E-02	Laboratory high food (see Hirst & Bunker 2002)
108	3.93E-02	Laboratory high food (see Hirst & Bunker 2002)
109	2.56E-02	Laboratory high food (see Hirst & Bunker 2002)
110	1.12E-02	Laboratory high food (see Hirst & Bunker 2002)
111	2.21E-02	Laboratory high food (see Hirst & Bunker 2002)
112	1.45E-02	Laboratory high food (see Hirst & Bunker 2002)
113	3.39E-02	Laboratory high food (see Hirst & Bunker 2002)
114	1.05E-02	Laboratory high food (see Hirst & Bunker 2002)
115	1.94E-02	Laboratory high food (see Hirst & Bunker 2002)
116	1.11E-02	Laboratory high food (see Hirst & Bunker 2002)
117	1.89E-02	Laboratory high food (see Hirst & Bunker 2002)
118	1.54E-02	Laboratory high food (see Hirst & Bunker 2002)
119	1.55E-02	Laboratory high food (see Hirst & Bunker 2002)
120	1.52E-02	Laboratory high food (see Hirst & Bunker 2002)
121	1.43E-02	Laboratory high food (see Hirst & Bunker 2002)
122	1.32E-02	Laboratory high food (see Hirst & Bunker 2002)
123	6.15E-02	Laboratory high food (see Hirst & Bunker 2002)
124	6.27E-02	Laboratory high food (see Hirst & Bunker 2002)
125	6.15E-02	Laboratory high food (see Hirst & Bunker 2002)
126	5.86E-02	Laboratory high food (see Hirst & Bunker 2002)
127	5.43E-02	Laboratory high food (see Hirst & Bunker 2002)
128	2.77E-02	Laboratory high food (see Hirst & Bunker 2002)
129	7.28E-02	Laboratory high food (see Hirst & Bunker 2002)
130	6.18E-02	Laboratory high food (see Hirst & Bunker 2002)
131	3.74E-02	Laboratory high food (see Hirst & Bunker 2002)
132	4.35E-02	Laboratory high food (see Hirst & Bunker 2002)
133	4.58E-02	Laboratory high food (see Hirst & Bunker 2002)
134	4.40E-02	Laboratory high food (see Hirst & Bunker 2002)
135	4.80E-02	Laboratory high food (see Hirst & Bunker 2002)
136	5.46E-02	Laboratory high food (see Hirst & Bunker 2002)
137	5.96E-02	Laboratory high food (see Hirst & Bunker 2002)

138	6.22E-02	Laboratory high food (see Hirst & Bunker 2002)
139	5.00E-02	Laboratory high food (see Hirst & Bunker 2002)
140	5.93E-02	Laboratory high food (see Hirst & Bunker 2002)
141	6.63E-02	Laboratory high food (see Hirst & Bunker 2002)
142	6.94E-02	Laboratory high food (see Hirst & Bunker 2002)
143	6.87E-02	Laboratory high food (see Hirst & Bunker 2002)
144	1.97E-02	Laboratory high food (see Hirst & Bunker 2002)
145	4.20E-02	Laboratory high food (see Hirst & Bunker 2002)
146	1.49E-02	Laboratory high food (see Hirst & Bunker 2002)
147	4.06E-02	Laboratory high food (see Hirst & Bunker 2002)
148	2.46E-02	Laboratory high food (see Hirst & Bunker 2002)
149	3.07E-02	Laboratory high food (see Hirst & Bunker 2002)
150	3.35E-02	Laboratory high food (see Hirst & Bunker 2002)
151	3.12E-02	Laboratory high food (see Hirst & Bunker 2002)
152	2.95E-02	Laboratory high food (see Hirst & Bunker 2002)
153	2.33E-02	Laboratory high food (see Hirst & Bunker 2002)
154	4.40E-02	Laboratory high food (see Hirst & Bunker 2002)
155	6.11E-02	Laboratory high food (see Hirst & Bunker 2002)
156	7.40E-02	Laboratory high food (see Hirst & Bunker 2002)
157	7.46E-02	Laboratory high food (see Hirst & Bunker 2002)
158	7.24E-02	Laboratory high food (see Hirst & Bunker 2002)
159	6.14E-02	Laboratory high food (see Hirst & Bunker 2002)
160	2.97E-02	Laboratory high food (see Hirst & Bunker 2002)
161	6.84E-02	Laboratory high food (see Hirst & Bunker 2002)
162	2.90E-02	Laboratory high food (see Hirst & Bunker 2002)
163	9.06E-02	Laboratory high food (see Hirst & Bunker 2002)
164	1.20E-01	Laboratory high food (see Hirst & Bunker 2002)
165	9.43E-02	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
166	1.07E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
167	1.16E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
168	1.28E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
169	1.34E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
170	1.39E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet

171	1.45E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
172	1.47E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
173	1.43E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
174	1.38E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
175	9.20E-02	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
176	1.02E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
177	1.10E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
178	1.18E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
179	1.23E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
180	1.25E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
181	1.26E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
182	1.24E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
183	1.17E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
184	1.08E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
185	8.64E-02	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
186	9.61E-02	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
187	1.05E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
188	1.16E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
189	1.23E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
190	1.26E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
191	1.29E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
192	1.28E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
193	1.20E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
194	1.09E-01	Fed Coscinodiscus until 200-300ugC in size, then fed Calanus, this reflects natural shift in diet
195	4.68E-02	Maintained on excess food
196	7.53E-02	Maintained on excess food
197	3.53E-02	Maintained on excess food
198	2.93E-02	Maintained on excess food
199	2.74E-02	Maintained on excess food
200	2.48E-02	Maintained on excess food
201	2.60E-02	Maintained on excess food
202	6.26E-02	Maintained on excess food
203	3.84E-02	Maintained on excess food

204	3.23E-02	Maintained on excess food
205	3.00E-02	Maintained on excess food
206	2.74E-02	Maintained on excess food
207	2.37E-02	Supplied with a surplus of Artemia nauplii as food.
208	2.25E-02	Supplied with a surplus of Artemia nauplii as food.
209	2.08E-02	Supplied with a surplus of Artemia nauplii as food.
210	1.26E-02	Supplied with a surplus of Artemia nauplii as food.
211	1.09E-02	Supplied with a surplus of Artemia nauplii as food.
212	7.53E-03	Supplied with a surplus of Artemia nauplii as food.
213	1.14E-02	Supplied with a surplus of Artemia nauplii as food.
214	6.20E-03	Supplied with a surplus of Artemia nauplii as food.
215	4.67E-03	Supplied with a surplus of Artemia nauplii as food.
216	7.28E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
217	6.48E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
218	6.81E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
219	5.20E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
220	5.37E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
221	4.12E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
222	4.53E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
223	3.95E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
224	3.32E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
225	2.42E-02	Phaeodactylum tricornutum fed once weekly 10^5 cells/ml
226	5.33E-02	Laboratory high food
227	7.30E-02	Laboratory high food
228	5.12E-02	Laboratory high food
229	7.75E-02	Laboratory high food
230	4.76E-02	Laboratory high food
231	5.90E-02	Laboratory high food
232	3.31E-02	Laboratory high food
233	1.83E-02	Laboratory high food
234	6.66E-02	Laboratory high food
235	6.16E-02	Laboratory high food
236	4.65E-02	Laboratory high food

237	5.39E-02	Laboratory high food
238	1.49E-02	Laboratory high food
239	1.11E-01	Laboratory high food
240	5.06E-02	Laboratory high food
241	4.84E-02	Laboratory high food
242	4.99E-02	Laboratory high food
243	1.57E-02	Laboratory high food
244	2.77E-02	Laboratory high food
245	8.37E-02	Laboratory high food
246	7.35E-02	Laboratory high food
247	5.00E-02	Laboratory high food
248	4.72E-02	Laboratory high food
249	2.76E-02	Laboratory high food
250	1.01E-02	Laboratory high food
251	5.52E-02	Laboratory high food
252	9.07E-02	Laboratory high food
253	3.51E-02	Laboratory high food
254	4.20E-02	Laboratory high food
255	2.53E-02	Laboratory high food
256	9.49E-02	Laboratory high food
257	2.70E-02	Laboratory high food
258	1.32E-02	Laboratory high food
259	5.69E-03	Laboratory high food
260	2.98E-03	Laboratory high food
261	2.46E-03	Laboratory high food
262	1.25E-03	Laboratory high food
263	6.32E-04	Laboratory high food
264	2.35E-02	Laboratory high food
265	1.16E-02	Laboratory high food
266	5.35E-03	Laboratory high food
267	2.80E-03	Laboratory high food
268	1.72E-03	Laboratory high food
269	5.82E-04	Laboratory high food

270	5.86E-04	Laboratory high food
271	6.85E-02	Artemia nauplii with supplementary frozen zoop to excess
272	6.29E-02	Artemia nauplii with supplementary frozen zoop to excess
273	5.89E-02	Artemia nauplii with supplementary frozen zoop to excess
274	5.50E-02	Artemia nauplii with supplementary frozen zoop to excess
275	5.18E-02	Artemia nauplii with supplementary frozen zoop to excess
276	4.86E-02	Artemia nauplii with supplementary frozen zoop to excess
277	4.60E-02	Artemia nauplii with supplementary frozen zoop to excess
278	4.30E-02	Artemia nauplii with supplementary frozen zoop to excess
279	4.05E-02	Artemia nauplii with supplementary frozen zoop to excess
280	3.80E-02	Artemia nauplii with supplementary frozen zoop to excess
281	3.53E-02	Artemia nauplii with supplementary frozen zoop to excess
282	7.86E-02	Artemia nauplii with supplementary frozen zoop to excess
283	7.23E-02	Artemia nauplii with supplementary frozen zoop to excess
284	6.76E-02	Artemia nauplii with supplementary frozen zoop to excess
285	6.31E-02	Artemia nauplii with supplementary frozen zoop to excess
286	5.94E-02	Artemia nauplii with supplementary frozen zoop to excess
287	5.58E-02	Artemia nauplii with supplementary frozen zoop to excess
288	5.70E-02	Artemia nauplii with supplementary frozen zoop to excess
289	4.95E-02	Artemia nauplii with supplementary frozen zoop to excess
290	4.65E-02	Artemia nauplii with supplementary frozen zoop to excess
291	4.35E-02	Artemia nauplii with supplementary frozen zoop to excess
292	4.05E-02	Artemia nauplii with supplementary frozen zoop to excess
293	6.60E-02	Artemia nauplii with supplementary frozen zoop to excess
294	6.07E-02	Artemia nauplii with supplementary frozen zoop to excess
295	5.67E-02	Artemia nauplii with supplementary frozen zoop to excess
296	5.30E-02	Artemia nauplii with supplementary frozen zoop to excess
297	4.98E-02	Artemia nauplii with supplementary frozen zoop to excess
298	4.69E-02	Artemia nauplii with supplementary frozen zoop to excess
299	4.42E-02	Artemia nauplii with supplementary frozen zoop to excess
300	4.15E-02	Artemia nauplii with supplementary frozen zoop to excess
301	3.89E-02	Artemia nauplii with supplementary frozen zoop to excess
302	3.65E-02	Artemia nauplii with supplementary frozen zoop to excess

303	3.39E-02	Artemia nauplii with supplementary frozen zoop to excess
304	6.86E-02	Natural assemblage but concentration unknown
305	1.88E-01	Natural assemblage but concentration unknown
306	9.71E-02	Natural assemblage but concentration unknown
307	3.35E-02	Natural assemblage but concentration unknown
308	4.52E-02	Natural assemblage but concentration unknown
309	1.48E-02	Natural assemblage but concentration unknown
310	4.97E-02	Natural assemblage but concentration unknown
311	4.31E-03	Natural assemblage but concentration unknown
312	1.03E-03	Natural assemblage but concentration unknown
313	3.01E-02	Natural assemblage but concentration unknown
314	6.72E-02	Natural assemblage but concentration unknown
315	1.36E-01	Natural assemblage but concentration unknown
316	1.88E-01	Natural assemblage but concentration unknown
317	4.45E-01	Natural assemblage but concentration unknown
318	5.08E-02	Natural assemblage but concentration unknown
319	6.45E-02	Natural assemblage but concentration unknown
320	2.85E-02	Natural assemblage but concentration unknown
321	8.35E-02	Natural assemblage but concentration unknown
322	2.04E-02	Natural assemblage but concentration unknown
323	8.77E-02	Natural assemblage but concentration unknown
324	1.43E-01	Natural assemblage but concentration unknown
325	1.49E-01	Natural assemblage but concentration unknown
326	2.11E-01	Natural assemblage but concentration unknown
327	1.05E-01	Natural assemblage but concentration unknown
328	6.27E-02	Natural assemblage but concentration unknown
329	9.65E-02	Natural assemblage but concentration unknown
330	1.58E-02	Natural assemblage but concentration unknown
331	1.25E-01	Deep tank, natural assemblage but concentration not givwn
332	1.49E-01	Deep tank, natural assemblage but concentration not givwn
333	1.10E-01	Deep tank, natural assemblage but concentration not givwn
334	4.28E-02	Deep tank, natural assemblage but concentration not givwn
335	5.95E-02	Deep tank, natural assemblage but concentration not givwn

336	3.23E-02	Deep tank, natural assemblage but concentration not givwn
337	5.31E-02	Deep tank, natural assemblage but concentration not givwn
338	1.43E-01	Deep tank, natural assemblage but concentration not givwn
339	1.35E-01	Deep tank, natural assemblage but concentration not givwn
340	7.00E-02	Deep tank, natural assemblage but concentration not givwn
341	2.93E-02	Deep tank, natural assemblage but concentration not givwn
342	1.93E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
343	7.65E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
344	1.10E-01	Rhodomonas and Thalassiosira (no more then 30% removed)
345	1.11E-01	Rhodomonas and Thalassiosira (no more then 30% removed)
346	1.07E-01	Rhodomonas and Thalassiosira (no more then 30% removed)
347	8.56E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
348	6.19E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
349	7.10E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
350	4.89E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
351	5.60E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
352	6.42E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
353	6.20E-02	Rhodomonas and Thalassiosira (no more then 30% removed)
354	1.32E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-13
355	1.22E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-14
356	3.33E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-15
357	3.95E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-16
358	2.97E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-17
359	3.74E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-18
360	3.77E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-19
361	4.13E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-20
362	1.67E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-21
363	2.37E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-22
364	1.67E-01	"Mixed diet"" - included gelatinous prey
365	1.72E-01	"Mixed diet"" - included gelatinous prey
366	2.23E-01	"Mixed diet"" - included gelatinous prey
367	1.96E-01	"Mixed diet"" - included gelatinous prey
368	1.61E-01	"Mixed diet"" - included gelatinous prey

369	1.50E-01	"Mixed diet"" - included gelatinous prey
370	6.81E-02	"Mixed diet"" - included gelatinous prey
371	3.42E-02	"Mixed diet"" - included gelatinous prey
372	1.08E-01	
373	9.39E-02	
374	5.28E-02	
375	5.69E-02	
376	6.24E-02	
377	9.04E-02	
378	6.88E-02	Artemia nauplii in excess
379	6.41E-02	Artemia nauplii in excess
380	4.22E-02	Artemia nauplii in excess
381	4.93E-02	Artemia nauplii in excess
382	2.30E-02	Artemia nauplii in excess
383	1.83E-01	Fresh copepods to excess
384	1.18E-01	Fresh copepods to excess
385	1.07E-01	Fresh copepods to excess
386	7.44E-02	Fresh copepods to excess
387	7.60E-02	Fresh copepods to excess
388	7.87E-02	Fresh copepods to excess
389	4.72E-02	Fresh copepods to excess
390	4.51E-02	Fresh copepods to excess
391	9.77E-02	100 Acartia l-1
392	9.90E-01	100 Acartia l-1
393	1.09E+00	100 Acartia l-1
394	5.13E-01	100 Acartia l-1
395	2.59E-01	100 Acartia l-1
396	1.79E-01	100 Acartia l-1
397	4.48E-01	100 Acartia l-1
398	4.89E-01	100 Acartia l-1
399	1.07E+00	100 Acartia l-1
400	2.63E-01	100 Acartia l-1
401	2.49E-01	100 Acartia l-1

402	1.56E-01	100 Acartia l-1
403	5.35E-01	101 Acartia l-1
404	7.26E-02	102 Acartia l-1
405	2.97E-01	103 Acartia l-1
406	2.00E-01	104 Acartia l-1
407	1.91E-07	105 Acartia l-1
408	9.09E-01	106 Acartia l-1
409	5.37E-01	107 Acartia l-1
410	2.74E-01	108 Acartia l-1
411	2.86E-01	109 Acartia l-1
412	8.30E-01	110 Acartia l-1
413	4.31E-01	111 Acartia l-1
414	9.53E-01	112 Acartia l-1
415	1.94E-01	113 Acartia l-1
416	7.41E-01	114 Acartia l-1
417	6.33E-01	115 Acartia l-1
418	6.58E-01	116 Acartia l-1
419	6.96E-01	117 Acartia l-1
420	6.69E-01	118 Acartia l-1
421	6.88E-02	
422	1.03E-01	
423	4.29E-02	
424	5.60E-01	
425	9.51E-03	
426	1.31E-02	
427	1.70E-02	
428	5.66E-02	
429	4.42E-02	
430	7.10E-02	
431	9.60E-02	
432	4.07E-02	Acartia/Paracalanus so that conc never dropped below 50%
433	9.12E-02	Acartia/Paracalanus so that conc never dropped below 50%
434	1.09E-01	Acartia/Paracalanus so that conc never dropped below 50%

435	9.73E-02	Acartia/Paracalanus so that conc never dropped below 50%
436	3.47E-02	Acartia/Paracalanus so that conc never dropped below 50%
437	1.01E-01	Acartia/Paracalanus so that conc never dropped below 50%
438	1.63E-01	Acartia/Paracalanus so that conc never dropped below 50%
439	8.45E-02	Acartia/Paracalanus so that conc never dropped below 50%
440	4.47E-02	Acartia/Paracalanus so that conc never dropped below 50%
441	2.52E-02	Acartia/Paracalanus so that conc never dropped below 50%
442	1.80E-01	Acartia/Paracalanus so that conc never dropped below 50%
443	4.77E-02	Acartia/Paracalanus so that conc never dropped below 50%
444	2.45E-02	Acartia/Paracalanus so that conc never dropped below 50%
445	5.32E-02	Acartia/Paracalanus so that conc never dropped below 50%
446	9.36E-02	Acartia/Paracalanus so that conc never dropped below 50%
447	4.86E-02	Acartia/Paracalanus so that conc never dropped below 50%
448	5.99E-02	Acartia/Paracalanus so that conc never dropped below 50%
449	3.73E-02	Acartia/Paracalanus so that conc never dropped below 50%
450	3.65E-02	Acartia/Paracalanus so that conc never dropped below 50%
451	1.26E-01	Acartia/Paracalanus so that conc never dropped below 50%
452	6.01E-02	Acartia/Paracalanus so that conc never dropped below 50%
453	3.78E-02	Acartia/Paracalanus so that conc never dropped below 50%
454	4.22E-02	Acartia/Paracalanus so that conc never dropped below 50%
455	4.92E-02	Acartia/Paracalanus so that conc never dropped below 50%
456	6.91E-02	Acartia/Paracalanus so that conc never dropped below 50%
457	5.01E-02	Acartia/Paracalanus so that conc never dropped below 50%
458	3.52E-02	Acartia/Paracalanus so that conc never dropped below 50%
459	1.96E-01	Acartia/Paracalanus so that conc never dropped below 50%
460	6.54E-02	Acartia/Paracalanus so that conc never dropped below 50%
461	7.44E-02	Acartia/Paracalanus so that conc never dropped below 50%
462	2.45E-01	Acartia/Paracalanus so that conc never dropped below 50%
463	2.30E-01	Acartia/Paracalanus so that conc never dropped below 50%
464	6.01E-02	Acartia/Paracalanus so that conc never dropped below 50%
465	1.41E-01	Acartia/Paracalanus so that conc never dropped below 50%
466	6.15E-02	Acartia/Paracalanus so that conc never dropped below 50%
467	3.02E-02	Acartia/Paracalanus so that conc never dropped below 50%

468	1.16E-01	Acartia/Paracalanus so that conc never dropped below 50%
469	1.62E-01	Acartia/Paracalanus so that conc never dropped below 50%
470	6.34E-02	Acartia/Paracalanus so that conc never dropped below 50%
471	1.33E-01	Acartia/Paracalanus so that conc never dropped below 50%
472	3.27E-01	Acartia/Paracalanus so that conc never dropped below 50%
473	4.99E-02	Acartia/Paracalanus so that conc never dropped below 50%
474	1.85E-01	Acartia/Paracalanus so that conc never dropped below 50%
475	6.05E-02	Acartia/Paracalanus so that conc never dropped below 50%
476	1.37E-01	Acartia/Paracalanus so that conc never dropped below 50%
477	6.42E-02	Acartia/Paracalanus so that conc never dropped below 50%
478	1.58E-01	200 copepods l-1
479	1.57E-01	200 copepods l-1
480	1.14E-01	200 copepods l-1
481	9.92E-02	200 copepods l-1
482	2.14E-01	200 copepods l-1
483	1.26E-01	200 copepods l-1
484	1.78E-01	Acartia so that conc never dropped below 50%
485	2.01E-01	1 Mnemiopsis l-1 (not satiated)
486	8.14E-08	1 Mnemiopsis l-1 (not satiated)
487	1.29E-01	1 Mnemiopsis l-1 (not satiated)
488	1.91E-01	1 Mnemiopsis l-1 (not satiated)
489	1.28E-01	1 Mnemiopsis l-1 (not satiated)
490	1.26E-01	1 Mnemiopsis l-1 (not satiated)
491	1.23E-01	1 Mnemiopsis l-1 (not satiated)
492	5.80E-02	1 Mnemiopsis l-1 (not satiated)
493	3.34E-03	1 Mnemiopsis l-1 (not satiated)
494	1.16E-01	1 Mnemiopsis l-1 (not satiated)
495	1.61E-01	1 Mnemiopsis l-1 (not satiated)
496	8.19E-02	1 Mnemiopsis l-1 (not satiated)
497	3.55E-01	1 Mnemiopsis l-1 (not satiated)
498	3.85E-01	1 Mnemiopsis l-1 (not satiated)
499	6.57E-02	1 Mnemiopsis l-1 (not satiated)
500	6.29E-02	1 Mnemiopsis l-1 (not satiated)

501	5.63E-09	1 Mnemiopsis l-1 (not satiated)
502	2.02E-07	1 Mnemiopsis l-1 (not satiated)
503	1.82E-07	1 Mnemiopsis l-1 (not satiated)
504	1.49E-01	1 Mnemiopsis l-1 (not satiated)
505	8.08E-02	1 Mnemiopsis l-1 (not satiated)
506	2.08E-01	1 Mnemiopsis l-1 (not satiated)
507	1.31E-01	1 Mnemiopsis l-1 (not satiated)
508	4.88E-08	1 Mnemiopsis l-1 (not satiated)
509	6.38E-02	1 Mnemiopsis l-1 (not satiated)
510	6.63E-02	1 Mnemiopsis l-1 (not satiated)
511	7.34E-02	1 Mnemiopsis l-1 (not satiated)
512	5.66E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-1
513	2.78E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-2
514	5.89E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-3
515	4.46E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-4
516	1.36E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-5
517	5.47E-03	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-6
518	5.64E-03	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-7
519	6.33E-03	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-8
520	3.01E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-9
521	2.88E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-10
522	2.14E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-11
523	2.51E-02	0.2-0.6 Isochrysis and 0.1-0.3 Peridinium l-12
524	9.41E-02	Rotifers = 6166 l-1
525	1.12E-01	>150 Artemia l-1 (saturated)
526	7.56E-02	>150 Artemia l-1 (saturated)
527	1.01E-01	>150 Artemia l-1 (saturated)
528	5.09E-02	>150 Artemia l-1 (saturated)
529	7.58E-02	>150 Artemia l-1 (saturated)
530	4.98E-02	Artemia in excess
531	7.77E-02	Artemia in excess
532	1.05E-01	Non-limiting Brachionus
533	9.21E-02	Non-limiting Brachionus

534	3.52E-02	Selco enriched Artemia to excess
535	4.48E-02	Selco enriched Artemia to excess
536	6.58E-02	Selco enriched Artemia to excess
537	6.46E-02	Selco enriched Artemia to excess
538	5.52E-02	Selco enriched Artemia to excess
539	3.91E-02	Selco enriched Artemia to excess
540	2.48E-02	Selco enriched Artemia to excess
541	8.48E-03	Selco enriched Artemia to excess
542	7.96E-03	Selco enriched Artemia to excess
543	1.01E-01	4500 rotifers 150 mnemiopsis (l-1)
544	3.20E-02	Excess Cassipoeia pieces
545	1.68E-02	Excess Cassipoeia pieces
546	2.55E-02	Excess Cassipoeia pieces
547	5.48E-03	Excess Cassipoeia pieces
548	5.95E-03	Excess Cassipoeia pieces
549	2.75E-03	Excess Cassipoeia pieces
550	1.80E-03	Excess Cassipoeia pieces
551	4.78E-02	Artemia, no detail on concentration
552	4.03E-02	Artemia, no detail on concentration
553	8.42E-02	Artemia, no detail on concentration
554	7.29E-02	Artemia, no detail on concentration
555	1.55E-02	Pieces of Cassiopeia
556	3.87E-03	Pieces of Cassiopeia
557	1.58E-02	Pieces of Cassiopeia
558	1.70E-02	Pieces of Cassiopeia
559	8.18E-03	Pieces of Cassiopeia
560	9.81E-03	Pieces of Cassiopeia

Record	Notes
1	Used average value for genus Sagitta from Kiorboe composition

2 Used average value for genus Sagitta from Kiorboe composition
3 Used average value for genus Sagitta from Kiorboe composition
4 Used average value for genus Sagitta from Kiorboe composition
5 Used average value for genus Sagitta from Kiorboe composition
6 Used average value for genus Sagitta from Kiorboe composition
7 Used average value for genus Sagitta from Kiorboe composition
8 Used average value for genus Sagitta from Kiorboe composition
9 Used average value for genus Sagitta from Kiorboe composition
10 Used average value for genus Sagitta from Kiorboe composition
11 Used average value for genus Sagitta from Kiorboe composition
12 Used average value for genus Sagitta from Kiorboe composition
13 Used average value for genus Sagitta from Kiorboe composition
14 Used average value for genus Sagitta from Kiorboe composition
15 Used average value for genus Sagitta from Kiorboe composition
16 Used average value for genus Sagitta from Kiorboe composition
17 Used average value for genus Sagitta from Kiorboe composition
18 Used average value for genus Sagitta from Kiorboe composition
19 Used average value for genus Sagitta from Kiorboe composition
20 Used average value for genus Sagitta from Kiorboe composition
21 Used average value for genus Sagitta from Kiorboe composition
22 Used average value for genus Sagitta from Kiorboe composition
23 Used average value for genus Sagitta from Kiorboe composition
24 Used average value for genus Sagitta from Kiorboe composition
25 Used average value for genus Sagitta from Kiorboe composition
26 Used average value for genus Sagitta from Kiorboe composition
27 Used average value for genus Sagitta from Kiorboe composition
28 Used average value for genus Sagitta from Kiorboe composition
29 Nauplii, calanoid cvol
30 Copepodites, calanoid cvol
31 All, calanoid cvol
32 Copepepodite, calanoid cvol
33 Copepepodite, calanoid cvol
34 Copepepodite, calanoid cvol

35 Copepodites, calanus cvol
36 Copepodites, calanus cvol
37 Nauplii
38 Copepodites
39 CIII-Adult, calanus cvol
40 CIII-Adult, calanus cvol
41 Nauplii
42 Copepodite
43 Copepodite
44 Copepodite
45 Copepodite
46 egg-NIV, calanus cvol
47 NV-CV, calanus cvol
48 CV-Female, calanus cvol
49 Copepodite
50 Copepodite
51 Copepodite
52 Copepodite
53 Copepodite
54 Copepodite
55 Copepodite
56 Copepodite
57 Copepodite
58 Copepodite
59 Copepodite
60 Copepodite
61 Nauplii, calanus cvol
62 Nauplii, calanus cvol
63 Nauplii, calanus cvol
64 Nauplii, calanus cvol
65 Nauplii, calanus cvol
66 CI and CII, calanus cvol
67 CI and CII, calanus cvol

68 CI and CII, calanus cvol
69 CI and CII, calanus cvol
70 CI and CII, calanus cvol
71 CIII and CIV, calanus cvol
72 CIII and CIV, calanus cvol
73 CIII and CIV, calanus cvol
74 CIII and CIV, calanus cvol
75 CIII and CIV, calanus cvol
76 CV, calanus cvol
77 CV, calanus cvol
78 CV, calanus cvol
79 CV, calanus cvol
80 CV, calanus cvol
81 Nauplii, calanoid cvol
82 Copepodites, calanoid cvol
83 Nauplii, calanoid cvol
84 Copepodites, calanoid cvol
85 Nauplii, calanoid cvol
86 Copepodites, calanoid cvol
87 All, calanoid cvol
88 All, calanoid cvol
89 All, calanoid cvol
90 All, calanoid cvol
91 All, calanoid cvol
92 CI-Adult, calanoid cvol
93 CI-Adult, calanoid cvol
94 CI-Adult, calanoid cvol
95 Copepodite, used Labidocera acutifrons cvol
96 Copepodite, used Labidocera acutifrons cvol
97 Copepodite, used Labidocera acutifrons cvol
98 Copepodite, used Labidocera acutifrons cvol
99 Copepodite, used Labidocera acutifrons cvol
100 Copepodite, used Labidocera acutifrons cvol

101 Copepodite, used Labidocera acutifrons cvol
102 Copepodite, used Labidocera acutifrons cvol
103 Copepodite, used Labidocera acutifrons cvol
104 Copepodite, used Labidocera acutifrons cvol
105 Copepodite, used Labidocera acutifrons cvol
106 Copepodite, used Labidocera acutifrons cvol
107 Copepodite, used Labidocera acutifrons cvol
108 Copepodite, used Labidocera acutifrons cvol
109 Copepodite, used Labidocera acutifrons cvol
110 Copepodite, used Labidocera acutifrons cvol
111 Copepodite, used Labidocera acutifrons cvol
112 Copepodite, used Labidocera acutifrons cvol
113 Copepodite, used Labidocera acutifrons cvol
114 Copepodite, used Labidocera acutifrons cvol
115 All
116 All
117 Copepodite
118 Nauplii, calanoid cvol
119 Nauplii, calanoid cvol
120 Nauplii, calanoid cvol
121 Nauplii, calanoid cvol
122 Nauplii, calanoid cvol
123 Copepodite, calanoid value
124 Copepodite, calanoid value
125 Copepodite, calanoid value
126 Copepodite, calanoid value
127 Copepodite, calanoid value
128 Nauplii, calanoid cvol
129 Copepodite, calanoid cvol
130 Copepodite, calanoid cvol
131 ?, calanoid cvol
132 ?, calanoid cvol
133 ?, calanoid cvol

134 ?, calanoid cvol
135 ?, calanoid cvol
136 ?, calanoid cvol
137 ?, calanoid cvol
138 ?, calanoid cvol
139 ?, calanoid cvol
140 ?, calanoid cvol
141 ?, calanoid cvol
142 ?, calanoid cvol
143 ?, calanoid cvol
144 Nauplii, calanoid cvol
145 Copepodite, calanoid cvol
146 Nauplii, calanoid cvol
147 Copepodite, calanoid cvol
148 Nauplii
149 Nauplii, calanoid value
150 Nauplii, calanoid value
151 Nauplii, calanoid value
152 Nauplii, calanoid value
153 Nauplii, calanoid value
154 Nauplii, calanoid value
155 Nauplii, calanoid value
156 Nauplii, calanoid value
157 Nauplii, calanoid value
158 Nauplii, calanoid value
159 Nauplii, calanoid value
160 Nauplii, calanoid cvol
161 Copepodites, calanoid cvol
162 Nauplii, calanoid cvol
163 CI-CIII/IV, calanoid cvol
164 CIII/IV-Adult, calanoid cvol
165 Used average value forfamily Amphipoda from Kiorboe composition

166 Used average value forfamily Amphipoda from Kiorboe composition

167 Used average value forfamily Amphipoda from Kiorboe composition

168 Used average value forfamily Amphipoda from Kiorboe composition

169 Used average value forfamily Amphipoda from Kiorboe composition

170 Used average value forfamily Amphipoda from Kiorboe composition

171 Used average value forfamily Amphipoda from Kiorboe composition

172 Used average value forfamily Amphipoda from Kiorboe composition

173 Used average value forfamily Amphipoda from Kiorboe composition

174 Used average value forfamily Amphipoda from Kiorboe composition

175 Used average value forfamily Amphipoda from Kiorboe composition

176 Used average value forfamily Amphipoda from Kiorboe composition

177 Used average value forfamily Amphipoda from Kiorboe composition

178 Used average value forfamily Amphipoda from Kiorboe composition

179 Used average value forfamily Amphipoda from Kiorboe composition

180 Used average value forfamily Amphipoda from Kiorboe composition

181 Used average value forfamily Amphipoda from Kiorboe composition

182 Used average value forfamily Amphipoda from Kiorboe composition

183 Used average value forfamily Amphipoda from Kiorboe composition

184 Used average value forfamily Amphipoda from Kiorboe

composition
Used average value forfamily Amphipoda from Kiorboe
185 composition
Used average value forfamily Amphipoda from Kiorboe
186 composition
Used average value forfamily Amphipoda from Kiorboe
187 composition
Used average value forfamily Amphipoda from Kiorboe
188 composition
Used average value forfamily Amphipoda from Kiorboe
189 composition
Used average value forfamily Amphipoda from Kiorboe
190 composition
Used average value forfamily Amphipoda from Kiorboe
191 composition
Used average value forfamily Amphipoda from Kiorboe
192 composition
Used average value forfamily Amphipoda from Kiorboe
193 composition
Used average value forfamily Amphipoda from Kiorboe
194 composition
Units of mass in carbon, mass and growth calculated from Table
195 2
Units of mass in carbon, mass and growth calculated from Table
196 2
Units of mass in carbon, mass and growth calculated from Table
197 2
Units of mass in carbon, mass and growth calculated from Table
198 2
Units of mass in carbon, mass and growth calculated from Table
199 2
Units of mass in carbon, mass and growth calculated from Table
200 2
Units of mass in carbon, mass and growth calculated from Table
201 2
Units of mass in carbon, mass and growth calculated from Table
202 2

203		Units of mass in carbon, mass and growth calculated from Table 2
204		Units of mass in carbon, mass and growth calculated from Table 2
205		Units of mass in carbon, mass and growth calculated from Table 2
206		Units of mass in carbon, mass and growth calculated from Table 2
207		
208		
209		
210		
211		
212		
213		
214		
215		
216		Data digitized from their Figure 3.
217		Data digitized from their Figure 3.
218		Data digitized from their Figure 3.
219		Data digitized from their Figure 3.
220		Data digitized from their Figure 3.
221		Data digitized from their Figure 3.
222		Data digitized from their Figure 3.
223		Data digitized from their Figure 3.
224		Data digitized from their Figure 3.
225		Data digitized from their Figure 3.
226		
227		
228		
229		Decapod value
230		Decapod value
231		Decapod value
232		Decapod value

233 Decapod value
234 Decapod value
235 Decapod value
236 Decapod value
237 Decapod value
238 Decapod value
239 Decapod value
240 Decapod value
241 Decapod value
242 Decapod value
243 Decapod value
244 Decapod value
245 Decapod value
246 Decapod value
247 Decapod value
248 Decapod value
249 Decapod value
250 Decapod value
251 Decapod value
252 Decapod value
253 Decapod value
254 Decapod value
255 Decapod value
256 Decapod value
257 Euphausid value
258 Euphausid value
259 Euphausid value
260 Euphausid value
261 Euphausid value
262 Euphausid value
263 Euphausid value
264 Euphausid value
265 Euphausid value

Euphausid value
Euphausid value
Euphausid value
Euphausid value
Euphausid value

299
300
301
302
303
304
305
306
307
308
309
310
311
312
313
314
315
316
317
318
319
320
321
322
323
324
325
326
327
328
329
330
331

332	
333	
334	
335	
336	
337	
338	
339	
340	
341	
342	Used Larson 86 cvol value for thaliaceans
343	Used Larson 86 cvol value for thaliaceans
344	Used Larson 86 cvol value for thaliaceans
345	Used Larson 86 cvol value for thaliaceans
346	Used Larson 86 cvol value for thaliaceans
347	Used Larson 86 cvol value for thaliaceans
348	Used Larson 86 cvol value for thaliaceans
349	Used Larson 86 cvol value for thaliaceans
350	Used Larson 86 cvol value for thaliaceans
351	Used Larson 86 cvol value for thaliaceans
352	Used Larson 86 cvol value for thaliaceans
353	Used Larson 86 cvol value for thaliaceans
354	Used value for thaliaceans from Larson 86 no reliable doliolid value
355	Used value for thaliaceans from Larson 86 no reliable doliolid value
356	Used value for thaliaceans from Larson 86 no reliable doliolid value
357	Used value for thaliaceans from Larson 86 no reliable doliolid value
358	Used value for thaliaceans from Larson 86 no reliable doliolid value
359	Used value for thaliaceans from Larson 86 no reliable doliolid value

Used value for thaliaceans from Larson 86 no reliable doliolid value
Used value for thaliaceans from Larson 86 no reliable doliolid value
Used value for thaliaceans from Larson 86 no reliable doliolid value
Used value for thaliaceans from Larson 86 no reliable doliolid value
AFDW =23%DW Larson 1986, CW=16% DW Kiorboe 2013

CW=1.5%DW, used length-mass regression from this study

Shiganova (unpublished) in Purcell et al. Hydrobiologia 2001
Shiganova (unpublished) in Purcell et al. Hydrobiologia 2002
Used paper value C=10.3% DW

Used C=5.64%DW Kiorboe composition average
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition

Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition
Used C=0.17% value for beroe ovata in kiorboe composition

1mg DW = 0.071 mg CW, incubated for 10 days
1 mg DW = 0.0071 mg CW Schneider

Used average C (% of DW) = 5.39% from Kiorboe Composition
Used average C (% of DW) = 5.39% from Kiorboe Composition
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
Converted using diameter to C (mg) in Olesen Purcell Stoecker
c converted from diameter C = 0.000215 Diam ^2.903

Used value from Pitt el a. 2013, c=0.55%WW, mean temperature

555
556
557
558
559
560

References

1. Anger K., Laasch N., Puschel C. and Schorn F. (1983) Changes in biomass and chemical composition of spider crab (*Hyas araneus*) larvae reared in the laboratory. *Marine Ecology Progress Series* 21 91-101.
2. Arai, M.N. (1980) Growth rates of *Aequorea medusae*. In: P. Tardent and R. Tardent (eds.) *Developmental and cellular biology of Coelenterates*. Elsevier, North Holland Biomedical Press.
3. Bamstedt, U., Lane, J. and Martinussen, M.B. (1999) Bioenergetics of ephyrae larvae of the scyphozoan jellyfish *Aurelia aurita* in relation to temperature and salinity. *Marine Biology* 135 89-98.
4. Berggreen, U., B. Hansen, and Kiørboe, T. (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Marine Biology* 99 341-352.
5. Buchholz, F. (1991) Moult cycle and growth of Antarctic krill *Euphausia superba* in the laboratory. *Marine Ecology Progress Series* 69 217-229.
6. Campbell, R.G., Wagner, M.M., Teegarden, G.J., Boudreau, C.A. and Durbin, E.G., (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Marine Ecology Progress Series* 221 161-183.
7. Clutter R.I. and Theilacker G.H. (1971) Ecological efficiency of a pelagic mysid shrimp: estimates from growth, energy budget, and mortality studies. *Fisheries Bulletin of the United States* 69 93-115.
8. Costello, J. (1991) Complete carbon and nitrogen budgets for the hydromedusa *Cladonema californicum* (Anthomedusae: Cladonemidae). *Marine Biology* 108 119-128.
9. Daan, R. (1986) Food intake and growth of *Sarsia tubulosa* (Sars, 1835), with quantitative estimates of predation on copepod populations. *Netherlands Journal of Sea Research* 20 67-74.
10. Dagg, M.J. (1976) Complete carbon and nitrogen budgets for the carnivorous amphipod, *Calliopius laeviusculus* (Kroyer). *International Review of Hydrobiology* 61 297-357.
11. Deibel, D. (1982) Laboratory determined mortality, fecundity and growth rates of *Thalia democratica* Forskal and *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea). *Journal of Plankton Research* 4 143-153
12. Escribano, R., Irribarren, C. and Rodriguez, L., (1997) Influence of food quantity and temperature on development and growth of the marine copepod *Calanus chilensis* from northern Chile. *Marine Biology* 128 281-288.

13. Escribano, R. and McLaren, I.A. (1992) Testing hypotheses of exponential growth and size-dependent molting rate in two copepod species. *Marine Biology* 114 31-39.
14. Frandsen, K.T. and Riisgard, H.U. (1997) Size dependent respiration and growth of jellyfish, *Aurelia aurita*. *Sarsia* 82 307-312.
15. Fryd, M., Haslund, O.H. and Wohlgemuth, O. (1991) Development, growth and egg production of the two copepod species *Centropages hamatus* and *Centropages typicus* in the laboratory. *Journal of Plankton Research* 13 683-689.
16. Gibson, D.M. and Paffenhofer, G.A. (2000) Feeding and growth rates of the doliolid, *Dolioletta gegenbauri* Uljanin (Tunicata, Thaliacea). *Journal of Plankton Research* 22 1485-1500.
17. Grove, M. and Breitburg, D.L. (2005) Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. *Marine Ecology Progress Series* 301 185-198.
18. Harris, R.P. and Paffenhöfer, G.A. (1976) Feeding, growth and reproduction of the marine planktonic copepod *Temora longicornis* Müller. *Journal of the Marine Biological Association of the United Kingdom* 56 675-690.
19. Heinle, D.R. and Flemer, D.A. (1975) Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Marine Biology* 31 235-247.
20. Hirota J (1972) Laboratory culture and metabolism of the planktonic ctenophore, *Pleurobrachia bachei* A. Agassiz. *In Biological oceanography of the Northern North Pacific Ocean* (A.Y. Takenouti, ed.) 465-484. Idemitsu Shoten, Tokyo.
21. Ikeda T, Dixon P and Kirkwood, J. (1985) Laboratory observations of moulting, growth and maturation in Antarctic krill (*Euphausia superba* Dana). *Polar Biology* 4 1-18.
22. Ikeda, T. (1991) Assimilated carbon budget for the Hyperiid amphipod *Themisto japonica* (Bovallius) from the Japan Sea as infleunced by temperature. *Journal of the Oceanographical Society of Japan* 47 7-16.
23. Jacobi, C.C. and Anger, K. (1985) Growth and respiration during the larval development of *Hyas coarctatus* (Decapod: Majidae). *Marine Biology* 87 173-180.
24. Kasuya, T., Ishimaru, T. and Murano, M. (2002) Laboratory study of growth of the lobate ctenophore *Bolinopsis mikado* (Moser). *Plankton Biology and Ecology* 49 81-87.
25. Kawahara, M., Uye, S.I., Ohtsu, K. and Iizumi, H. (2006) Unusual population explosion of the giant jellyfish, *Nemopilema nomurai*, (Scyphozoa: Rhizostomeae) in East Asian waters. *Marine Ecology Progress Series* 307 161-173.
26. Kideys, A.E., Finenko, G.A., Anninsky, B.E., Shiganova, T.A., Roohi, A., Tabari, M.R., Youseffyan, M., Rostamian, M.T., Rostami, H. and Negarestan, H. (2004) Physiological characteristics of the ctenophore *Beroe ovata* in Caspian Sea water. *Marine Ecology Progress Series* 266 111-121.
27. Kimmerer, W.J. and McKinnon, D., 1987. Growth, mortality, and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnology and Oceanography* 32 14-28.
28. Kimoto, K., S. Uye, and T. Onbé (1986) Egg production of a brackish-water calanoid copepod *Sinocalanus tenellus* in relation to food abundance and temperature. *Bulletin of Plankton Society of Japan (1986).*

29. Klein Breteler, W.C., H.G. Fransz, and S.R. Gonzalez. (1982) Growth and development of four calanoid copepod species under experimental and natural conditions. *Netherlands Journal of Sea Research* 16 195-207.
30. Kremer, P. and Reeve, M.R. (1989) Growth dynamics of a ctenophore (Mnemiopsis) in relation to variable food supply II. Carbon budgets and growth model. *Journal of Plankton Research* 11 553-574.
31. Larson, R.J. (1986) The feeding and growth of the Sea Nettle, *Chrysaora quinquecirrha* (Desor) in the laboratory. *Estuaries* 9 376-379.
32. Larson, R.J. (1987) A note on the feeding and reproduction of the epipelagic scyphomedusa *Pelagia noctiluca* (Forskal). *Biological Oceanography* 4 447-454.
33. Lasker R (1966) Feeding, growth, respiration and carbon utilization of a Euphausiid crustacean. *Journal of Fisheries Research Board of Canada* 23 1291-1317.
34. Logan D.T. and Epifano C.E. (1978) A laboratory energy balance for the larvae and juveniles of the American lobster *Homarus americanus*. *Marine Biology* 47 381-389.
35. Moller, L.F., and Riisgard, H.U. (2007) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. *Marine Ecology Progress Series* 346 167-183.
36. Olesen, N.J., Purcell, J.E. and Stoecker, D.K. (1996) Feeding and growth by ephyrae of scyphomedusae *Chrysaora quinquecirrha*. *Marine Ecology Progress Series* 137 149-159.
37. Olesen, N.J., Frandsen, K. and Riisgard, H.U. (1994) Population dynamcis, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. *Marine Ecology Progress Series* 105 9-18.
38. Paffenhofer, G.A. (1976) Feeding, growth, and food conversion of the marine planktonic copepod *Calanus helgolandicus*. *Limnology and Oceanography* 21 39-50.
39. Paffenhöfer, G.A. (1993) On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *Journal of Plankton Research* 15 37-55.
40. Peterson, W.T. (1986) Development, growth, and survivorship of the copepod *Calanus marshallae* in the laboratory. *Marine Ecology Progress Series* 61-72.
41. Reeve M.R. and Baker, L.D. (1975) Production of two planktonic carnivores (chaetognath and ctenophore) in South Florida inshore waters. *Fisheries Bulletin* 73 238-248.
42. Reeve M.R. and Walter, M.A. (1976) A large-scale experiment on the growth and predation potential of ctenophore populations. In *Coelenterate ecology and behaviour* (G. Mackie ed.), pp 187-199. Plenum Press, New York
43. Reeve, M. R. (1970). The biology of chaetognatha I. Quantitative aspects of growth and egg production in *Sagitta hispida*. In "*Marine food chains*" (H. Steele, ed), pp. 168-189. Oliver and Boyd, Edinburgh.
44. Reeve, M.R., Walter, M.A. and Ikeda, T. (1978) Laboratory studies of ingestion and food utilisation of lobate and tentaculate ctenophores. *Limnology and Oceanography* 23 740-751.
45. Ross M (1982) Energetics of *Euphausia pacifica*. II. Complete carbon and nitrogen budgets at 9^{o} and 12^{o}C throughout the life span. *Marine Biology* 68 15-23

46. Sabatini, M. and Kiørboe, T. (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis*. *Journal of Plankton Research* 16 1329-1351.
47. Senjie, L. and Song, L., (1990) Development rate of *Labidocera euchaeta* Giesbrecht in Xiamen Harbor. *Acta Oceanologica Sinica* 9 439-447.
48. Uye, S., Iwai, Y. and Kasahara, S., (1983) Growth and production of the inshore marine copepod *Pseudodiaptomus marinus* in the central part of the Inland Sea of Japan. *Marine Biology* 73 91-98.
49. Uye, S.I. (1988) Temperature-dependent development and growth of *Calanus sinicus* (Copepoda: Calanoida) in the laboratory*. Hydrobiologia* 167 285-293.
50. Vidal, J. (1980) Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus sp*. *Marine Biology* 56 111-134.
51. Widmer, C.L. (2005) Effects of temperature on growth of north-east Pacific moon jellyfish ephyrae, *Aurelia labiata* (Cnidaria: Scyphozoa). *Journal of the Marine Biology Association of the United Kingdom* 85 569-574.

Appendix III – L4 measurements and indices

Measurements and bloom indices for the zooplanktonic taxa sampled at the L4 study site. Coeffvar = coefficient of variation in abundance, Coeffvar NO 0 = coefficient of variation in abundance of all non-zero records, Interval = the number of days between the 25th and 50th cumulative percentiles of abundance, 2 INC MAX = maximum value for increase rate index over two successive increases (on 3 point running mean data, index detailed in Chapter 4), 3 INC MAX = maximum value for increase rate index over three successive increases (on 3 point running mean data, index detailed in Chapter 4), 4 INC MAX = maximum value for increase rate index over two successive increases (on 3 point running mean data, index detailed in Chapter 4), Interannual var = coefficient of variation of mean annual abundance, Interannual var AA = maximum annual abundance / minimum (non-zero) abundance, Non-zero records = total number of records of non-zero abundance, FDC = frequency distribution coefficient (calculated as described in Chapter 4).

Record	Name	Group	Carbon percentage
1	Noctiluca scintillans	Protist	0.54
2	Foraminifera	Protist	0.54
3	Acantharia	Protist	0.54
4	Tintinnida	Protist	0.54
5	Pleurobrachia pileus	Ctenophora	0.15
6	Solmaris corona (Narcomedusae)	Hydromedusae	0.49
7	Aglantha digitale	Hydromedusae	0.37
8	Liriope tetraphylla	Hydromedusae	0.49
9	Hydromedusae unidentified	Hydromedusae	0.49
10	Actinula larvae	Hydromedusae	2
11	Amphinema spp	Hydromedusae	0.49
12	Bougainvillia muscus	Hydromedusae	0.49
13	Clytia hemisphaerica	Hydromedusae	0.31
14	Corymorpha nutans	Hydromedusae	0.49
15	Coryne prolifer	Hydromedusae	0.49
16	Cosmetira pilosella	Hydromedusae	0.49
17	Eirene viridula	Hydromedusae	0.49
18	Eutima gracilis	Hydromedusae	0.49
19	Hydractinia borealis	Hydromedusae	0.49
20	Leukartiara octona	Hydromedusae	0.49
21	Lizzia blondina	Hydromedusae	0.49
22	Lovenella clausa	Hydromedusae	0.49
23	Mitrocomella brownei	Hydromedusae	0.49
24	Obelia spp.	Hydromedusae	0.49
25	Phialella quadrata	Hydromedusae	0.31
26	Podocoryne hartlaubi	Hydromedusae	0.49
27	Rathkea octopunctata	Hydromedusae	0.49
28	Sarsia prolifera	Hydromedusae	0.49
29	Sarsia spp.	Hydromedusae	0.49
30	Turritopsis nutricula	Hydromedusae	0.49
31	Zanclea costata	Hydromedusae	0.49
32	Muggiaea kochi (polygastric)	Siphonophora	0.44
33	Muggiaea atlantica (polygastric)	Siphonophora	0.44
34	Muggiaea sp. (eudoxid)	Siphonophora	0.44
35	Siphonophore unidentified	Siphonophora	0.44
36	Nanomia cara (nectophore)	Siphonophora	0.44

37	Agalma elegans (nectophore)	Siphonophora	0.44
38	Anemone larvae	Scyphomedusae	4
39	Planula larvae	Scyphomedusae	2
40	Polyp	scyphomedusae	2
41	Aurelia aurita ephyrae	Scyphomedusae	1
42	Scyphozoan ephyrae	Scyphomedusae	1
43	Chaetognath unidentified	Chaetognatha	3.5
44	Parasagitta elegans	Chaetognatha	3.5
45	Parasagitta setosa	Chaetognatha	3.5
46	Nematoda	Worms	5
47	Flatworm larvae (Platyhelminth)	Worms	5
48	Polychaete larvae unidentified	Worms	5
49	Tomopteris helgolandica	Worms	5
50	Phoronida actinotroch larvae	Worms	7
51	Nemertea pilidium larvae	Worms	5
52	Gastropod larvae	Molluscs	7
53	Limacina retroversa	Molluscs	7
54	Bivalvia	Molluscs	7
55	Lamellaria echinospira larvae	Molluscs	7
56	Gymnosome larvae	Molluscs	7
57	Clione	Molluscs	1.36
58	Cephalopoda larvae	Molluscs	9.3
59	Echinoderm larvae unidentified	Echinoderms	7
60	Ophiopluteus larvae	Echinoderms	7
61	Ophiuroid juvenile	Echinoderms	7
62	Echinopluteus larvae	Echinoderms	7
63	Echinoid Juvenile (Sea urchin larvae)	Echinoderms	7
64	Asterioid bipinnaria/brachiolaria	Echinoderms	7
65	Asteroid juvenile	Echinoderms	7
66	Luidia sp. larvae	Echinoderms	7
67	Auricularia larvae (Holothuria)	Echinoderms	7
68	Doliolaria larvae (Holothuria)	Echinoderms	7
69	Tornaria larvae (Hemichordata)	Chordata	7
70	Branchiostoma (Cephalochordata)	Chordata	7
71	Ascidian tadpole	Chordata	7
72	Doliolida	Chordata	3.8
73	Appendicularia	Chordata	9.3
74	Fish larvae	Chordata	9.3
75	Cirripede nauplii	Crustacean (other)	10
76	Rhizocephalan nauplii	Crustacean (other)	10
77	Cirripede cyprid	Crustacean (other)	10
78	Evadne spp.	Crustacean (other)	10
79	Podon spp.	Crustacean (other)	10
80	Penilia avirostris	Crustacean (other)	10
81	Isopoda	Crustacean (other)	10
82	Gammariida	Crustacean (other)	10
83	Hyperiida	Crustacean (other)	12
84	Caprellida	Crustacean (other)	10
85	Tanaid	Crustacean (other)	10
86	Cumacea	Crustacean (other)	10
87	Mysida	Crustacean (other)	10
88	Euphausiid	Crustacean (other)	12
89	Decapod larvae unidentified	Crustacean (other)	10
90	Brachyuran larvae	Crustacean (other)	10
91	Porcellanid larvae	Crustacean (other)	10
92	Metridia lucens	Copepoda	11.38

93	Acartia	Copepoda	11.38
94	Candacia armata	Copepoda	11.38
95	Centropages chierchiae	Copepoda	11.38
96	Centropages hamatus	Copepoda	11.38
97	Centropages typicus	Copepoda	11.38
98	Isias clavipes	Copepoda	11.38
99	Anomalocera patersoni	Copepoda	11.38
100	Parapontella brevicornis	Copepoda	11.38
101	Labidocera wollastoni	Copepoda	11.38
102	Temora longicornis	Copepoda	11.38
103	Calanoides carinatus	Copepoda	15.18
104	Calanus helgolandicus	Copepoda	15.18
105	Calanus finmarchicus female	Copepoda	15.18
106	Calocalanus spp.	Copepoda	11.38
107	Para/Pseudo/Cteno/Clausocalanus	Copepoda	11.38
108	Clausocalanus spp.	Copepoda	11.38
109	Ctenocalanus vanus	Copepoda	11.38
110	Paracalanus parvus	Copepoda	11.38
111	Pseudocalanus elongatus	Copepoda	11.38
112	Subeucalanus spp.	Copepoda	11.38
113	Microcalanus spp.	Copepoda	11.38
114	Diaixis hibernica	Copepoda	11.38
115	Paraeuchaeta hebes	Copepoda	11.38
116	Scolecithricella spp.	Copepoda	11.38
117	Oithona spp.	Copepoda	11.38
118	Oncaea spp.	Copepoda	11.38
119	Ditrichocorycaeus anglicus	Copepoda	11.38
120	Microsetella sp	Copepoda	11.38
121	Euterpina acutifrons	Copepoda	11.38
122	Goniopsyllus clausi	Copepoda	11.38
123	Harpacticoid unidentified	Copepoda	11.38
124	Siphonostomatoida	Copepoda	11.38
125	Copepod nauplii	Copepoda	11.38
126	Bryozoa cyphonautes larvae	Other	7
127	Acarid mites	Other	10

Record	Carbon mass	Coeffvar	Coeffvar NO 0	Interval	2 inc MAX
1	0.44	4.171974	2.5775506		42411.66683
2	0.25	17.860571			
3	0.04	8.855122	2.7682652		87.666667
4	0.01	16.510876	1.5321988		17.666667
5	154.39	3.189028	1.8510907	14	249.000001
6	0.34	4.404215	1.6373121		1227.666671
7	18.58	6.887805	3.0713492		327.666668
8	4.18	3.089988	2.0979639	21.42857143	1007.000004
9	17.63	3.968731	2.0684167	50.42857143	406.333335
10	110	17.640141	1.699987		161.666666
11	18.03	6.824537	1.6370514		94.333334
12	11.29	9.993486	1.8319611		81
13	8.08	2.952828	2.0690174	62.85714286	47.181818
14	21.03	4.194894	0.8066907		21.666667
15	0.76	5.944168	0.7182102		3.666667
16	223.99	10.573023	2.2246001		211.666667
17	10.18	17.860571			
18	0.77	7.560033	2.1030846		16.789474

19	11.29	14.297603	2.1740191		89
20	393.8	4.383941	0.893259		10.333333
21	0.5	6.789789	3.6427184	20.85714286	5041.000019
22	21.73	4.134109	0.6992341		11.666667
23	14.21	5.889583	0.4995272		3
24	4.02	2.760604	2.4556441	55.57142857	1319.431378
25	3.12	4.794177			53.571429
26	0.17	17.860571	2.0392153		1.666667
27	6.48	9.170453	1.789565		
28	71.25	9.815297	0.9950881		6.041667
29	71.25	8.682225	1.9931368		15.666667
30	11.29	17.860571			
31	4.71	12.256083	2.0345388		44.333333
32	16.74	9.583955	2.7182056	34	373.000001
33	16.74	2.460584	1.9783334	35	207.666667
34	3.6	2.303288	1.9559388		2109.000008
35	3.97	4.949632	1.7904418		321.000001
36	3.97	3.742768	1.6696326		131.666667
37	3.97	7.18343	1.3186719		26.333333
38	10.55	3.854738	1.7613834		771.000003
39	14.8	7.179445	1.1827307		961.000004
40	45	10.903852	2.3885276		83.666667
41	45	17.860571			
42	45	14.717303	0.8485281		
43	6.31	1.403587	1.3495304	50.85714286	41.285714
44	46.73	2.7476	1.916103	108.7142857	429.000002
45	46.73	1.611533	1.4612694	119.7142857	265.000001
46	0.31	10.574026	1.1568369		
47	0.34	11.753077	3.8257343		462.333335
48	11.17	10.903852	2.3885276	36.57142857	83.666667
49	182	5.630048	3.1014167	15.57142857	55.666667
50	0.25	3.256658	1.537281		23.545455
51	1.59	4.10931	1.7514912	41.57142857	158.333334
52	0.46	6.375057	5.5803652		156.333334
53	0.46	3.331886	2.6556524	57.42857143	301.000001
54	0.45	1.436457	1.3033944	95.71428571	72.333334
55	0.34	4.92513	2.0092546		114.333334
56	0.73	8.057498	2.3149905		229.380953
57	4.12	9.139916	1.1280879		42.333333
58	228	17.860571			1.666667
59	0.16	4.634608	1.4628677		101.75
60	0.16	6.140067	4.0658623	27	701.000003
61	0.16	4.730977	2.0433127		563.666669
62	0.16	3.32345	1.6936747	16	2201.000008
63	0.16	6.450789	1.0338538		23.666667
64	0.16	3.613308	1.3566719		275.999999
65	0.16	7.065047	1.4613795		3.909091
66	0.16	6.770815	2.0243472		234.333334
67	0.16	4.065341	1.5782107		185.666666
68	0.16	8.434577	2.5327689		67
69	19.6	7.892154	3.0443973		850.999998
70	8.6	5.792242	0.9422565		17
71	6.16	17.369242	2.15915		401.000001
72	2.03	4.739835	1.9560143		1966.333341
73	4.28	1.537644	1.4603445	57.14285714	104.2
74	339.29	2.098018	1.9170105	37.14285714	24.282051

75	1.98	4.579803	4.0292531	12.85714286	701.000003
76	0.37	14.292203	1.8489279		
77	2.14	4.696775	2.8158759	10.71428571	8526.333363
78	3.43	3.382658	2.3428862	32.42857143	2481.00001
79	2.36	2.052913	1.4466116	36.71428571	138.333333
80	3.43	17.860571			1.666667
81	195.75	3.333518	1.6547725	80.28571429	106.333334
82	195.75	2.656163	2.0328107	41.57142857	117
83	167	6.996976	2.8629756		91.666667
84	195.75	12.90581	1.2080386		11.666667
85	195.75	17.860571			
86	69	16.258654	1.7575758		
87	975	4.577201	1.7607552		14.333333
88	133.65	3.450565	2.1729471	18.85714286	126.333334
89	30.72	1.629231	1.5684107	43.42857143	13
90	30.72	1.497185	1.476708	50.14285714	12.712329
91	30.72	2.322197	1.6099894	32.85714286	29.8
92	12.74	3.321743	1.9220118	14.14285714	137.000001
93	2.49	2.349384	2.2245388	39.71428571	281.000001
94	20.91	3.104156	2.0607579	86	181.000001
95	19.06	14.331414	0.7614996		
96	19.06	5.561603	1.7801309		21.857143
97	15.4	2.890649	2.7559331	28.85714286	331.666668
98	2.76	5.344397	1.5467939		219.666667
99	2.76	10.866217	1.5031076		11.666667
100	7.01	6.99981	0.3307189		3
101	53.5	17.860571		62.28571429	
102	7.55	2.119822	2.0497456		1057.000004
103	44.22	8.224284	1.023159		24.6
104	42.35	1.670697	1.6706968	65.57142857	16.171084
105	47.89	4.714121	1.7246577		15.666667
106	2.29	15.993421	1.0999439		
107	1.54	1.315622	1.315622	82	14.575221
108	6.64	3.325223	2.1817144	87.71428571	286.333334
109	5.87	2.083482	1.1608711	73.42857143	701.000003
110	3.17	6.99981	0.3307189	56.57142857	3
111	3.17	1.341953	1.3155453	51.14285714	29.236842
112	54.21	4.11747	2.0921082		97
113	0.87	10.782835	1.1994204		21.24
114	5.51	16.777951	1.2374369		11
115	66.49	3.556195	1.6816812		337.000001
116	4.1	17.860571			
117	0.41	1.089001	1.0858509	46.71428571	7.837209
118	0.98	1.613525	1.5199187	71.28571429	63
119	3.66	1.768006	1.6509142	51.28571429	375.999999
120	3.56	6.692259	1.6384913		14.333333
121	3.56	1.366294	1.1869189	117.7142857	801.000003
122	3.56	2.238328	1.3320598	64.71428571	506.333335
123	3.56	3.756278	1.365538		571.000002
124	0.14	12.609458	0		
125	0.72	1.628826	1.5273696		201.000001
126	0.97	1.42818	1.2879819	68.14285714	153.666667
127	0.47	12.123126	1.0643611		11

Record	3 inc MAX	4 inc MAX	Interannual var	Interannual var AA
1	67931.66693	221521.00	1.197800523	235.351583
2			2.645751311	
3	1304.333333	124.69	1.692990629	137.4311384
4	18.333333		2.645751311	
5	731.666669	758.33	0.632815527	12.89166659
6	1521.000006	3022.33	1.343504023	381.8462129
7	439.857143	1467.67	1.772786536	267.5052631
8	1179.000005	1377.00	0.61664527	14.63555242
9	636.333336	389.00	0.76561442	6.823317132
10			2.645751311	15.53762882
11			1.871530874	4.166425539
12			1.26696303	
13	85	47.32	0.702682833	
14	11.666667	9.00	0.487445695	4.000000119
15			1.128825412	6.66628306
16	245.000001		2.190864247	4.997709324
17			2.645751311	8.049599855
18	3.909091		1.039771976	3.899999459
19			2.28455065	4.997710065
20	15.666667		1.149662305	5
21	5861.000023	4337.00	1.469140288	
22	6.333333		0.707775743	4.923114116
23			1.251338288	3.333146973
24	1597.862751	111.00	0.73875917	6.298973579
25	13.666667		0.942455389	5.293462411
26			2.645751311	1.936822713
27			1.219272535	1.142857155
28	12.083333		1.777876273	11.11122428
29	6.333333		1.30638698	4.648160119
30			2.645751311	
31	8.333333		2.270802917	4.507949938
32	387.666668	37.00	1.355018083	2.203111447
33	1223.000005	1403.00	0.685976545	7.24637316
34	3559.000013	18351.00	0.622069907	
35	401.000002		1.767824508	5
36	235.666668	249.00	0.933177166	13.79999858
37			1.518136742	20.20873382
38	971.000004	902.33	0.80513235	21.75128201
39			2.40927212	17.64898206
40			2.068845611	5.665553045
41			2.645751311	2.658699432
42			2.094437077	2.606553408
43	96.333333	58.41	0.131062308	9.949063805
44	221.666668	271.67	0.873124481	16.15278478
45	297.000001	734.33	0.353985824	24.18603282
46			1.342390363	11.71590909
47	465.000002		1.951507706	10.04020767
48			0.428037042	21.08075293
49	159.285714	371.67	1.045566084	2.926564475
50	101.666667	122.33	0.571681717	5.742616037
51	621.000002	701.00	0.661065634	2.944231517
52	415.666668	1209.00	2.15986147	6.46694215
53	701.000003	719.67	0.637756578	269.7577917
54	132.333334	176.33	0.215971578	4.61823558

55	154.333334	43.86	0.94562015	1.976279701
56	241.380953	29.67	1.469339385	5.537295379
57			1.727061094	5.841471518
58			2.645751311	3.305790961
59	112.416667	4.64	2.582212863	
60	2021.000008	6303.67	1.053038265	618.3367806
61	670.333336	687.67	1.160855301	8.598580599
62	2521.00001	3381.00	0.915622438	19.22967798
63	35		1.42899961	9.081148564
64	106.333333	44.14	0.719575144	2.911637361
65	8.6		1.377809967	4.523431768
66	102.333334		1.563750096	16.84278448
67	585.666665	875.67	1.1415365	7.499989214
68	49.666667		1.025011182	13.0047598
69	1030.999998	1042.33	1.527925435	16.93091105
70	49		0.610192331	47.06390978
71	403.666668		2.640686296	2.999999599
72	3113.000012	4597.67	1.3996171	1.644736836
73	188.200001	330.60	0.363941173	133.5749809
74	38.454545	46.33	0.421293056	5.142847001
75	13101.00005	26981.00	0.602509684	3.737190083
76			2.051572365	8.300605732
77	14606.33339	21881.00	0.850668453	5.104702918
78	4081.000016	18301.00	0.640109035	25.45945346
79	1065.800001	2283.86	0.537020784	11.35858932
80			2.645751311	32.32427864
81	111.666667	49.00	0.762889842	
82	166.333334	120.33	0.635019291	8.491017962
83	94.333334	235.67	1.45905139	12.87591234
84			1.88199441	6.494166335
85			2.645751311	2.285731221
86			2.367518179	
87	14.333333		0.827103573	3.333147039
88	69	186.33	0.865134318	5.280464218
89	17	39.67	0.802014403	4.763098968
90	14.849315	22.09	0.468155434	7.540609136
91	62.2	80.67	0.417992341	3.482439423
92	40.927273	49.35	1.570258221	4.227289286
93	303.666668	712.33	0.790190752	33.78412574
94	786.333336	870.33	0.846674108	9.278400569
95			2.024991782	10.72193877
96	17.444444	27.71	1.171729103	2.999827466
97	353.000001	1467.67	0.654579773	15.99188262
98	346.333335		1.973716057	30.20536748
99			1.577211521	15.68300324
100	3.666667		1.280868845	3.333146973
101			2.645751311	4.997709324
102	1094.333337	1545.00	0.778891048	
103	41	58.33	1.717676693	16.46710047
104	23.383275	32.78	0.42218097	1.2
105	27.333333	109.67	1.713457518	15.80955341
106			2.320954819	7.673825162
107	19.376471	36.98	0.213032056	1.250002032
108	786.333336	1681.00	0.959181594	14.06914708
109	901.000003	1101.00	0.702884342	133.5315301
110	3.666667		0.371596529	14.90185281

111	41.542105	54.43	0.539600293	11.76892589
112	118.333334	398.33	0.993302517	88.75273615
113	48.12		2.645751311	13.0972122
114			2.458245055	
115	577.000002	749.00	1.120719055	1.500083808
116			2.645751311	20.03348211
117	11.395604	17.32	0.342792255	
118	237	711.00	0.487441022	2.771407849
119	429.333332	525.03	0.424060291	15.79168284
120	11.666667		1.124904322	125.443284
121	1301.000005	1741.00	0.373084371	2.999999596
122	606.333336	46.49	0.540092065	17.43498633
123	791.000003	821.00	1.233749709	7.546675038
124			2.645751311	18.53092005
125	670.215689	2316.29	0.322903333	
126	210.800001	450.80	0.349566403	17.69982439
127			2.574682241	2.380956585

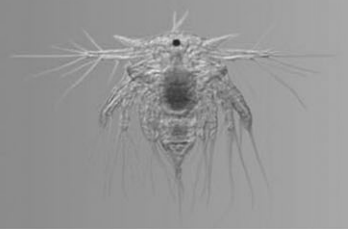
Record	Non-zero records	FDC
1	132	-19.91
2	1	
3	34	-23.94
4	3	
5	126	-13.98
6	57	-17.04
7	68	-20.69
8	163	-14.24
9	100	-20.58
10	3	
11	24	
12	13	
13	173	-16.57
14	28	-34.34
15	13	
16	16	
17	1	
18	29	-23.98
19	8	
20	28	-27.34
21	96	-24.10
22	26	-43.24
23	11	
24	260	-12.57
25	68	-21.90
26	1	
27	15	
28	6	
29	20	
30	1	
31	10	
32	28	-27.80
33	222	-11.05
34	244	-11.93
35	52	-18.64
36	80	-16.66

37	16	
38	82	-17.33
39	14	
40	17	
41	1	
42	2	
43	303	-6.09
44	174	-12.77
45	278	-10.62
46	6	
47	35	-29.28
48	17	
49	103	-20.70
50	92	-12.36
51	72	-23.42
52	246	-21.86
53	212	-17.77
54	281	-6.18
55	63	-19.92
56	30	-26.69
57	8	
58	1	
59	44	-15.49
60	144	-23.31
61	70	-23.47
62	102	-13.66
63	15	
64	64	-17.61
65	19	
66	34	-23.64
67	63	-18.73
68	32	-32.16
69	51	-26.48
70	17	
71	5	
72	65	-18.99
73	297	-8.64
74	276	-16.08
75	250	-18.43
76	6	
77	123	-15.35
78	166	-15.44
79	189	-9.64
80	1	
81	98	-19.72
82	203	-13.91
83	58	-24.33
84	4	
85	1	
86	4	
87	59	-22.05
88	141	-18.19
89	302	-7.96
90	313	-7.93
91	179	-13.16
92	124	-15.61

93	291	-11.97
94	157	-13.77
95	2	
96	41	-22.65
97	293	-18.00
98	36	-22.48
99	8	
100	7	
101	1	
102	302	-9.73
103	9	
104	319	-11.34
105	54	-18.81
106	2	
107	319	-6.86
108	152	-17.75
109	140	-12.32
110	7	
111	311	-5.84
112	95	-17.26
113	6	
114	2	
115	89	-14.88
116	1	
117	318	-3.29
118	293	-8.57
119	288	-10.08
120	25	
121	268	-6.49
122	147	-12.49
123	60	-20.06
124	2	
125	291	-9.20
126	279	-7.33
127	4	

Appendix IV – Published work

JPR Advance Access published December 29, 2016



Journal of
Plankton Research

plankt.oxfordjournals.org

J. Plankton Res. (2016) 00(00): 1–11. doi:10.1093/plankt/fbw094

Disentangling the counteracting effects of water content and carbon mass on zooplankton growth

KRISTIAN MCCONVILLE[1,2]*, ANGUS ATKINSON[1], ELAINE S. FILEMAN[1], JOHN I. SPICER[2] AND ANDREW G. HIRST[3,4]

[1]PLYMOUTH MARINE LABORATORY, PROSPECT PLACE, PLYMOUTH PL1 3DH, UNITED KINGDOM, [2]MARINE BIOLOGY & ECOLOGY RESEARCH CENTRE, SCHOOL OF MARINE SCIENCE & ENGINEERING, PLYMOUTH UNIVERSITY, DRAKE'S CIRCUS, PLYMOUTH PL4 8AA, UNITED KINGDOM, [3]SCHOOL OF BIOLOGICAL AND CHEMICAL SCIENCES, QUEEN MARY UNIVERSITY OF LONDON, MILE END ROAD, LONDON E1 4NS, UNITED KINGDOM AND [4]CENTRE FOR OCEAN LIFE, NATIONAL INSTITUTE FOR AQUATIC RESOURCES, TECHNICAL UNIVERSITY OF DENMARK, KAVALERGARDEN 6, CHARLOTTENLUND 2920, DENMARK

*CORRESPONDING AUTHOR: krm@pml.ac.uk

Received February 26, 2016; editorial decision November 30, 2016; accepted December 12, 2016

Corresponding editor: Marja Koski

Zooplankton vary widely in carbon percentage (carbon mass as a percentage of wet mass), but are often described as either gelatinous or non-gelatinous. Here we update datasets of carbon percentage and growth rate to investigate whether carbon percentage is a continuous trait, and whether its inclusion improves zooplankton growth models. We found that carbon percentage is continuous, but that species are not distributed homogenously along this axis. To assess variability of this trait *in situ*, we investigated the distribution of biomass across the range of carbon percentage for a zooplankton time series at station L4 off Plymouth, UK. This showed separate biomass peaks for gelatinous and crustacean taxa, however, carbon percentage varied 8-fold within the gelatinous group. Species with high carbon mass had lower carbon percentage, allowing separation of the counteracting effects of these two variables on growth rate. Specific growth rates, g (d^{-1}) were negatively related to carbon percentage and carbon mass, even in the gelatinous taxa alone, suggesting that the trend is not driven by a categorical difference between these groups. The addition of carbon percentage doubled the explanatory power of growth models based on mass alone, demonstrating the benefits of considering carbon percentage as a continuous trait.

KEYWORDS: water content; zooplankton; gelatinous; carbon percentage; growth

INTRODUCTION

Gelatinous zooplankton are a phylogenetically broad and ecologically important group of taxa found throughout the world's oceans. Their prey range from bacteria to fish (Sutherland *et al.*, 2010) and they exhibit an equally diverse range of life history strategies and body compositions. The high water content characteristic of this group

available online at www.plankt.oxfordjournals.org

can be expressed as carbon percentage (carbon mass as % of wet mass), with some taxa having carbon mass as low as 0.01% of their wet mass (Clarke *et al.*, 1992; Harbison, 1992; Lucas *et al.*, 2011; Kiørboe, 2013).

Interest in gelatinous zooplankton is linked to a growing appreciation of their impact on pelagic ecosystems and human activities (Richardson *et al.*, 2009; Purcell, 2012, Gibbons and Richardson, 2013). For example, the introduction of the ctenophore, *Mnemiopsis leidyi* to the Black Sea has had considerable financial implications for fisheries in the area (Shiganova and Bulgakova, 2000). Research on gelatinous zooplankton has grown apace with basic ecological interest in the physiology, trophic ecology and bloom dynamics of this group (Møller and Riisgård, 2007; Condon *et al.*, 2013; Gemmell *et al.*, 2013).

Based on a compilation of zooplankton body composition, Kiørboe (2013) found that most zooplankton species are either gelatinous (~0.5%) or non-gelatinous (5–10%), with comparatively few intermediates. Indeed, much research has been directed toward comparing and contrasting gelatinous versus non-gelatinous zooplankton. For example, compared to other planktonic animals, gelatinous zooplankton have higher carbon mass-specific feeding rates (Hamner *et al.*, 1975; Acuña, 2001; Acuña *et al.*, 2011), lower locomotion costs and higher specific growth rates (Hirst *et al.*, 2003; Pitt *et al.*, 2013). Indeed, gelatinous taxa such as salps are amongst the fastest growing metazoans (Bone, 1998).

The use of a categorical approach to zooplankton body composition (i.e. gelatinous versus non-gelatinous) contrasts with the treatment of carbon mass (Peters, 1983), which is used as a continuous variable in many models of growth (Hansen *et al.*, 1997; Gillooly *et al.*, 2002, Hirst *et al.* 2003). However, the carbon percentage of zooplankton species also varies widely, even among gelatinous taxa (Molina-Ramirez *et al.* 2015). A recent review suggested that water content was second only to body size in determining key aspects of the biology of zooplankton (Andersen *et al.*, 2015b). So far, empirical models of zooplankton growth use equations that are specific to various taxonomic groups (Hirst *et al.* 2003; Kiørboe and Hirst, 2014) and these equations have not yet been unified. As carbon mass and carbon percentage are both variable traits, it is important to consider them together in empirical models of zooplankton growth. Furthermore, quantifying the relationship between growth rate and carbon percentage may help to explain how carbon percentage functions as an evolutionary trait, and, e.g. why there are gelatinous representatives from six phyla found in the plankton.

In this study we have used both a meta-analyses approach and an *in situ* time series of zooplankton from weekly sampling at the Plymouth L4 time series (Smyth *et al.* 2015). We had three objectives. The first was to quantify the degree of variability in carbon percentage both in 'trait space' from the meta-analysis dataset and in a natural plankton assemblage, to gauge whether it was appropriate to treat water content as a continuous variable. The second aim was to investigate the degree of collinearity between carbon mass and carbon percentage, again both in a meta-assemblage and in the L4 assemblage. Dependent on the outcome of these two objectives, the third aim was to construct a simple empirical model of zooplankton growth that combines carbon mass and carbon percentage.

METHOD

Carbon percentage data

Ratios of wet mass to carbon mass were combined from a series of recent compilations (Kiørboe, 2013; Pitt *et al.*, 2013; Molina-Ramirez *et al.*, 2015). The amalgamated dataset with their sources is presented in Supplementary Information 1 online. Only concurrent measurements of carbon and wet mass of the same individual were used to calculate carbon percentage.

The degree of tissue dilution of zooplankton taxa has been expressed previously as body carbon content (Molina-Ramirez *et al.*, 2015). However, to avoid confusion with carbon mass, throughout this article it is referred to as 'carbon percentage' (carbon mass as a percentage of wet mass). For our comparisons the levels of taxonomic organization were selected based on functional diversity and body form (e.g. phylum for Chaetognatha, but orders Cydippida and Lobata).

In situ analysis

To investigate how species biomass was distributed along the spectrum of carbon percentage an *in situ* community, the L4 zooplankton time series (Western Channel Observatory, Plymouth) was used. The L4 sampling site is approximately 15 km south–west of Plymouth and undergoes seasonal stratification (Harris, 2010). Sampling at the L4 site consists of a pair of vertical hauls with a 200 μm WP-2 zooplankton net from 50 m to the surface (maximum depth 54 m). The nets are retrieved at 20 cm s^{-1} and are immediately fixed in 4% formaldehyde solution (Maud *et al.*, 2015). The zooplankton are then subsampled, counted and identified (Eloire *et al.* 2010). This zooplankton abundance times series has high resolution both temporally (weekly sampling) and taxonomically, with many taxa

consistently identified to species level since 2009. To determine zooplankton biomass, a total of 3780 individuals from the formalin-preserved catches at L4 taken throughout 2014 and 2015 were measured. From standard length measurements (e.g. cnidarian bell height or diameter, copepod prosome length), length-carbon mass relationships from the literature were used to estimate carbon mass per individual. These length measurements were then aggregated into seasons, namely spring (March–May), summer (June–August), autumn (September–November) and winter (December–February) to account for the high intraspecific variability in length observed at L4 (Atkinson *et al.*, 2015). This allowed us to derive season-specific mean carbon masses per individual, which were multiplied by numerical densities to estimate biomass density (mg C m^{-3}). Previously measured, L4-specific seasonal values of individual carbon biomass were used, when available (e.g. *Calanus helgolandicus;* Pond *et al.* 1996).

Of the approximately 189 taxa recorded at L4, only 22 contributed more than 0.5% to the total biomass for all species. To examine how biomass was distributed across the spectrum of carbon percentage, these taxa were assigned to $\log_2$ classes (0.1–0.2%, 0.2–0.4%, 0.4–0.8%, 0.8–1.6%, 1.6–3.2%, 3.2–6.4%, 6.4–12.8%, >12.8%) using the carbon percentage data in Supplementary Information 1 online. The distribution of carbon biomass in each carbon percentage category across the seasons was then calculated.

Growth rate data

Using the references from the appendices of Kiørboe and Hirst (2014) as a starting point, zooplankton growth rate data were extracted from the original sources and augmented by searching the literature. All growth rate data used here are in Supplementary Information 2 online.

To improve comparability of source data we restricted the meta-analysis to data from laboratory incubations with food available in high (assumed non-limiting) concentrations. By using only data collected under these conditions we suggest that the measurements are more directly comparable, with the observed patterns more likely to reflect the intrinsic biology of the species than external factors.

Published growth rates are normally expressed either as increase in length or body mass over time. When organism size was expressed as length, published length-mass regressions were used to convert to body carbon mass (Hirst, 2012; Kiørboe and Hirst, 2014). To express growth rates in the terms commonly used for zooplankton (as an exponential rate; see Hirst and Forster 2013), the mass-specific growth rate, g (d^{-1}) was determined as follows:

$$g = (\ln M_t - \ln M_0)/d$$

where M_t is mass at time, t, M_0 is mass at the previous time point, and d is the time period between the two measurements of mass (in days).

Growth data were temperature-corrected to 15°C using a Q_{10} of 2.8 (following Hansen *et al.*, 1997; Kiørboe and Hirst, 2014). General linear models (GLMs) were constructed in R (R Core Team, 2014) to determine the relationships between growth rate, carbon percentage and carbon mass. To determine whether there was collinearity between the predictor variables we examined the condition indices for the variables in the model using the *colldiag* function in the *perturb* package in R (Hendrickx, 2012). A condition index of greater than 30 is considered large (Belsley *et al.*, 1980) and suggests that the variable should be removed from the model.

When growth data were available for a species but carbon percentage values were not, the latter was estimated using the mean value for the highest level of taxonomic relatedness available. For instance, if composition values for a species were not available, then the composition values for all other species within the genus were averaged and used as an estimate. The estimates were typically at the genus level but no lower relatedness than family (38% estimated at family level, primarily for copepods).

Growth rate analysis

Four analyses were performed; the first two were based on mean and maximum growth rates for all zooplankton taxa in the dataset, the second two as above but for the classical gelatinous taxa only (Cnidaria, Ctenophora and Thaliacea). Maximum growth values were defined as the highest temperature-adjusted growth rate value available for each species. Issues of non-independence between data were avoided by using single growth rate values per species per study. For illustrative purposes only (i.e. the plots in Fig. 4), we adjusted all growth rates to a fixed body carbon mass of 1 mg C after correcting to 15°C. This mass correction was performed assuming $\log_{10}$ mass-specific growth (g) scales against $\log_{10}$ mass with a slope of −0.25 (Brown *et al.* 2004).

RESULTS

Variability in carbon percentage across the zooplankton

The range in body volume for two animals of equal carbon mass but at either end of the carbon percentage spectrum is show in Fig. 1. For the compiled dataset, the range in carbon percentage extended over four orders of magnitude, from 0.01% in the lobate ctenophore, *Bathycyroe fosteri*, to 19.02% in the copepod, *Calanus hyperboreus* (Figs 1 and 2a, Supplementary Information 1 online). The intervals between adjacent ranked species were small relative to the range covered (Fig. 2a), suggesting that water content could be considered as a continuous variable. The largest interval between species coincided with the shift from the classic gelatinous taxa to other zooplankton (i.e. from Thaliacea to Chaetognatha). However, this difference between species constituted a relatively small fraction of the total range (6.8%). In addition, there was overlap of classic gelatinous and non-gelatinous groups. For example, some chaetognaths were within the traditional gelatinous range (1.27 and 1.35% for *Pseudosagitta lyra (as P. scrippsae)* and *Pseudosagitta* (as *Sagitta) gazellae* respectively), whereas one tunicate had a carbon percentage which lay within the non-gelatinous range (3.87% for *Doliolum denticulatum*). This overlap of taxonomic groups was extensive across the spectrum of water content, as can be seen by the mixing of colour across Fig. 2. This was particularly the case among the Ctenophora and Thaliacea with the range of both taxa approaching two orders of magnitude in carbon percentage.

The wide variation in body carbon percentage observed at a species level in Fig. 1a is also summarized at the broader taxon level in Fig. 2b. Median values for groups do loosely cluster into gelatinous and non-gelatinous taxa following the bimodal distribution of species suggested by Kiørboe (2013). The ranges of all adjacent taxa (excluding lobate ctenophores) overlapped, with Thaliacea and Chaetognatha bridging the gap between the classical gelatinous and non-gelatinous taxa. The variability within groups was greater for gelatinous taxa, with the greatest range in the scyphomedusae, closely followed by the thaliaceans. The gelatinous taxa sort into their respective phyla when ranked (i.e. Lobata, Nuda, Cydippida for the Ctenophora, then Hydromedusae and Scyphomedusae for Cnidaria) suggesting that taxa within phyla are on average more similar to each other than with other phyla.

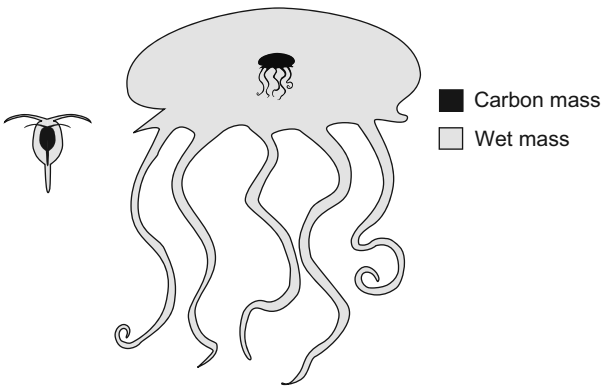


Fig. 1. Comparison of the relative carbon (black) and wet masses (grey) of *Calanus hyperboreus* (left, carbon percentage = 19.02%) and *Bathycyroe fosteri* (right, carbon percentage = 0.01%). The relative area of each shade is scaled as volume so the silhouettes are representative of true size.

In the natural assemblage sampled at the Plymouth L4 site (Figure 3) we have an alternative picture, namely how biomass is distributed along this spectrum of carbon percentage. At L4, biomass is distributed bimodally. The biomass is primarily concentrated in the categories that are either highly gelatinous (carbon mass 0.1–0.8% of wet mass) or non-gelatinous (6.4–>12.8%) However, there is considerable variability within the carbon percentage categories, as some gelatinous taxa are as much as 8 times larger in wet mass for the same carbon mass as others. The biomass in the intermediate categories (0.8–1.6 and 1.6–3.2%) was very low and below our threshold for inclusion. This area of the spectrum is populated by thaliaceans and large rhizostome scyphomedusae, which are either not commonly recorded at L4 (thaliaceans) or are rarely or poorly sampled by the 0.57 cm diameter nets used. Gelatinous taxa comprise a greater proportion of biomass in summer than the other seasons. In winter, chaetognaths (3.56%) have similar total biomass to the dominant copepods. There is also a broad trend of increasing carbon percentage through the year within the gelatinous taxa. In spring, the cydippids (the most gelatinous group frequently encountered at L4) are dominant, followed by Nuda (Beroe) in summer and finally hydromedusae and siphonophores in autumn.

Relationship between carbon mass and carbon percentage

There were negative relationships between carbon mass and carbon percentage, both in the meta-dataset (Fig. 4a) and in the *in situ* dataset (Fig.4b). While the more gelatinous taxa tended to have higher carbon mass there was considerable variability, with some organisms of similar carbon mass differing 100-fold in carbon percentage (Fig. 4). To ensure that collinearity was not influencing the growth model the condition

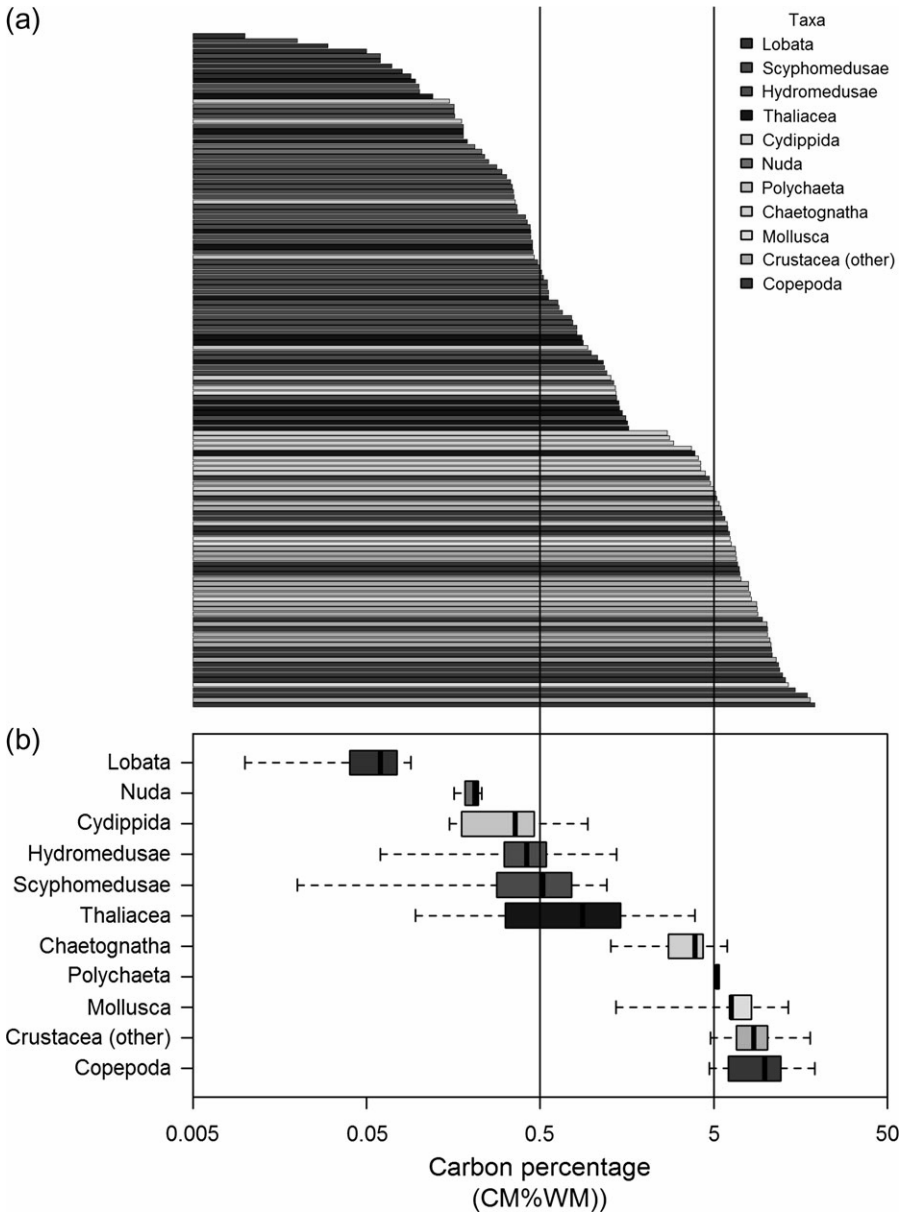


Fig. 2. (**a**) Zooplankton species ranked according to their carbon percentage (CM%WM; $\log_{10}$ scale), each horizontal bar represents a single species. Colours indicate taxonomic groups as detailed in the legend. (**b**) Zooplankton taxonomic groups ranked according to their carbon mass (as % of wet mass; $\log_{10}$ scale). Boxes indicate median, lower and upper quartiles with whiskers showing the range. (Vertical lines at 0.5 and 5 CM%WM represent the composition of the gelatinous and non-gelatinous taxa defined by Kiørboe (2013).).

indices for the variables were inspected. The highest condition index observed was 3.05, lower than the threshold of 30 suggested by Belsley *et al.* (1980) confirming that carbon mass and carbon percentage can be used in combination in models of zooplankton growth. As gelatinous and small organisms tend to grow fastest, the tendency for more gelatinous taxa to have higher carbon mass underlines the need to include both as covariates in our growth model.

Relationship between carbon percentage and growth rate

We first conducted GLMs on the subset of data comprising the classical gelatinous taxa alone. These showed that mean growth rate declined with increasing mass and increasing body carbon percentage. The GLMs on the whole dataset established that $\log_{10}$ mass-specific mean and maximum growth rate was significantly correlated with both $\log_{10}$ carbon mass and $\log_{10}$ body

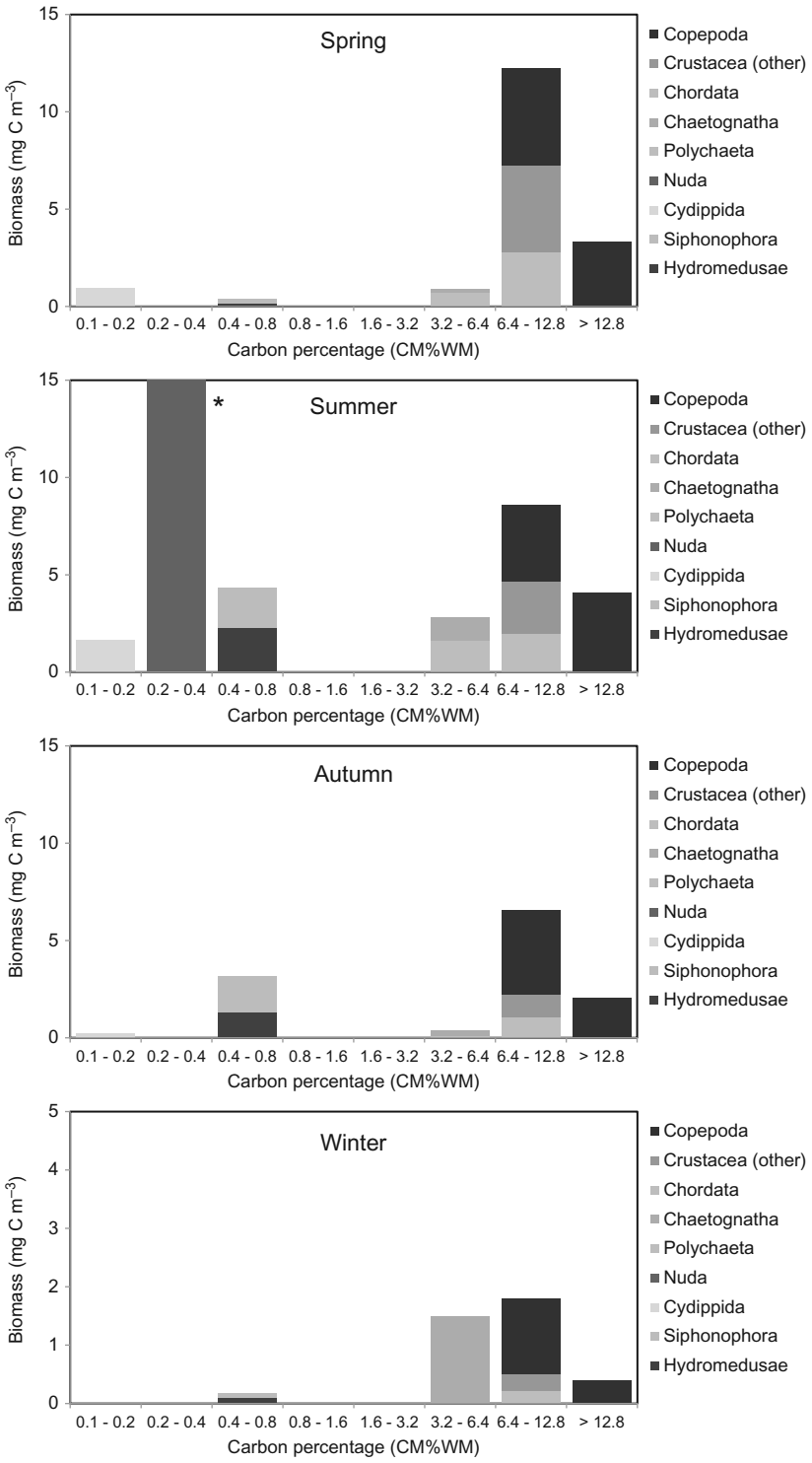


Fig. 3. Distribution of carbon biomass (mg C m^{-3}) between log_2 carbon percentage (CM%WM) categories through spring, summer, autumn and winter (2009–2015) at the L4 sampling site, Western Channel Observatory, Plymouth. The same colour coding of taxa is used as in Fig. 1—see legend. *Biomass value for the category 0.4–0.8 exceeds the scale in summer (34.4 mg C m^{-3}) as a result of 7 high abundance observations of *Beroe spp*. (of total 318 samples). Upper limit of biomass scale in winter is 5 mg C m^3.

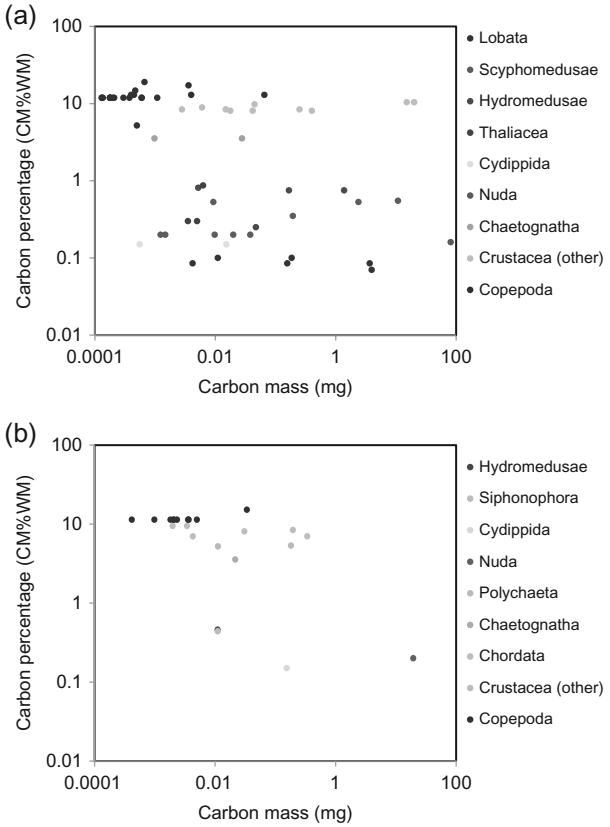


Fig. 4. Carbon percentage (CM%WM) as a function of carbon mass (mg) for the meta-analysis dataset (A, log carbon percentage = −0.26 * log carbon mass −0.18, $P = 0.0001$, $R^2 = 0.21$, df = 60) and the L4 assemblage (B, log carbon percentage = −0.34* log carbon mass −1.1, $P = 0.0026$, $R^2 = 0.3429$, df = 20). Taxonomic groups coloured as indicated in the legends.

carbon percentage (Fig. 5 and Table I). As expected, there was a negative relationship between $\log_{10}$ mass-specific growth rate (g), and $\log_{10}$ carbon mass, consistent with the results of Kiørboe and Hirst (2014). In the analyses of all zooplankton taxa, mean and maximum growth rate decreased with increasing carbon mass and carbon percentage.

In all analyses, the addition of body carbon percentage to models of growth based on carbon mass alone increased the explanatory power (Table II). The second order Akaike criterion, AICc, (Burnham and Anderson, 2002) was lower in the model including water content in all analyses, supporting the inclusion of this factor in analyses of zooplankton growth. In the maximum analysis including all taxa, Akaike weights (ω_i) were approximately 10 times higher in the models including body carbon percentage (mass $\omega_i = 0.08$, mass + carbon percentage $\omega_i = 0.92$). This suggests that these models were significantly better than models based on mass alone (Royall, 1997). A similar pattern was observed in the analysis of maximum growth rates of the gelatinous taxa however it was not observed for mean growth rates (mass $\omega_i = 0.02$, mass + GI $\omega_i = 0.98$).

DISCUSSION

Our study provides strong support for body carbon percentage being a continuous trait, for a negative relationship between body carbon percentage and growth rate, and for considerable increases in model predictive power as a result of inclusion of this trait for zooplankton. Below we discuss the implications of each of these findings in turn.

Kiørboe (2013) demonstrated that if zooplankton are arranged in a frequency distribution based on body composition, that most taxa are either gelatinous (carbon mass is ~0.5% of wet mass) or non-gelatinous (~5–10%), with little overlap. Our study would appear to contradict this, since we found a fairly continuous distribution of carbon percentage. However, this does not conflict with the findings of Kiørboe (2013), since in that study it was emphasized that most taxa are either highly gelatinous or non-gelatinous. Rather, we highlight that, while most species fall into one of these two groups, there is considerable variability in carbon percentage within each group and there are representatives across much of this spectrum. The distribution of zooplankton biomass at L4 supports both of these views. Biomass is clustered at either end of the spectrum as described previously, and this could suggest that the fitness landscape for this trait favours extremes. However, at either end of the spectrum there is considerable variability. The traditional gelatinous group alone spans an 8-fold range in carbon percentage, with implications for growth rate. For example, there is a trend of increasing carbon percentage among the gelatinous zooplankton through the year, with cydippids being replaced by beroids in summer and finally by hydromedusae and siphonophores in autumn.

In the meta-analysis compilation, the largest interval occurs between taxa typically considered as gelatinous and intermediate, between the pelagic tunicate, *Thalia* (as *Salpa*) *democratica* (1.6% body carbon percentage) and a chaetognath, *Eukrohnia hamata* (2.7 % body carbon percentage). Molina-Ramirez *et al.* (2015) stressed that considerable variation in carbon percentage existed even within the classic gelatinous taxa (Cnidaria, Ctenophora and Tunicata). Our results are in agreement, albeit with even higher degree of variability (at 350-fold). Taken together, the relatively small interval between values for gelatinous and non-gelatinous species and the high variability observed within the gelatinous

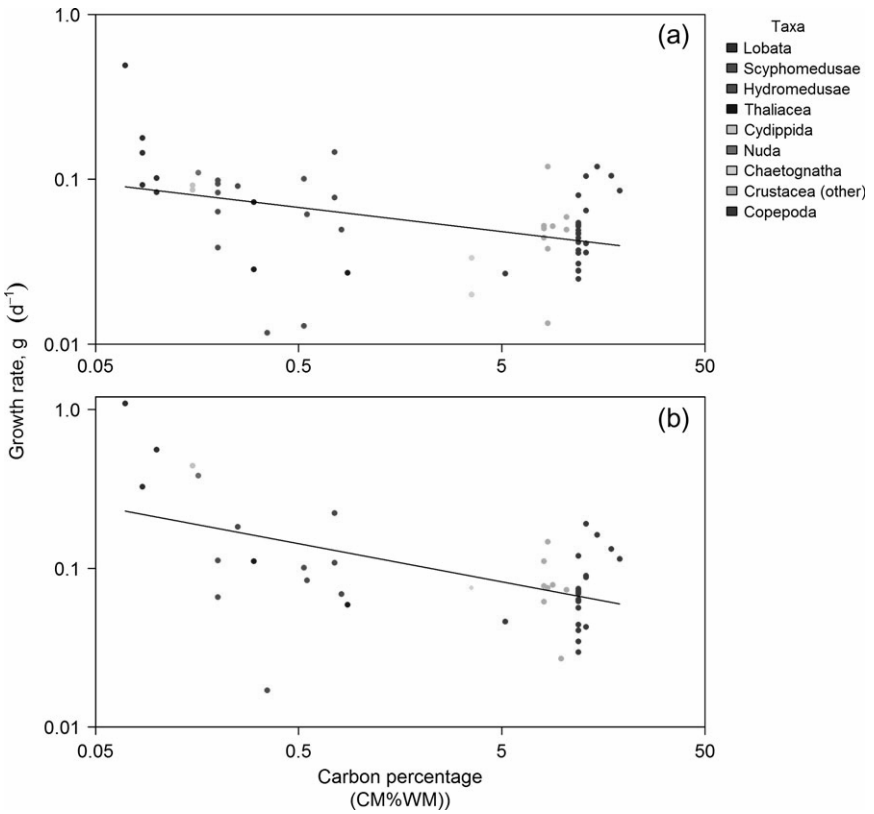


Fig. 5. Specific growth rate, g (d^{-1}) as a function of body carbon percentage (CM%WM). Growth values were temperature-adjusted to 15°C, mass adjusted to 1 mg C and then averaged for each species in each study. (**a**) Mean mass-specific growth rate values for each species in each study and (**b**) maximum specific growth rate values for each species.

Table I: General linear models predicting log_{10} mean specific and log_{10} maximum specific growth rate, g (d^{-1}), as a function of both log_{10} carbon mass (mg) and log_{10} body carbon percentage (100(CM/WM))*

Group		Factor	df	*P*	Slope	Intercept	Adj R^2
All zooplankton	Mean growth rate, *g*	log_{10} carbon mass	58	<0.0001	−0.17	−1.12	0.43
		log_{10} carbon percentage		0.036	−0.18		
	Max growth rate, *g*	log_{10} carbon mass	42	<0.0001	−0.16	−0.81	0.31
		log_{10} carbon percentage		0.013	−0.16		
Gelatinous taxa only	Mean growth rate, *g*	log_{10} carbon mass	22	0.027	−0.19	−1.18	0.33
		log_{10} carbon percentage		0.038	−0.17		
	Max growth rate, *g*	log_{10} carbon mass	13	0.011	−0.16	−1.15	0.42
		log_{10} carbon percentage		0.018	−0.72		

All models pertain to growth rate data that were first Q_{10}-adjusted to 15°C.

taxa suggest that growth models can indeed incorporate carbon percentage as a continuous trait.

When log_{10} mass-specific growth rate was regressed against log_{10} body carbon percentage as a continuous variable, a negative relationship was observed. Crucially, the pattern persisted when considering the gelatinous taxa alone (Table II). The existence of the relationship among the gelatinous taxa alone, is important as this demonstrates that the relationship is not due to a categorical difference between gelatinous organisms and non-gelatinous organisms.

One potential mechanism that could explain the relationship between body carbon percentage and growth rate is enhanced feeding rate (Acuña *et al.*, 2011). These authors suggested that the large dilute bodies of gelatinous zooplankton facilitate higher carbon-specific feeding rates than other zooplankton taxa of the same carbon mass. If this increased feeding rate drives faster growth,

Table II: Changes to measures of explanatory power of models of growth based solely on carbon mass when body carbon percentage (CC) was added as a factor

		R^2		AICc			ω_i	
Group	g	Mass	Mass + CC	Mass	Mass + CC	Δ_i	Mass	Mass + CC
All zooplankton	Mean	0.39	0.43	18.63	16.67	2.47	0.19	0.81
	max	0.22	0.31	21.99	17.57	4.42	0.076	0.92
Gelatinous taxa only	mean	0.33	0.33	18.51	19.96	1.44	0.54	0.46
	max	0.09	0.42	21.55	16.26	5.29	0.019	0.98

AICc is the corrected Akaike information criterion, Δ_i is the AIC difference, and ω_i is the Akaike weight. Models with Akaike weight values 10 times greater than that of the other models being compared are considered statistically significant as optimal models (mass + GI for mean and max all zooplankton and max gelatinous taxa only). All models pertain to growth data that were first Q_{10}-adjusted to $T = 15$°C.

then this might explain the relationship of increasing growth rate with decreasing carbon percentage (Fig. 2). As many gelatinous taxa are filter or ambush feeders that rely on capture surfaces to feed, assuming that feeding rate scales with surface area, then we may expect the scaling exponent between surface area and body carbon percentage to match the exponent for growth rate and body carbon percentage. To investigate this we used a simple geometric calculation. Assuming isomorphic growth, surface area (SA) scales with body volume with a power of 0.67. By altering degree of gelatinousness for a fixed amount of body carbon, SA then scales with carbon percentage with a power of −0.67. Hence, with an assumption that growth rate is a fixed proportion of feeding rate, this would give the same slope of −0.67 for $\log_{10}$ mass-specific growth versus $\log_{10}$ carbon percentage (Fig. 2). The exponents that we determined empirically across the various zooplankton taxa are less steeply negative than −0.67 (at −0.18 and −0.16 for mean and maximum respectively), i.e. increasingly gelatinous organisms increase their growth rate less rapidly than these surface considerations would predict. This could indicate a potential feeding inefficiency associated with decreasing carbon percentage or that factors additional to surface area may also be important.

In common with Ikeda (2014), we found that species with larger total carbon mass also tended to be more watery. Furthermore, as the larger organisms are typically more watery the effects of carbon mass and carbon percentage tend to counteract, underscoring the need to include these variables together in order to better predict growth. Molina-Ramirez *et al.* (2015) found a similar result for tunicates but found that body carbon percentage was invariant with increasing mass for cnidarians and ctenophores. The authors suggested that this might be due to differences between internal filter feeding in tunicates and external ambush or cruise feeding in the other groups. It has been suggested that feeding modes decrease in efficiency with increasing size (Kiørboe, 2011), so high water content may help to mitigate this decrease in efficiency and maintain relatively higher carbon-specific feeding rate at large carbon masses. This is supported by the findings of Acuña *et al.* (2011), suggesting that gelatinous plankton had higher carbon-specific feeding rates than other zooplankton of a similar carbon mass. Together with higher growth rates, these factors could help to explain how gelatinous zooplankton are capable of forming such high localized increases in species biomass (blooms).

While the increase in capture surface area and associated feeding and growth rates is one potential advantage of the gelatinous body form, there are other implications. There are potential negative implications also, especially with regard to limited swimming speed and escape responses. While medusae have potential defences in the form of nematocysts, many gelatinous taxa such as ctenophores do not, and may have limited ability to escape from potential predators as a result of their large dilute bodies (Acuña *et al.* 2011). Understanding why some taxa are gelatinous is not always straightforward. The most gelatinous mollusc in this analysis is *Clione limacina*, a gymnosome predator that feeds on almost exclusively on *Limacina helicina*. *Clione* does not rely on large capture surfaces or on generating a feeding current as it ambushes individual, relatively large prey items. In this case, water content does not appear to be a derived trait to increase body volume relative to carbon for feeding, suggesting that this may not be the only driver of high water content in zooplankton. It has been suggested that potential other causes include physical or ecological factors such as transparency to impair visual predation (Hamner *et al.*, 1975) or the efficiency of neutral buoyancy (Kiørboe, 2013). Together these factors may help to explain why semi-gelatinous bodies are observed in at least six major planktonic phyla (Cnidaria, Ctenophora, Chordata, Annelida, Chaetognatha, Mollusca, see Supplementary Information 1).

CONCLUSIONS

Body size is often described as a master-trait, and is frequently used as the sole intrinsic variable in empirical and simulation models involving zooplankton growth (Kiørboe and Hirst, 2014; Andersen *et al.*, 2015a). But what do we mean by 'body size'? Carbon mass is often used as the unit for size, but both our meta-analysis and the real assemblage data show that carbon percentage also varies greatly. It may even vary negatively with carbon mass, levering an opposing effect on growth. We argue that carbon mass and carbon percentage are both key traits, both are intrinsic to the zooplankton and since they are possible to estimate, then we should disentangle their separate effects in a unified growth model. By including carbon percentage in models of growth based on carbon mass alone, we substantially increased their explanatory power, with smaller body masses and lower body carbon percentages leading to higher specific growth rates. Building on the work of previous publications (Kiørboe, 2013; Pitt *et al.*, 2013; Molina-Ramirez *et al.*, 2015) we provide a carbon percentage dataset in Supplementary Table 1. By using these source data alongside carbon mass, the maximum growth rate equation in Table 1 may then be used as a starting point to estimate growth rates attainable by zooplankton.

Alongside the 'size' based simplifications used for modelling, there has also been an increase in 'trait-based' modelling in which categorical variables or functional groups are allowed to vary continuously. A purpose of this article is to allow water content also to be used as a continuous trait; to facilitate its inclusion alongside carbon mass and other traits such as feeding mode (Litchman *et al.*, 2013; Andersen *et al.* 2015a; Hérbert *et al.*, 2016). Since we found that growth rate depended on carbon percentage even among the gelatinous taxa alone, we hope that considering and modelling water content as a continuous trait will reveal the ecological and evolutionary factors that influence the water content of zooplankton.

SUPPLEMENTARY DATA

Supplementary data can be found online at *Plankton Research* journal.

ACKNOWLEDGEMENTS

We thank the numerous authors (cited in Supplementary Tables 1 and 2) whose measurements of body composition and growth rate have made this meta-analysis possible. We also thank the crew of the RV *Plymouth Quest* and Anderson Rachel Harmer and Andrea McEvoy who analysed the zooplankton data. We thank Martin Lilley for help with the length-mass conversions of the gelatinuous taxa.

FUNDING

K.M. was in receipt of a Natural Environment Research Council National (NERC) funded studentship, and was partly funded together with A.A., E.F. and A.G.H. by the NERC and Department for Environment, Food and Rural Affairs (Grant no. NE/L003279/1, Marine Ecosystems Research Program).

REFERENCES

Acuña, J.L. (2001) Pelagic tunicates: why gelatinous? *Am. Nat.*, **158**, 100–106.

Acuña, J.L., López-Urrutia, A. and Colin, S. (2011) Faking giants: the evolution of high prey clearance rates in jellyfishes. *Science*, **333**, 1627–1629.

Andersen, K.H, Aksnes, D.L., Berge, T., Fiksen, Ø. and Visser, A. (2015a) Modelling emergent trophic strategies in plankton. *J. Plankton Res.*, **37**, 862–868.

Andersen, K.H., Berge, T., Goncalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C. *et al.* (2015b) Characteristic sizes of life in the oceans, from bacteria to whales. *Annu. Rev. Mar. Sci.*, **8**, 3.1–3.25 2016.

Atkinson, A., Harmer, R.A., Widdicombe, C.E., McEvoy, A.J., Smyth, T.J., Cummings, D.G., Somerfield, P.J., Maud, J.L. *et al.* (2015) Questioning the role of phenology shifts and trophic mismatching in a planktonic food web. *Prog. Oceanogr.*, **137**, 498–512.

Bone, Q. (1998) *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Burnham, K. P. and Anderson, D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.

Clarke, A., Holmes, L.J. and Gore, D. J. (1992) Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. *J. Exp. Mar. Biol. Ecol.*, **155**, 55–68.

Condon, R.H, Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R., Mianzan, H.W., Bogeberg, M. *et al.* (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proc. Natl. Acad. Sci. U.S.A.*, **110**, 1000–1005.

Belsley, D., Kuh, E. and Welsch, R. (1980) Regression Diagnostics. Wiley, Hoboken, New Jersey, USA.

Eloire, D., Somerfield, P.J., Conway, D.V.P., Halsband-Lenk, C., Harris, R. and Bonnet, D. (2010) Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. *J. Plankton Res.*, **32**, 657–679.

Gemmell, B.J., Costello, J.H., Colin, S.P., Stewart, C.J., Dabiri, J.O., Tafti, D. and Priya, S. (2013) Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. *Proc. Natl. Acad. Sci. U.S.A.*, **110**, 17904–17909.

Gibbons, M.J. and Richardson, A.J. (2013) Beyond the jellyfish joyride and global oscillations: advancing jellyfish research. *J. Plankton Res.*, **35**, 929–938.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. and Charnov, E.L. (2002) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.

Hamner, W.M., Madin, L.P., Alldredge, A.L., Gilmer, R.W. and Hamner, P.P. (1975) Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. *Limnol. Oceangr.*, **20**, 907–917.

Hansen, P.J., Bjørnsen, P. K. and Hansen, B.W. (1997) Zooplankton grazing and growth: scaling within the 2–2000 μm body size range. *Limnol. Oceanogr.*, **42**, 687–704.

Harbison, G.R. (1992) The gelatinous inhabitants of the ocean interior. *Oceanus*, **35**, 18–23.

Harris, R. (2010) The L4 time series: the first 20 years. *J. Plankton Res.*, **32**, 577–583.

Hendrickx, J. (2012). *Perturb: Tools for Evaluating Collinearity*. R package version 2.05. http://CRAN.R-project.org/package=perturb

Hérbert, M-P., Beisner, B.E. and Maranger, R. (2016) Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. *J. Plankton Res.*, **00**, 1–10.

Hirst, A.G. (2012) Intra-specific scaling of mass to length in pelagic animals: ontogenetic shape change and its implications. *Limnol. Oceanogr.*, **57**, 1579–1590.

Hirst, A.G. and Forster, J. (2013) When growth models are not universal: evidence from marine invertebrates. *Proc. R. Soc. B*, **280**, 20131546, http://dx.doi.org/10.1098/rspb.2013.1546.

Hirst, A.G., Roff, J.C. and Lampitt, R.S. (2003) A synthesis of growth rates in marine epipelagic invertebrate zooplankton. *Adv. Mar. Biol.*, **44**, 1–142.

Ikeda, T. (2014) Synthesis toward a global model of metabolism and chemical composition of medusae and ctenophores. *J. Exp. Mar. Biol. Ecol.*, **456**, 50–64.

Kiørboe, T. (2011) How zooplankton feed: mechanisms, traits and trade-offs. *Biol. Rev.*, **86**, 311–339.

Kiørboe, T. (2013) Zooplankton body composition. *Limnol. Oceanogr.*, **58**, 1843–1850.

Kiørboe, T. and Hirst, A.G. (2014) Shifts in mass scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. *Am. Nat.*, **183**, 118–130.

Litchman, E., Ohman, M.D. and Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. *J. Plankton Res.*, **35**, 473–484.

Lucas, C.H., Pitt, K.A., Purcell, J.E., Lebrato, M. and Condon, R.H. (2011) What's in a jellyfish? Proximate and elemental composition and biometric relationships for use in biogeochemical studies. *Ecology*, **92**, 1704–1704.

Maud, J.L., Atkinson, A., Hirst, A.G., Lindeque, P.K., Widdicombe, C.E., Harmer, R.A., McEvoy, A. and Cummings, D.G. (2015) How does *Calanus helgolandicus* maintain its population in a changing climate? Analysis of a 25-year time series from the English Channel. *Prog. Oceanogr.*, **137**, 513–523.

Molina-Ramirez, A., Caceres, C., Romero-Romero, S., Bueno, J., Ignacio Gonzalez-Gordillo, J., Irigoien, X., Sostres, J., Bode, A. *et al.* (2015) Functional differences in the allometry of the water, carbon and nitrogen content of gelatinous organisms. *J. Plankton Res.*, **35**, 989–1000.

Møller, L.F. and Riisgård, H.U. (2007) Feeding, bioenergetics and growth in the common jellyfish *Aurelia aurita* and two hydromedusae, *Sarsia tubulosa* and *Aequorea vitrina*. *Mar. Ecol. Prog. Ser.*, **346**, 167–177.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Pitt, K.A., Duarte, C.M., Lucas, C.H., Sutherland, K.R., Condon, R. H., Mianzan, H., Purcell, J.E., Robinson, K.L. *et al.* (2013) Jellyfish body plans provide allometric advantages beyond low carbon percentage. *PLoS One*, **8**, e72683.

Pond, D.W., Harris, R.P., Head, R.N. and Harbour, D. (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, U.K.. *Mar. Ecol. Prog. Ser.*, **143**, 45–63.

Purcell, J.E. (2012) Jellyfish and Ctenophora blooms coincide with human proliferations and environmental perturbations. *Annu. Rev. Mar. Sci*, **4**, 209–235.

R Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Richardson, A.J., Bakun, A., Hays, G.C. and Gibbons, M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.*, **24**, 312–322.

Royall, R.M. (1997) *Statistical Evidence: A Likelihood Paradigm*. Chapman and Hall, New York, NY.

Shiganova, T.A. and Bulgakova, Y.V. (2000) Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. *ICES J. Mar. Sci.*, **57**, 641–648.

Smyth, T., Atkinson, A., Widdicombe, S., Frost, M., Allen, I., Fishwick, J., Quieros, A., Sims, D. and Barange, M. (2015) The Western Channel. *Prog. Oceanogr.*, **137**, 335–341.

Sutherland, K.L., Madin, L.P. and Stocker, R. (2010) Filtration of submicrometer particles by pelagic tunicates. *Proc. Nat. Acad. Sci. U.S.A.*, **107**, 15129–15134.